ADAPTIVE COLORATION
IN ANIMALS

Hugh B. Cott *pinx.*

Bombinator igneus
Atelopus stelzneri
Phrynomerus bifasciatus

Hyperolius marmoratus
Salamandra maculosa

Dendrobates tinctorius
Dendrobates tinctorius
Dendrobates tinctorius

Adaptive Coloration in Animals

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WITH AN INTRODUCTION BY

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TO

MY WIFE

'The day has passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist, who, for the first time, has wandered by himself in a Brazilian forest. . . . To a person fond of natural history, such a day brings with it a deeper pleasure than he can hope to experience again.'

DARWIN

'Happy the man whose lot it is to know
The secrets of the earth. He hastens not
To work his fellows' hurt by unjust deeds,
But with rapt admiration contemplates
Immortal Nature's ageless harmony,
And how and when her order came to be.'

EURIPIDES

INTRODUCTION

AMONG a certain section of experimental biologists, any time in these last thirty years, it has been fashionable and indeed almost a matter of professional conscience to display a radical scepticism on the subject of adaptations, especially colour adaptations, and most particularly mimetic adaptations. Upholders of the theories of protective and warning coloration and of mimicry have often been attacked as 'armchair theorists' (whereas they have in fact almost invariably been first and foremost field naturalists), insufficiently acquainted with modern work in genetics, which for some unexplained reason is held to do away with adaptive interpretations.

Thus, for instance, to cite but one recent author, A. F. Shull in his book on *Evolution* (1936) writes (p. 212):

> if the doctrine [of natural selection] can emerge minus its sexual election, its warning colors, its mimicry and its signal colors, the reaction over the end of the century will have been a distinct advantage. These special forms of the selection idea . . . seem destined to be dropped, or at least relegated to very minor places in Evolution discussion.

Elsewhere (p. 175) he states that the theories of aggressive and alluring resemblance 'must probably be set down as products of fancy belonging to uncritical times'.

Dr. Cott, in this important book, has turned the tables with a vengeance on objectors of this type. He has shown that it is they who are the armchair critics, or, one might say, the laboratory-bench critics. Had they taken the trouble to acquaint themselves with even a fraction of the relevant facts to be found in nature, they could never have ventured to enunciate such sweeping criticisms: their objections are a measure of their ignorance. Further, by applying optical and psychological principles, he has pushed the analysis of visual allæsthetic characters to a new level, and shown that many of them constitute adaptations of a quite unsuspected degree of refinement. Far from genetics in any way throwing doubt on their adaptive interpretation, the facts of cryptic, warning and mimetic coloration pose searching questions to the geneticist, and demand a recasting of many current views on the efficacy and mechanisms of selection.

This analysis is the most original part of Dr. Cott's book. With the aid of his own remarkable drawings and photographs, he demonstrates how nature—in this case via the operation of natural selection—employs the most elaborate optical-psychological devices to enhance conspicuousness where conspicuousness is advantageous, to reduce it where obliteration is the biological aim.

Cases in which an unusual resting position is adopted provide beautiful evidence of his contentions. Counter-shading is reversed in fish which swim upside-down and caterpillars which rest inverted. Bark-haunting moths have their markings running parallel with the vertical cracks of the bark, whether they rest with body vertical or horizontal, with wings folded or expanded.

The correlation of behaviour and markings, indeed, as Poulton long ago pointed out, is one of the strongest supports for theories of adaptive coloration. Even if it were possible for a case-hardened sceptic to dismiss as accidental such isolated facts as the co-existence, in various stingless insects, of a resemblance to bees or wasps on the one hand and on the other of motions simulating stinging, and even of the protrusion of an imitation sting, the enormous array of less spectacular but equally significant correlations provided by Dr. Cott is overwhelming.

Dr. Cott is a true follower of Darwin in driving his conclusions home by sheer weight of examples. Faced with his long lists of demonstrative cases, the reader is tempted to wonder why adaptive theories of coloration have been singled out for attack by anti-selectionists. As Dr. Cott observes, physiologists and geneticists do not deny that wings exhibit characters which make them suitable as mechanisms for flying, or that legs, beaks and teeth are adaptively correlated with mode of life.

A proper analysis, such as that undertaken in this book, demonstrates conclusively that optical-psychological principles promoting increase or decrease of conspicuousness in correlation with mode of life are just as effectively employed in animal coloration as are aerodynamic principles in the construction of flying animals. There is no more justification for denying the functional (and therefore adaptive) significance of the one than of the other.

Let it not be supposed, however, that the experimental approach has been neglected. Here again the anti-Darwinian critics of the theories of adaptive coloration seem not to have taken the trouble to acquaint themselves with the facts. The experimental data conclusively demonstrate that cryptic, warning and mimetic forms do in point of fact enjoy a degree of immunity from predators which constitutes a considerable selective advantage in the struggle for existence. Some of the recent work is especially convincing.

Another novel and interesting feature of this book is the constant cross-reference to human affairs. Dr. Cott shows how the same optical principles automatically utilized by natural selection in animal coloration have over and over again been employed deliberately and of set purpose by men to achieve the same effects. It is good to know that he has been called on to apply the principles he has studied to such good effect in animals to the practice of camouflage in war.

Adaptive Coloration in Animals is perhaps the most satisfactory book yet written on adaptation. It brings together great masses of data, from the field, the museum and the laboratory, analyses them in the light of established physical and psychological principles, and deals satisfactorily with the methodological problem of establishing proof of their adaptive nature. It is a worthy successor to Sir Edward Poulton's *The Colours of Animals*, published nearly half a century ago. The one was a pioneer study, the other is in many respects the last word on the subject. It is very gratifying to see that one of the great traditions of British biology—the tradition of scientific natural history, in which the comparative treatment of patiently accumulated data is made to yield generalizations of first-class importance—is being so worthily upheld.

JULIAN S. HUXLEY

PREFACE

THERE are many ways of regarding living creatures. They appear very differently to different men. What we see in an animal depends both upon our outlook and experience. To the morphologist, it presents problems of structure and descent ; to the systematist, it raises questions of relationship and classification ; the embryologist interests himself in its development ; the psychologist, in its behaviour ; to the stock-farmer, it has market value ; to the artist, beauty ; to the naturalist, a place to live and a part to play in the world of life. Even within the confines of a specialized study, like that of animal coloration, the same wide differences in approach and outlook exist. Here the biochemist is concerned with chemical problems of pigmentation ; the physicist, with the optics of structural colours ; the geneticist attempts to analyse colour-characters in terms of heredity ; the systematist traces in them an indication of relationship ; the physiologist studies their functions in the body ; the naturalist, their functions in the field.

In the interrelationships between animals of the same, or of different species —as between predator and prey, between rival males, or the opposite sexes, between parent and offspring, or between members of the group—characters which exert their influence from a distance, by sound, by sight, or scent, take a prominent place. To such characters Julian Huxley has applied the useful and comprehensive term Allæsthetic. In this volume I have intentionally confined myself to a special study of the various manifestations and functions of coloration in the interspecific relations of animals—that is to say, in the relations between predator and prey. Thus it will be apparent at the outset that auditory and olfactory characters have not been dealt with, except in so far as their mention may be relevant to my purpose ; and that, on the other hand, I have excluded as beyond the scope of the present volume that large and important class of coloration-phenomena whose function has to do with intraspecific relations—coloration, in other words, used for threat by rival males, for courtship by members of the opposite sex, and for recognition, by members of the family, or flock.

One of the fundamental facts affecting living creatures is the interspecific warfare known to biology as the struggle for existence. Animals, like men, are beset by many and great dangers. The problem of self-preservation in the field is very real, very urgent, and often difficult enough to solve ; but it is one with which all forms of animal life are faced. Broadly speaking, individual survival depends upon the satisfaction of two vital needs—security and sustenance. These are the two primary claims of life. In a world peopled with potential enemies and pregnant with hunger and the possibility of starvation, if an animal is to survive, it must eat, and avoid being eaten. It is the old question of the relation between the aggressor and the victim of aggression, between hunter and hunted.

The very urgency of this central biological problem of self-preservation is reflected in the variety and specialization of nature's adaptive experiments in offence and defence, as it is also in the parallel inventions and contrivancies of man. Indeed, the primeval struggle of the jungle, and the refinements of civilized warfare, have here very much the same story to tell. In both realms we see the results of an armament race and an invention race, which has led to a state of preparedness for offence and defence as complex as it is interesting. In both, methods mainly similar are employed : we have the evolution of speed, on land, in the air, and under water, by pursuer and pursued ; the employment of stealth and surprise, of deception and ambush ; the display of warning signals and of alluring baits ; the elaboration of smoke-screens, traps, nets, parachutes, of electrocution and booby-traps ; the adoption of fossorial and nocturnal habits ; the development of poison, and of deadly apparatus in the form of fangs or stings or arrows for its injection into the bodies of enemies or prey ; the protection afforded by armour-plating, spines and barbed wire ; the use of chemical warfare, which is practised, for instance, by certain insects ; and of poison gas, by creatures like the skunk.

Among all these evolutionary achievements, perhaps none are more important, more widely used, and more highly developed, than those characters which serve to elude, to attract, or to deceive the eye, and so to facilitate escape from enemies or the pursuit of prey. Indeed, it is no exaggeration to say that the modification of outward appearance by visual characters, directed towards a seeing public, and serving either to facilitate recognition or to frustrate it, has been one of the main results attained in the evolution of the higher animals ; and such characters comprise some of the most outstanding examples of adaptation in the whole field of biology.

In most spheres of modern warfare man has now, though in some cases only very recently, advanced far ahead of the so-called brute creation in his equipment for protection and aggression—in regard, for instance, to the development of armour and mobility, to the use of projectiles, and of devices such as the balloon-barrage and submarine-net (which in principle are gigantic spiders' webs), of smoke-screens (which are employed with effect by cuttle-fishes), and of delicate instruments like range-finders and sound-detectors. Yet, while there is the closest analogy between the needs for concealment and deception in nature and in war, in this sphere the coloration of animals has attained a degree of perfection far beyond the comparatively crude attempts at camouflage with which we are too easily satisfied—attempts which often neglect to make use of the very principles revealed in the coloration of innumerable snakes, caterpillars, birds, fishes and other organisms.

Because of recent developments in aerial warfare, and the ever-increasing part played by aircraft in military and naval operations of all kinds—for reconnaissance, photography, and bombing—camouflage has assumed to-day a new and vital function, whose significance can scarcely be overstated. But we have lagged far behind nature, and have much leeway to make up before we can approach the efficiency attained by different forms of wild life in the field. We should do well, therefore, to follow advice from the Book of Job : ‘ But ask now the beasts, and they shall teach thee ; and the fowls of the air, and they shall tell thee . . . and the fishes of the sea shall declare unto thee.’

A satisfactory system of classification, while primarily a matter of convenience, is nevertheless one of great importance to the serious study of any phenomena. Many of us had an early introduction to classification when, as children, we learned to play the game ‘ Animal, Vegetable and Mineral ’. Now the phenomena of adaptive coloration likewise fall into three main classes, according to the visible results produced. I have accordingly divided the present work into parts devoted, respectively, to questions of concealment, of advertisement, and of disguise. The biological function of these elusive, attractive, or deceptive devices varies widely according to circumstance, Through reduced visibility, they may facilitate the capture of food, or escape from the aggressor. Through increased conspicuousness, they may serve as a warning, or as bluff, to potential enemies, or as an allurement to prey. Through deceptive or mimetic effects, they may mislead the observer as to an animal’s whereabouts, attitude, or identity.

It would be great presumption for any one to attempt a book on functional aspects of animal coloration without acknowledging a deep debt of gratitude to Sir Edward Poulton, D.Sc., F.R.S., whose classical work on *The Colours of Animals* appeared just half a century ago. Whatever the subsequent developments of our knowledge in this field of natural history, Poulton’s analysis and classification of the phenomena must remain the essential structure upon which others may build. The great array of facts which have since been accumulated are largely due to his untiring labours, and in the preparation of the present work I have time and again had occasion to refer to his writings. Reference has been made in the text to the original publications from which I have drawn examples and evidence.

Although such a study as this is somewhat specialized, it is nevertheless one bearing directly upon that central problem of biology—the mechanism of evolution. In this book I have been less concerned with the origin of adaptive coloration, than with its various manifestations and uses. Nevertheless, those who are more interested in questions of origin, than in effects and applications, will find assembled in these pages a body of facts and evidence from which they may draw their own conclusions. The theory of natural selection is to-day receiving support from a number of sources. One of these sources is the scientific study of natural history, and in particular of adaptive coloration. Indeed, in the light of modern knowledge, the claim may well be repeated and emphasized, which was made in 1898 by Poulton, when he wrote that ‘ the explanation of these deeply interesting facts, which form so fascinating and important a department of natural history in the tropics, is one of the most notable triumphs ever won by the great Theory of Natural Selection ’.

In a book which deals, as this book deals, with optical principles and outward appearances, illustrations must take an important place, and I have spared no pains in the preparation of a series of photographs and drawings which will, I trust, materially add to any usefulness the work may possess. I have heard the view expressed that photographs do not provide reliable evidence as to the effectiveness of concealing coloration, since, it is argued, animals are more difficult to detect in the photographs than they would be in the field. Now this opinion does contain an element of truth when applied to some photographs—bad photographs. Every one has seen reproductions intended to illustrate some cryptic insect or bird, in which the creature remains unfound, not because of its cryptic coloration, but because the picture is technically deficient—lacking in clarity of outline, or in range of tones, or in scale, or because it is badly printed on vile paper. On the other hand, with illustrations of good quality—and in these days of ultra-rapid sensitive materials and ultra-precise cameras there is really no excuse for indifferent photography—the reverse is certainly true. In the sphere of aerial reconnaissance, it is the camera, and not the observer, which yields the exact data so necessary for the detection of camouflage. The photographic record is more accurate and discriminating than the retinal record, and camouflage is more readily spotted from the former than from the latter. Moreover, the limited field over which the eye must explore greatly facilitates the detection in a print of a cryptic insect which in nature may well escape observation since not even its approximate whereabouts is known. I hope, therefore, that the photographs reproduced in this volume will be of real value as a scientific record of the wonderful power of cryptic and deceptive coloration in nature. They have been obtained over a period of some fifteen years, from many parts of the world, and, unless otherwise stated, they represent wild animals, free and in their natural surroundings.

All the figures in the text I have drawn specially for the book. Figs. 8, 24(1), 28(2), 48, 50, 54, 69(2), 73, 75, 82 and 83(2, 3 and 4) are copies in line of existing half-tone illustrations whose source is named in the text. Fig. 56 is based partly upon photographs of the Crested Rat in display, kindly given me by Mr. David Seth Smith, of the Zoological Society of London. Fig. 69(1), representing the cryptic attitude of *Zabrochilus australis*, is taken from a photograph of the living insect by Mr. A. J. Nicholson, who generously supplied me both with a print and with a specimen of this remarkable grasshopper. In Fig. 74 the cryptic attitude of the Poor-me-one is taken from a photograph by A. Muir, published in the *Ibis*, 1925. The remaining figures are original.

Sir John Graham Kerr, F.R.S., M.P., has paid me the compliment of showing a lively interest in this work since it began to take shape, nearly five years ago, in the Department of Zoology, Glasgow University; and his never-failing encouragement, guidance, and friendship, backed by his own exceptional store of knowledge and experience both as a field naturalist and as an authority on questions of camouflage, have contributed much towards the confident spirit in which I have been able to approach the work. In addition to the untiring support he has given me, he has generously found time to read through and correct the entire proofs. To Dr. Julian S. Huxley, D.Sc., F.R.S., I am also under very real obligations. He, too, has read the whole book in proof, and has spared no pains in giving helpful criticism. I appreciate my good fortune in having had the benefit of advice and numerous valuable suggestions from one whose own important contributions to knowledge in the field of adaptive coloration is so widely recognized.

It is not possible to mention here the names of all those who, in one way or another, have generously given advice or assistance. They know, and I appreciate, in what ways they have helped. To various officials of the British Museum (Natural History) I am indebted for facilities which they have so courteously granted, and in particular I wish to thank Mr. H. W. Parker, M.A., and Mr. J. R. Norman, of the Department of Zoology, and Mr. W. E. China, of the Department of Entomology, for giving me access to specimens in their charge, and for helpful suggestions and many kindnesses. At Oxford, Professor G. D. Hale Carpenter, M.D., has kindly allowed me to examine and photograph specimens in the Hope Department. I am also especially indebted to my friend and former travelling companion, Mr. L. C. Bushby, of the Zoological Society of London, for the opportunities he has afforded for the study of living insects in the Society's Gardens.

I owe a debt of gratitude to the Colston Research Society, Bristol University, for a grant towards expenses incurred during a zoological expedition to the Canary Islands in 1931 ; and to the Carnegie Trustees for the Universities of Scotland, for financial assistance received in 1937–38 during my tenure of a Carnegie Teaching Fellowship in the University of Glasgow.

To my publishers I should like to express my indebtedness for the courteous consideration they have shown me, and for the care which they have bestowed on the book in all stages of its production.

Finally, I must record a deep sense of gratitude to my wife, who has typed part of the manuscript, checked the final proofs, helped me to compile the index, and who in innumerable other ways has lightened my work.

This book was written in a period of unsettled peace, in which the nations of Europe were preparing for, or against, war. Now the war has come, and with it an intensification of industrial energy and of that preoccupation with machines which has long been an accompaniment of modern life. In these days that lie ahead, when too exclusive an interest in mechanical and scientific contrivancies must tend to encourage the development of what Lord Dawson once called the 'gadget-mind', which is restless, unreflective, and unemotional, the study of natural history provides a welcome antidote—not indeed as a way of escape from reality, but rather as a means of seeing, as from a mountain-top, and in clearer and wider perspective, that struggle for existence which is the lot of men not less than of animals.

In war, as in peace, to young and old alike, animals may be, and should be, a fount of joy and inspiration. It was Thomas à Kempis who said : ‘ If indeed thy heart were right, then would every creature be to thee a mirror of life, and a book of holy doctrine.’ All men, provided they are not too ignorant, too proud, or too sophisticated, are bound to take a delight in animal life ; and fortunate are those who have learned to see, in the wild things of nature, something to be loved, something to be wondered at, something to be reverenced, for they will have found the key to a never-failing source of recreation and refreshment.

Unmindful of the affairs of men, the pageant of nature marches on : we can recognize and give names to most of the actors ; but of their make-up, their parts, and their inner lives we still know little enough. In whatever direction we look, there appear problems, old and new, awaiting investigation. Much, then, remains to be done. For the research worker with patience, resolution, and imagination, the future is full of promise. Experimental embryologist and biochemist, physiologist and psychologist, systematist and ecologist, each views the players from a different angle ; each has a special light to shed upon them ; each may help to banish the dark shadows and dusty corners into which we cannot yet see clearly. I hope that with the present volume I have been successful in sending a ray or two across this old stage of nature—a stage crossed by so fine and varied a cast that those privileged for a few fleeting years to see the show may well look on in wonder, and in gratitude.

HUGH B. COTT

UNIVERSITY MUSEUM OF ZOOLOGY,
CAMBRIDGE
January, 1940

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PART I

CONCEALMENT

INTRODUCTORY

> It is the glory of God to conceal a thing: but the honour of kings is to search out a matter.
>
> PROVERBS XXV, 2

SHORTLY before sunset on a clear evening in summer, when foliage is fresh and full, the leaves of an oak are seen from certain directions to be aflame with orange light: the familiar tree becomes transmuted into a veritable burning bush—though only the elect have eyes to see it so. This reality may readily be proved by holding a flame-coloured nasturtium petal between the tree and the eye and comparing the tints thus brought together. But most of us make a mental reservation, based upon long years of experience, and we reject the evidence of the senses. Leaves, we know, are green in summer, not golden; and unless we are specially observant or specially trained, we refuse to accept the facts of colour as they are—we refuse to see that the distant firs are pale grey, or that the snow on the hills is blue where it lies in shade and warmly tinted where bathed in sunlight, that indeed it may be almost any tint except the white which we think it is. Experience has taken much of the colour and variety out of life, and we go on our way almost unconscious of the real appearance of the visual signs we have learned from earliest childhood to construe.

So accustomed are we to reject what the eye sees in nature, so dull and dead have we become as a result of visual experience, that to appreciate the wonder and wealth of colour around us we must be shown our surroundings in some novel or unusual manner—in a picture, for instance, or as they appear when we stand on our heads, or when seen inverted in the focusing screen of a camera. Indeed, so largely does experience enter into and modify our perception of objects, that many people are quite unable to accept what the eye gives them, but only what they have learned to expect it is giving them: they *see* only what they *know*. They have lost that power which artists by patient striving have recovered, and which Ruskin calls the 'innocence of the eye'. These remarks are true not merely of colour phenomena. All the sensations which enable us to appreciate depth and distance, modelling and texture of the objects around us come to have their special significance only as a result of individual experience. Thus we interpret the effects of light and shade in terms of sculpturing and relief; we project perspective into three-dimensional space; we translate separate patches of colour into objects with separate surfaces.

Now what I wish to emphasize here is that these processes in the psychological plane cause us to overlook the fact that in the physical plane all optical effects whatsoever are fundamentally due to differences of colour and brightness, and of light and shade. They are solely due, in other words, to radiations differing in frequency and intensity. All the varied signs which enable us to perceive objects are capable of analysis into these simple terms. Once this important matter is grasped, we are in a position to appreciate not only the visual phenomena upon which recognition depends, but to understand the optical methods by which recognition can be delayed or altogether prevented. For these must depend ultimately upon modifications of the visual signs which reach the observer's eye.

To put the matter in another way: vision rests upon a threefold basis lying in the realms of psychology, physiology and physics. There are the physical facts which happen in the world outside the eye; the physiological reactions which occur within it; and the psychological processes which take place behind it. Now the visual effects making for concealment, or camouflage, while of course producing their results through the operation of the eye and the attributes of the mind, are fundamentally those of the physical properties of light—*they are nothing more than effects of colour variously shaded.*

Before considering the methods by which different animals are rendered so wonderfully inconspicuous and difficult to detect in the field, it will therefore be helpful first to enquire what are the optical principles upon which recognition by sight depends. How is it that we are able to isolate and recognize any single object from the surroundings which form its immediate background? What do the various visual clues amount to—clues which the eye receives from the outer world and which we have learned to interpret and project in the language of solidity and space?

All solid objects which we see in the world about us are presented to the eye merely as patches of colour occupying a particular area in the visual field. These patches may differ widely from one another in various respects—notably in their saturation or dilution, in their darkness or paleness, in their size and texture and form. Actually, we *see* nothing but flat stains of colour—variously shaded and variously shaped.

When we recognize anything by sight—a leaf, for instance—the means by which the eye is enabled to distinguish it are fourfold, and it is essential for the proper understanding of our subject that these should be clearly appreciated. Firstly, the object appears in the field of vision as a continuous area of *colour*, differing more or less markedly in *hue* and *purity* and *depth* from its immediate surroundings, against which it is therefore seen to stand out in contrast. The leaf may appear, for instance, as a dark green shape against the blue sky, or as a brown patch lying on the lawn.

Secondly, owing to the effect of unequal illumination on an uneven surface, the leaf is not seen simply as a wash of flat colour—even when in actual fact it may be uniform in colour. For it is thrown into *relief* by the effect of *light* and *shade*, which enables the eye to detect surface curvature, modelling, texture and such details or irregularities as the midrib, lateral veins, and so on.

Thirdly, although natural objects are not, or are but rarely, bounded by lines—in the way that an outline drawing is—nevertheless the surface of every visible body is framed by a *contour* or outline which divides the area where it is from the area where it is not in the visual field. And this contour frequently has a characteristic or familiar shape, enabling the *form* of a familiar object to be recognized : it may tell us, for instance, that the leaf we are looking at is oak or elm, or holly, or some other kind.

Fourthly, under certain conditions of illumination a *shadow* will be thrown by the object upon its background. Shadows are caused when opaque bodies intercept light upon some surface other than their own, and are not to be confused with shade, which is found on parts of the body that are turned away from the light. By framing the outline of the object, as well as by virtue of their own shape and conspicuousness, shadows tend to facilitate recognition.

The point which cannot be too strongly emphasized here is that *visible form can only be distinguished when it is exhibited by differences of colour or tone, or of light and shade : with the reduction of such differences an animal or any other object becomes more and more difficult to recognize : in their absence it becomes unrecognizable.*

It follows from these theoretical considerations, that four fundamental steps towards effective camouflage must lie in the direction (1) of *colour resemblance*—i.e. the agreement in colour between an object and the background against which it is seen ; (2) of *obliterative shading*—i.e. counter lightening and darkening which abolishes the appearance of roundness or relief due to light and shade ; (3) of *disruptive coloration*—i.e. a superimposed pattern of contrasted colours and tones serving to blur the outline and to break up the real surface form, which is replaced by an apparent but unreal configuration ; and (4) by *shadow elimination*—i.e. the effacement of cast shadows by modifications of form or adaptive orientation.

Now it is a very remarkable fact, and one of much significance, that these theoretical principles of colour resemblance, obliterative shading, disruptive coloration and shadow elimination, together with various additional devices and instincts, are those actually found to operate in nature, whereby different animals —fishes and wild-fowl, toads and tree-frogs, dabs and crabs, cats and caterpillars and innumerable others—are rendered so extraordinarily difficult to recognize when seen in their natural surroundings.

THE METHODS BY WHICH CONCEALMENT IS ATTAINED IN NATURE

1. GENERAL COLOUR RESEMBLANCE

> There are also divers other kinds of worms, which for colour and shape alter even as the ground out of which they are got.
>
> IZAAK WALTON

I. GENERAL RESEMBLANCE IN DIFFERENT ENVIRONMENTS

THE general resemblance borne by various animals to the different surroundings in which they live is a theme more or less familiar to every one. The Ptarmigan nesting among the lichen-covered rocks of the mountain summit; the Golden Plover on the neighbouring moorland; the Woodcock among the bracken and fallen oak leaves; the Ringed Plover on its pebble beach; the Stone-Curlew in its native breckland; the Bittern standing motionless among the tawny reeds; the Parrakeet screaming from the luxuriant foliage of a mango tree; the Saharan Nightjar crouching invisible in a barren waste; the Frogmouth perched on some rotten tree-stump—each is afforded concealment by the hues and tones demanded of its particular environment.

It is, of course, easy to point to exceptions: but the fact remains that innumerable animals, inhabiting all kinds of surroundings, tend to wear on their bodies a cryptic dress. The traveller who visits one of the arid regions of the earth, such as the Kalahari, Sahara, or the deserts of North-western India or Southern California, will look there in vain for the brilliant greens which beautify many tree-dwellers all the world over—parrots and woodpeckers, tree-frogs and tree-snakes, chameleons and iguanas, grasshoppers and mantids: he will look almost in vain for the blue tints of tunny and mackerel and flying fish which are typical of many inhabitants of the ocean's surface waters: nor will he find there the immaculate white dresses worn by members of the snowland fauna.

Instead he will observe that those creatures hardy enough to eke out an existence in such inhospitable places are, with few exceptions, clad in colours borrowed from the desert itself—ochre, buff, brown and sandy-grey, broken perhaps with patterns of dark-brown, black and white. Moreover, these colours prevail in distantly related groups of animals: they are seen alike in the fur of mammals, such as Jackal and Fennec, Gerbil and Jerboa; they are reproduced in the feathers of birds—the Desert and Crested Larks, the Egyptian Nightjar, Houbara, Cream-coloured Courser, Sand-Grouse and Quail: they are repeated on the scales of desert lizards—geckos, skinks, monitors, ‘ horned toads ’, and many others ; and of snakes like the Horned Viper : and they occur once more in the chitinous covering of many desert insects.

It is a significant fact, to which I have referred on another page, that the only other major environment where somewhat similar colours predominate is one the very opposite in most respects from the desert, namely, the mud of estuaries and the sandy and gravelly bottom of inshore seas. And here again the fauna, though so entirely different from that we have been considering, wears the same sober hues of brown and orange, ochre and grey, such as are seen in flatfish like the Flounder and Plaice, and in many crustaceans and cephalopods. Here, too, we find that the colours and patterns worn are not indiscriminately brown or buff or yellow, for there is generally a marked colour-harmony between the animal and the particular bottom on which it rests.

Facts such as these, regarding general cryptic resemblance in the major environments of the world, are too well known to require detailed description here. Certain controversial aspects of the subject will be deferred until a later page. The broad facts are clear enough. In every well-illuminated region having a dominant type of colour, the tendency is apparent for a considerable percentage of the fauna to reproduce more or less closely its prevailing colours and tones. For instance, green—which occurs so widely and so vividly in the colour scheme of foliage haunting birds, lizards, snakes, frogs, beetles, bugs, grasshoppers, mantids, moths, caterpillars and other forms from evergreen forests—is found to predominate in other regions only where green is also a constant feature of the environment, namely, on land among grass and ground herbage generally, and in the sea among sea grass and green algæ. There is no environment in the world where white is predominantly worn by the fauna except in the frozen North, where white is also the dominant colour of the landscape.

Not least remarkable in this connexion is the evolution of transparency in the surface waters of the sea, a feature shared in the larval or adult state by such widely different pelagic organisms as cœlenterates, Gastropod molluscs, Polychæte worms, crustaceans, tunicates and fishes—members of which in this particular differ completely from their opaque and pigmented nearest relatives, or adult stages, dwelling on the sea bottom and seashore.

II. CONVERGENCE IN COLOUR RESEMBLANCE : COMMON CRYPTIC COLORATION

The phenomena of general cryptic resemblance involve many striking demonstrations of the principle of convergence—which implies a superficial similarity (in this case of colour) that is independent of affinity but correlated with similar conditions of life. As with all types of adaptive convergence, the superficial resemblance between different animals seen in Common Cryptic Coloration (for which Poulton has introduced the term Syncryptic) is quite incidental, and in this respect utterly different both in function and origin from mimetic resemblances where the superficial similarity between different animals appears to have been developed as an end in itself.

(1) **Green Coloration in Tropical Tree-Snakes**—We may illustrate the point by reference to the green coloration of tropical tree-snakes, which has arisen on a number of different occasions, in several remotely related families, and in every tropical region of both Old and New Worlds. The following table indicates the systematic position of various genera containing vividly green arboreal species—of which a single example from each genus is cited. The list could, of course, be considerably extended, and is merely intended to show the widespread occurrence of a colour which every one with experience of tropical nature knows to be highly effective as a cryptic dress among foliage.

Family.	Sub-family.	Genus.	Species.	Distribution.
Boidæ	Boinæ	*Boa*	*B. canina*	South America
	Pythoninæ	*Chondropython*	*C. viridis*	Papua
Colubridæ	Colubrinæ	*Leimadophis*	*L. viridis*	South America
		Leptophis	*L. mexicanus*	Mexico
		Chlorophis	*C. neglectus*	Tropical Africa
		Philothamnus	*P. nitidus*	Tropical Africa
		Gastropyxis	*G. smaragdina*	Africa
		Elaphe	*E. prasina*	China
		Opheodrys	*O. æstivus*	North America
	Boiginæ	*Passerita*	*P. prasina*	South-East Asia
		Oxybelis	*O. fulgidus*	Central America
		Philodryas	*P. viridissimus*	Peru
Elapidæ		*Dendraspis*	*D. viridis*	West Africa
Viperidæ	Viperinæ	*Atheris*	*A. squamigera*	Tropical Africa
	Crotalinæ	*Trimeresurus*	*T. albolabris*	Asia
		Bothrops	*B. bicolor*	Central America

The above list embodies several striking cases of convergence—of form as well as colour: for example, as between the Bush Vipers (*Atheris*) of tropical Africa and the Palm Vipers (*Bothrops*) of tropical America—the former being true vipers (Viperinæ) and the latter pit vipers (Crotalinæ).

Parallel phenomena are of world-wide occurrence among other members of the forest fauna, as seen in the green uniforms evolved independently in numerous genera and families of lizards, frogs, and birds, not to mention Coleoptera, Lepidoptera, Hemiptera and Orthoptera.

(2) **Green Coloration due to a Variety of Causes**—A further series of facts which lends indirect support to the adaptive interpretation of green colour

concerns the wide variety of methods, both physical and chemical, by which the appearance of green is itself produced in different groups of animals.

Many years ago Poulton proved that the green coloration of various caterpillars was due to a modified chlorophyll derived from their food, and present in their blood (499). It is remarkable, as he points out, that this colouring matter, unlike any other known solution of chlorophyll, is stable under the prolonged action of light, and that spectroscopically the green blood shows a closer resemblance to the unaltered chlorophyll in the leaf, than the latter does to chlorophyll in alcoholic solution—a fact which seems the more striking when account is taken of chemical processes involved in the passage of the pigment through the wall of the alimentary tract.

It is interesting to note that in cases like *Smerinthus ocellatus* the green larval pigment passes by way of the pupa into the eggs, and so to the young larvæ, which are thereby rendered green on hatching before they have had the opportunity of acquiring fresh chlorophyll from the food plant (525).

Sometimes, as in caterpillars of the Angle Shades Moth (*Phlogophora meticulosa*), the green coloration is caused by the food in the alimentary tract showing through the transparent body wall (496). In other cases green pigments are synthesized by the insect, being developed independently of the nature of the food even in phytophagous species, and betraying no close relation to chlorophyll. This is shown by their production in stick insects, locusts and many caterpillars when reared upon food containing no pigment (170, 207, 412). And their independent nature has been confirmed spectroscopically. Thus Faure (170) finds that in green individuals of the solitary phase of the African Migratory Locust (*Locusta migratoria* subsp. *migratoroides*) the pigment involved differs from chlorophyll in showing a single absorption band with its centre at 6,700 Å, and no trace of red fluorescence. In contrast to what has been said above, we have to note that various leaf-mining dipterous larvæ, which have no need of cryptic resemblance, do not assume a green coloration though feeding upon chlorophyll-bearing tissue (281).

The independent nature of the green pigment in certain crustaceans has been demonstrated by Gamble (198), who showed that the development of green coloration in specimens of *Hippolyte varians*, when reared against a background of green weed, was uninfluenced by diet; for prawns fed with colourless substances, with red ovary, and with fine brown weed, became green under these conditions.

Green in mature insects is frequently either structural in nature, or produced by the combined effect of pigment and structure. Thus Onslow (449) has shown that the brilliant green of the butterfly *Ornithoptera poseidon* is due to the modification of a yellow pigment by a structural blue; and that the green colour of beetles such as *Heterorrhina elegans* and *H. africana* is due to a similar cause.

Coloration in the Amphibia depends upon the arrangement of three kinds of pigment cells or chromatophores—namely, melanophores, lipophores and guanophores, whose pigments are black or brown, yellow or red, and white respectively. Now it is interesting to find that by means of, and in spite of so limited a palette, many foliage-haunting tree-frogs, such as *Hyla arborea* and *Leptopelis johnstoni*, are able to appear dressed in brightest leaf-green tints. This effect is due partly to the selective absorption of rays of greater wave-length by the deep-seated background of melanophores, and partly to the action of the guanophores, which reflect back the waves of shorter length. This scattered light would appear blue, for the same reason that the sky is blue, were it not for the filtering action of the overlying colour screen formed by the layer of lipophores, which transmit only the green light (445).

In the case of snakes, it appears that nothing has yet been published on the nature of green coloration. However, Mr. H. W. Parker, of the British Museum (Natural History), informs me that green snakes react in alcohol in two different ways. Either they remain green ; or else they become blue. In the former case, the alcohol is liable to be discoloured green ; in the latter, it is discoloured yellow. He points out that presumably this different behaviour is due to different methods of producing green colour—the first by a green pigment slightly soluble in alcohol ; the second by a combination of structural blue which is unaffected by alcohol, and a soluble yellow pigment.

Similar conditions appear to obtain among lizards. Many species belong to the second category, and in certain cases post-mortem colour changes have led to mistaken ideas of the true coloration in life. A striking instance of this came to my notice in Brazil. A rare and very handsome lizard of the most brilliant green hue which I took on Marajó Island was subsequently identified with a species known to science by the inappropriate name of *Urocentron azureum*, whose colour had repeatedly been described in systematic literature as ' un beau bleu '—doubtless owing to its appearance in spirit (107).

With birds, especially among arboreal species, green is a common colour. In the Musophagidæ, or Plantain-eaters, this is due to a green pigment containing iron. In all other birds, green is a structural colour—being produced by a combination of yellow or grey or brown pigment associated with a special colourless superstructure (439). Its nature is well seen in species like the Blue-fronted Amazon Parrot, whose green feathers turn a dull brown when the bird is thoroughly drenched after a bath.

Finally, we may mention here the well-known, not to say highly curious case of the South American Sloths *Bradypus tridactylus* and *Cholœpus didactylus*, whose coarse, shaggy hair is given a greenish-grey tint by the presence of a symbiotic alga of the *Protococcus* group.

(3) **Green Coloration and Infra-red Radiation**—A very interesting question bearing upon the nature and quality of light reflected from green animals is opened up by the comparatively new technique of infra-red photography. It is well known that chlorophyll reflects light in the infra-red region of the spectrum, and that as a consequence grass or foliage appear snowy-white in the infra-red photograph. But different green animals, which to the eye appear

similar in tone and colour both to one another and to their surroundings, differ greatly in their absorption of infra-red light. Consequently when twin photographs of these are taken respectively on panchromatic and on infra-red plates, the results in certain cases are most illuminating—those forms which absorb infra-red rays becoming in the latter case strongly differentiated from their environment, and appearing as dark objects standing out conspicuously from their light surroundings.

This is well seen in the photographs of the Tettigoniid grasshopper (*Leptophyes punctatissima* (Plate 3), which stands out vividly as a dark patch against the light infra-red rendering of the rhubarb leaf on which it is resting. A similar effect is obtained with the Eider Duck (Plate 4), which in the infra-red photograph becomes as conspicuous as it is in normal circumstances inconspicuous.

There is an aspect of this subject of practical importance. During the Great War the development of aerial photography and reconnaissance rendered the concealment of ammunition dumps, battery positions, concentrations of troops, and other objectives a matter of vital importance. To this end various devices were used, such as the erection of overhead cover of a suitable colour and texture, and disposed so as to eliminate shadows, approaches, spoil, blast-marks and so forth. Because such screens are effective against direct observation and ordinary photography, by no means does it follow that they will be hidden in the infra-red photograph. Comparison of aerial photographs taken simultaneously on panchromatic and infra-red plates will reveal much that before the advent of this new technique would have been adequately camouflaged, and a new difficulty has thus been added to the difficult problem of concealment by deception.

Now, when we return to the problem in its bearing upon animals, it is found that this difficulty is one which can be, and has been, solved in nature. In the first place, as might be expected, certain green caterpillars like *Smerinthus ocellatus*, whose green coloration is due to a modified chlorophyll, do not thus become differentiated in the infra-red plate from the leaves among which they are resting, but retain their cryptic appearance (Plate 5).

However, something much more remarkable is seen in the case of certain tree-frogs, such as *Hyla cœrulea* (Plate 6). Here the green coloration is purely subjective, being due—as already mentioned—to a combination of pigment and structure. Yet in the infra-red photograph the skin is rendered *as though* its coloration were due to chlorophyll (with which, of course, it has no physical or chemical relation whatsoever). Thus in the infra-red picture, or to the infra-red-sensitive eye, it retains the harmony of tone upon which its inconspicuousness depends, appearing in waxy white pallor amidst the snow-white foliage.

In view of the possibility that certain animals may have a visual range which extends to, or lies within, the deep-red and infra-red region of the spectrum—as claimed by Vanderplank (639) in the case of the Tawny Owl[1]—the whole

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[1] In a recent letter to *Nature* (1939, **143**, 983), L. Harrison Matthews and Bryan H. C. Matthews describe experiments which lend no support to the view that owls can see a

subject becomes one of deep interest to the naturalist, as it is of necessity to the camouflage expert; and it obviously opens up a profitable field for future investigation.

III. ADAPTIVE RADIATION IN COLOUR RESEMBLANCE

The same principle may be studied from the complementary point of view, namely, that of the adaptive range of coloration exhibited by particular groups of animals whose habits and relationships are such as to place a premium on concealment, whether for offensive or defensive purposes. The fact is that with such species the divergent colour differences exhibited within different families and orders is commonly correlated with the diversity of surroundings occupied by the several species and genera. Such a relation is found, for instance, in groups so diverse in habits and affinity as spiders, lizards, and cats.

(1) **General Resemblances among Spiders**—Various members of the first group well illustrate the point. Thus species that live on bark, like *Marpessa muscosa*, are commonly brown; others, like *Salticus scenicus*, which haunt stone walls and granite rocks, wear a disruptive dress of black and white; others, such as *Trochosa picta*, which dwell on sandy ground, are sandy in hue, and vary in different localities according to the shade of sand prevalent in their particular neighbourhood; others again, like *Sitticus pubescens*, which commonly frequent walls and fences, are greyish in colour; lichen-haunting species, such as the North American *Epeira prompta*, often bear a close resemblance to lichen; many grass-frequenting species, like the South American *Tetragnatha extensa*, are dressed in green; while certain flower-loving forms, like *Misumena vatia*, are whitish, pink, yellow or pale green according to the colour of their immediate surroundings.

(2) **General Resemblances among Lizards**—Lizards show the same general relation between habits, haunts and habiliment in a striking manner. In the forest, as already mentioned, many species living among twigs and foliage are predominantly green; and this coloration bears no particular relation to the animals' systematic position. It occurs, for instance, in a number of Iguanid genera such as *Anolis*, *Iguana* and *Polychrus* (Plate 1); in many Agamidæ, such as *Cophotis ceylanica*, a species found on moss-covered tree-trunks in Ceylon; in a number of Geckos such as *Phelsuma*; and typically among Chameleons like the little South African *C. pumilus* and the East African *C. dilepis*. Other lizards, living on boughs and trunks, are variegated with browns and greys and resemble bark and lichen, as, for instance, in the East African *Agama atricollis*, in *Corythophanes cristatus* (Plate 1) from Southern Burma, and in *Ptychozoon kuhli* from the Malay Peninsula. Other species such as the Brazilian *Ameiva surinamensis*, living on the light-flecked ground, are dark-hued with light spots. In the

small mammal in darkness by its own infra-red radiation. These authors detected no response in the Tawny Owl's eye to radiation from a black body at temperatures between 40° C. and 400° C.; and they found that transmission through the eye practically ceases for long infra-red wave-lengths.

savannah, spotted liveries tend to give place to a striped dress harmonizing with the linear configuration of grasses, as seen in the African Skink *Mabuia quinquetæniata*.

In the desert, stripes are discarded for drab dustcoats, which with their darker markings so well blend with the weathered rock and sand of a sun-baked wilderness. Such species seem almost invariably to be coloured like their surroundings, irrespective of the family to which they belong. As examples the following may be cited—*Phrynocephalus maculatus* (Agamidæ) from Persia; *Phrynosoma modestum* (Iguanidæ) from Mexico; *Palmatogecko rangei* (Gekkonidæ) from South-West Africa; and *Varanus griseus* (Varanidæ) from Arabia and North-West India.

We may also note in passing a point that will be taken up again later in connexion with Mammals, Birds and Insects, that different races and species frequently show the closest possible resemblance to the colour of the particular ground on which they occur. This is well seen in lizards of the genus *Phrynosoma*, the well-known horned lizard of the United States. Bryant (65) states that this lizard resembles the colour of the substratum so closely that it is practically invisible except when in motion. The large *P. douglassii ornatissimum* resembles the vari-coloured rocks of the Painted Desert of Arizona; *P. d. douglassii* the uni-coloured soil of Oregon; *P. platyrhinos*, at Ash Meadows in the Amargosa Desert, occurs as a very white form living on white alkali soil; others from the black lava belts are almost black in colour; and *P. blainvillii frontale*—the only known horned lizard which inhabits the forest belt near Pacific Grove, Monterey County, simulates the colour of the pine-needle carpet.

(3) **General Resemblances among Cats**—Analogous colour schemes have been evolved in different Mammalian orders. Thus among members of the Felidæ, colour and pattern are generally related to habit and environment. The Snow Leopard (*Felis uncia*), whose long fur is white in ground colour, is confined to the almost treeless highlands of Central Asia. The vertical tawny-orange and black stripes of the Tiger (*F. tigris*) assimilate with the tall parallel grass stems and reeds of the swamps and grassy plains where it lives. The more arboreal cats, both large and small, are boldly marked with disruptive spotted or streaked patterns: this is especially true of the South American Jaguar (*F. onça*), whose tawny-yellow and reddish coat, broken with black spots, constitutes an effective anticryptic disguise for forest foliage. A modification of this dress is worn by the handsome Ocelot (*F. pardalis*), exclusively a forest animal, also from South America; and by the Clouded Leopard (*F. nebulosa*), a thoroughly arboreal forest species from South Eastern Asia. The Fishing Cat (*F. viverrina*), of the same region, whose general ground colour of grey is broken by elongated dark spots and stripes, lives in lake-side and river-side thickets where its coloration is doubtless highly cryptic. The coat of the British Wild Cat (*F. silvestris*) is similarly adapted to close country. In less degree we find the relation exhibited by the Leopard (*F. pardus*) which frequently inhabits wooded districts and is partly arboreal. On the other hand, species living in open barren

country tend to be uniformly coloured, or but lightly marked: this is, of course, the case with the Lion (*F. leo*), primarily an inhabitant of sandy plains and rocky places with low scrub; and with such smaller species as the Caracal (*F. caracal*), a uniformly coloured fawn or rufous species from India and Arabia, Pallas's Cat (*F. manul*), a greyish or buff-coloured form from the Mongolian desert, and the Pampas Cat (*F. pajeros*), a yellowish-grey species with oblique straw-coloured bands on the flanks, found in the grassy regions of Argentina.

IV. COLOUR RESEMBLANCE IN DIFFERENT LOCALITIES: LOCAL RACES

A refinement of the principle we have been considering is found in the close colour adaptation presented by different animals to the particular locality which they frequent. We shall here refer to a few of the more striking instances provided by mammals, birds, and insects.

(1) **Local Races among Mammals**—The existence of pale races of wild animals upon isolated beaches, sandy islands, and patches of desert, has been recorded by many writers. In 1898 Jameson (285) published an account of a pale-coloured race of the House Mouse (*Mus musculus*) found inhabiting sandhills on a small island called the North Bull, in Dublin Bay. It appears that this island first arose between 1775 and 1800, and the race had evidently evolved during the intervening hundred years or so. Jameson observed that in autumn and winter the sandhills were frequented by Short-eared Owls, and that hawks from the mainland were regular visitors and could be seen any day in pursuit of prey on the North Bull. He concluded that the protectively coloured race owes its origin to the selective elimination by these birds (both of which hunt by sight) of the more conspicuous dark mice, combined with the effect of isolation in preventing immigration of the darker type from the mainland.

Many similar observations have been recorded in North America. W. H. Osgood, in his valuable Revision of the Mice of the American Genus *Peromyscus* (450), described a pale sub-race of the Deer-mouse (*Peromyscus maniculatus rubidus*) inhabiting a practically isolated sandy peninsula near Samoa, Humboldt Bay, on the northern Californian coast. The occurrence of this pallid form and the related darker Deer-mice from the redwoods of the mainland adjoining has since been analysed by Sumner (595), who discusses the rôle of isolation in the formation of the narrowly-localized pallid race.

Conversely, as is now well known, there is a prevailing tendency for different mammals living on black lava beds to become deeply pigmented. Dark forms of mice and other rodents, differing in their dusky coloration from their nearest relatives of the lighter-hued adjacent desert, have been described from blackish lava beds by Merriam (408), Goldman (210), Osgood (450), Sumner and Swarth (602), Benson (46), and others.

For example, Merriam (408) mentions three mammals captured in the lava fields of Arizona—a Squirrel (*Citellus spilosoma obsidianus*), a Mouse (*Onychomys leucogaster fuliginosus*), and a Pocket-mouse (*Perognathus flavus fuliginosus*)—which differed strikingly from their relatives of the neighbouring desert.

Broadly speaking, it would seem that we must look either to atmospheric or to optical factors for an explanation of the facts. The correlation between dark pigment and high humidity, and between pale coloration and arid conditions, has long been recognized, not only among different mammals and birds but also in various reptiles and insects. Distributional studies have led some authorities to support the first hypothesis—namely, that the pallid hues of desert animals stand in some direct relation to the low humidity of their surroundings.

Sumner's earlier studies of rodents on the North Californian Coast (595) and in the Mojave Desert (596) led him to doubt the validity of protective coloration as an explanation of the phenomena—as inapplicable to animals which are almost wholly nocturnal in their habits ; which (in the case of Gophers) spend most of their time beneath the ground ; and which show depigmentation in parts of the body (soles of the feet and fur of the belly) not exposed to view.

Moreover, he describes the occurrence (596), on an isolated and dark-coloured lava field in the Mojave Desert, of *Peromyscus crinitus stephensi*, whose pale coat colour showed no difference as compared with a control series of Deer-mice from pale sand in another part of the same desert. On these and other grounds he inclined to the view that the observed colour differences are probably correlated with climatic factors, and especially with differences of atmospheric humidity.

Dice's (141) investigations in the distribution of rodents in the Tularosa Basin, New Mexico—an area peculiarly well suited to biogeographical studies—appear to support the adaptive interpretation. He describes certain colour forms, occurring in close proximity and under almost identical climatic conditions, which closely harmonize with two extreme types of background—namely, black lava and white sand. The prevailing colours of the mammals living on the desert plains and slopes are the pale buff and tawny hues of the soil. But on an extensive lava flow in this region the White-throated Wood-rat and the Rock Pocket-mouse, characteristic of the adjacent mountain slopes, are replaced by black races (*Neotoma albigula melas* and *Perognathus intermedius ater*) : these black races appear to be restricted to the lava formation. On the neighbouring White Sands region there occurs a small nearly white pocket-mouse (*Perognathus gypsi*), whose colour closely approaches that of the gypsum dunes where it lives : this species was not taken elsewhere than on the White Sands. Dice concludes that the presence of these peculiar species and subspecies cannot be correlated with climatic differences, since the desert and lava stations lie but a few miles apart in the same valley, and at practically the same elevation. He believes that the coloration is in some way correlated with the colour of the surroundings.

In 1931 Benson (47) carried out a more detailed survey of the mammalian fauna of the same region ; and in his paper on ' Concealing Coloration among some Desert Rodents of the Southwestern United States ' discusses the possible effect of background upon the coloration of mammals inhabiting the white sand-dune and black lava flow areas. His observations support and extend those of Dice, and confirm the view that the observed colour differences are not due to climatic factors. The author concludes that : ' The hypothesis of the operation of natural selection toward producing protective coloration, together with the factor of isolation, appears to be the best explanation of the development of the races peculiar to the dunes and to the lava . . .'

It now seems clear that in certain cases at any rate depigmentation results from a life on a pallid background; and it is very evident that an appeal to the physical effects of light or atmosphere involve great difficulties. More recent researches by Sumner led him to modify his earlier conclusions. In an important paper dealing with the subspecies of *Peromyscus* (598) he brings forward evidence which points towards the operation of visual rather than physical factors, and he admits that earlier arguments for the direct responsibility of atmospheric agents in bringing about pallid hues have lost some of their cogency.

Thus, on an isolated reef of pure white quartz sand off North-west Florida he found *Peromyscus polionotus polionotus* of the mainland represented by a distinct and extraordinarily pallid race, *P. p. leucocephalus*. In this race most of the hair was white, and the pigment of the skin was greatly reduced. Yet the environment is one of high rainfall and high atmospheric humidity. Here, then, the relation between humidity and pigmentation is reversed, while that between the coloration of the Mice and that of their background provides a striking example of approximation. Sumner expresses the opinion that, in the absence of direct evidence, protective coloration, achieved through differential survival of the paler variants, seems to be the most plausible hypothesis to meet this case.

Reviewing the phenomena, Sumner appears to favour a ' compromise verdict ' between the alternative interpretations. ' It is not improbable ', he says, ' that both of these explanations must be reckoned with. Pronounced differences of atmospheric humidity may be capable of bringing about genetic changes in pigment formation, independently of selection, while selection, on the basis of concealing coloration, may enhance these effects in the case of many desert animals.'

Dice and Blossom (141*a*) discuss a number of instances of local, non-climatic colour-adaptation in their comprehensive work on mammalian ecology of south-western North America. For instance, a most complete series of colour-races is presented by the Rock Pocket-mouse (*Perognathus intermedius*), the Cactus Mouse (*Peromyscus eremicus*), the White-throated Wood-rat (*Neotoma albigula*) and the Cactus Wood-rat (*N. lepida*). All occur in parallel series of pale, intermediate, and dark-coloured races on pale, intermediate and dark-coloured rocks; and the authors point out that this correspondence cannot be the result of coincidence, nor can it be due to differences of climate or vegetation.

The facts, then, point unmistakably towards adaptation, and it is difficult to avoid the conclusion that the coloration of these mammals is to be explained in terms of concealment from predators.

(2) **Local Races among Birds**—Many analogous facts are known in other groups of animals. I have referred elsewhere to the similarity exhibited by lizards of the genus *Phrynosoma* to different surroundings. Among birds, a classical instance is afforded by Desert Larks of the genus *Ammomanes*, whose

local races are wonderfully adapted to the colour of the ground on which they nest (94). On the desert between Ammam and Baghdad Meinertzhagen found an almost black race (*A. deserti annæ*) on a narrow belt of black iron-pan rock. On the neighbouring sandy plain this was replaced by a pale race (*A. d. coxi*). Both exactly matched the colour of the soil on which they lived, and doubtless nested. Major Cheesman points out that: 'It cannot be contended that these two forms are due to humidity, as the climate is exactly the same for both.' This author found another subspecies (*A. d. azizi*), the palest of the genus, on white chalky sandstone hills at Hufuf, where he states that the harmony of colour between the bird and the pinky-white rubble was marvellous.

What is in some respects one of the most singular cases yet recorded of colour adaptation to a particular background has been described by Stuart Baker (13), and relates to the eggs of the Yellow-wattled Lapwing (*Lobipluvia malabarica*). Breeding throughout the greater part of India, this bird nests on the bare ground, the eggs usually being placed in a slight depression absolutely in the open: but their earthy coloration and dark markings render them very inconspicuous and difficult to find. Search for nests in 1915 by Mr. J. Stuart on a narrow sandy strip along the Malabar coast, where the soil consists of brick-red laterite with scattered nodules of black ironstone, led to the discovery that throughout this particular area the Yellow-wattled Lapwing lays a curious erythritic form of egg—from pale to deep buff-red in ground colour, with blackish-brown or reddish-brown specks and blotches. These eggs are 'exactly like the ground upon which they are deposited', and when in situ are practically invisible. In subsequent years a large series of eggs was collected both from the red laterite and from the dark-soiled surrounding country. In the latter region the eggs were of the normal earthy type: on the red laterite they were almost consistently of the erythritic form. 'On the rare occasions on which eggs were found on soil contrasting with their colour, they stood up so conspicuously that it was obvious they must have speedily attracted the attention of vermin passing anywhere close by.'

(3) **Local Races among Insects**—Among insects also many cases are known of colour races which closely harmonize with the prevailing hues of the particular region which they inhabit. A notable example is provided by the Geometrid moth *Camptogramma bilineata*—a widely spread and common British species. On a small rock islet called Dursey Island, off the Kerry coast, Kane (299) discovered a melanic variety (var. *isolata*), which had in that locality wholly superseded the yellow type. Melanism was advanced, both fore and hind wings being a 'uniform sooty black', which harmonized with the local dark slate formation. Kane attributed its existence to the effect of isolation and to the selective agency of bats, Rock Pipits, Wheatears and smaller gulls which haunted the rock in active pursuit of insects. It will be remembered that these moths habitually rest on the rock-face with outstretched wings, and he believed that the intense struggle for existence on a small exposed area out at sea had led to the thinning out of the paler individuals, and to the survival of the better con-

cealed dark form. Although Kane produces no direct evidence to support this explanation, its probability is supported by evidence of the selective value of concealing coloration and of discrimination by insectivorous enemies which will be considered on a later page. What we may notice here are the further significant facts that dark aberrations of *C. bilineata* were also found on the dark cliffs of the adjoining mainland, and also on the dark peat bogs of Connemara; but that on the pale grey limestone tracts of Galway Bay and in the neighbouring Aran Islands, the same species, varying procryptically in the opposite direction, had assumed a light patternless form.

Of special interest is the well-known phenomenon of industrial melanism in Lepidoptera, recently reviewed by E. B. Ford (181*a*). Many different species of moths, belonging to several very distinct groups, have become black in industrial areas in England and on the Continent. The change has been brought about during the last eighty years. It is still actively proceeding. And, as Ford remarks, ‘ It represents one of the few evolutionary modifications ever actually witnessed in nature, and is certainly the most considerable of them.’

The earliest instance was provided by the Pepper and Salt Moth (*Biston betularia*), whose melanic (and almost entirely black) variety *carbonaria* was apparently first noticed in 1850 at Manchester. It has now completely replaced the typical form in English industrial areas, whence it has also spread into neighbouring country districts.

Good examples are seen in the Geometrid moths *Boarmia extersaria* and *B. punctinalis*. The first occurs in southern England, and here its black variety *cornelseni* is rare; but in Germany this has replaced the normal form where the species occurs in manufacturing districts, though not elsewhere in unpolluted country. Similarly, the black variety *humperti* of *B. punctinalis* has established itself where the species occurs in German industrial areas.

The distribution of such melanic varieties, coinciding as it often does with industrialism, is very significant. So is the fact that the melanic forms have not, or have but rarely, become established, even though they are present, in rural districts like the South of England—and this although it has been demonstrated that in a number of cases the black variety is actually hardier than the normal form.

This is apparently to be accounted for, in Ford's view, by the counterbalancing disadvantage of conspicuousness—for black coloration would be a handicap in unpolluted areas, but not so in the smoke-blackened countryside of many manufacturing districts. Consequently in the latter the physiological advantages inherent in melanism, perhaps aided by the ecological advantage of inconspicuousness, have apparently led to its replacement of the normal form.

V. COLOUR RESEMBLANCE IN DIFFERENT SEASONS: SEASONAL DIMORPHISM

Various insects having more than one annual brood exhibit seasonal dimorphism, the colours of successive broods being correlated with the changing conditions produced by seasonal phenomena. In the following brief reference to the subject, I have drawn my information mainly from Poulton's *Essays on Evolution*. Among butterflies, well-marked differences often occur between wet- and dry-season broods, involving modifications both of form and colour. Typically, the latter may be characterized by an elongated and bent apex to the fore wing, and by the much-produced angle of the hind wing, which gives an outline more in keeping with the curled and warped leaves of the dry period.

Such modifications, which are well seen in the Indian *Kallima* (43), have been developed independently in a number of groups—Satyrinæ, Nymphalinæ and Pierinæ. They also occur in various northern species, such as *Selenia bilunaria*. In Africa, where—as compared with India—the two seasons are more distinctly contrasted, the differences between seasonal phases of butterflies, especially as regards colour, tend to be more marked. Of these two phases, that of the dry season is usually the one better adapted for concealment. Moreover it sometimes happens, as with *Precis sesamus*, *P. antilope* and *P. actia*, that the two phases differ from one another very markedly—the dry forms having the under wing surfaces highly cryptic in appearance, while those of the wet form are highly conspicuous.

Poulton has correlated this striking difference with the conditions of life in the two seasons. During the wet season, butterflies are plentiful; they are much on the wing; and they are less subject to long periods of rest. The dry season, on the other hand, is one of comparative scarcity for insectivorous foes. Insects are then much reduced in numbers and are in greater demand. They are also less upon the wing; more inclined to a state of hibernation; and obliged to face the risks of longer periods of enforced repose. Also, the succession of broods is almost at a standstill, so that individuals must face the hazards of life for longer periods. Hence the dry season is a time of far greater stress. These considerations led Poulton to conclude that while conspicuousness may be advantageous to relatively distasteful species in the wet season, when more palatable food is plentiful, concealment is a necessity during the time of drought,—when food is scarce and the struggle for existence especially severe.

VI. COLOUR RESEMBLANCE DUE TO CHOICE OF APPROPRIATE BACKGROUNDS

A number of cases are known in which colour harmony is dependent upon a definite escape instinct, which leads animals—including such diverse types as grasshoppers and butterflies, fishes and molluscs—to seek shelter in appropriately coloured surroundings. I shall refer to this habit on a later page, in connexion with special cryptic resemblances, and will confine myself here to a single instance observed by Doflein in Martinique (152).

This relates to three species of lizards, belonging to the genus *Anolis*, which were found occupying one part of the island. Though coloured very differently—being respectively brownish, green and light grey marbled with darker spots—they lived in the same surroundings and were in the habit of hunting together for insects over the same ground. When disturbed, however, Doflein noticed that they would dart off for a short distance and then disappear from view. After a little time he recognized that this was due to a peculiar sorting of the lizards, each species seeking refuge in surroundings of appropriate colour; the green individuals running to the green vegetation, the brown to dry withered bushes, and the grey species to cover among the grey tree-trunks, whose sun-flecked bark corresponded closely with their own marbled coloration. Having gained the protection of these surroundings, the three species would remain completely motionless, as though in the knowledge that they were perfectly safe.

We may also include here cases in which colour harmony appears to be correlated with special nesting habits. There is evidence that certain ground-nesting birds select a special type of site whose coloration is in closer harmony with that of their eggs than are the general surroundings. Thus the eggs come to be better concealed than would be possible in a site chosen indiscriminately.

The Four-banded Sand-Grouse (*Pterocles quadricinctus quadricinctus*) lays pinkish eggs which would seem to make them conspicuous, since they are laid on bare ground. However, Mr. A. L. Butler (cited Bannerman 18) observed in the Sudan 'the interesting fact that all the nests he found were amongst the scattered fallen leaves of the Camel's Foot Tree (*Bauhinia*), which dry exactly the same clay-pink as the eggs, and amongst which the eggs are very difficult to detect'.

It appears that Lapwings may obtain similar protection for their eggs when nesting on pasture, where they show a tendency to deposit them among the scattered droppings of farm animals. In May 1938 I found in a large grass field near Strathaven, Lanark, a number of Lapwings nesting, and the immediate association of the nests with the scattered brown droppings of horses requires some comment. In several cases the nests and eggs were situated right in the centre of the scattered excrement, and in this situation they were undoubtedly less conspicuous than when surrounded by clean grass. The distribution in this case was as follows:

5 nests containing eggs: 4 in horse dung; 1 in grass.
12 empty nests or scrapes: 6 in horse dung; 6 in grass.

The area of this field actually covered by droppings was possibly about 1 per cent., and was sufficiently small to exclude altogether the explanation of these results as due to chance; and the facts seem to point to definite selection of a particular site.

The above facts acquire additional significance when they are considered in relation to the known selection by cuckoos of particular foster parents, whose eggs are similar in colour to their own. This subject will be considered under the heading of Mimicry. I merely wish here to draw attention to the common end achieved by these nesting instincts, so widely different in other respects, but both of which lead to colour-resemblance between the eggs and their immediate surroundings—a resemblance which in the one case is protective, in the other mimetic.

2. VARIABLE COLOUR RESEMBLANCE

> As a vesture shalt thou change them, and they shall be changed.
>
> PSALM CII, 26

We now come to an important class of cases, in which cryptic resemblance depends upon adaptive colour changes in the individual. The nature of these adjustments in appearance differs widely according to circumstances. They may be permanent, or temporary; specific and unvarying, or adjustable and capable of repetition; correlated with the life cycle, or with the cycle of the seasons; built up gradually, or assumed in an instant.

I. CHANGES OF COLOUR CORRELATED WITH THE LIFE HISTORY

Adaptive changes associated with the life history are presented by many insects and other animals which, in the succeeding stages of their lives, bear a strong resemblance to the successive stations which they occupy. Among Lepidoptera, for instance, examples are familiar to every one. Many Geometridæ, like the Oak Beauty (*Pachys strataria*), bear in the larval form a wonderful similarity, exact to the smallest detail, to twigs of the food plant on which they rest; as pupæ, occurring in and wearing the colour of the soil; while the habits and coloration of the adult are admirably adapted for concealment on bark.

Many Sphingidæ, like the Pine Hawk Moth (*Hyloicus pinastri*), are dressed in the similitude of the needles, soil, and bark with which they are intimately associated in the larval, pupal and adult states. In certain Brazilian butterflies of the genus *Ageronia*, where the pupæ are suspended among leaves in full view of enemies, this stage is elaborately modified both in form and colour, so that it bears an even closer resemblance to a rolled leaf than the adult does to the grey bark of a tree.

Poulton has pointed out that fully fed larvæ of the Privet Hawk Moth (*Sphinx ligustri*) change from green to brown and are thus rendered inconspicuous on brown earth prior to burying for pupation. At a corresponding period larvæ of the August Thorn Moth (*Eunomos angularia*) undergo exactly the reverse change from brown to green, preparatory to pupating in a cocoon of elm leaves (496).

Frequently particular phases of early life are correlated with special temporary habits and attitudes. An interesting example has been described by Hale Carpenter from Uganda. When very young the larvæ of the Bombycid moth *Triloqua obliquissima* are chalky white in colour, and since they feed crowded together on the *surface* of a leaf, they simulate a bird's dropping. But with growth their appearance and habits alter. They become 'rich brown, like the petioles, with greenish and purplish mottlings and numerous excrescences like scales at the bases of the petioles': and now they no longer crowd together, but feed on the edge of the leaves and rest individually on the twigs and petioles (87).

Several instances of a similar nature are given by Poulton in *The Colours of Animals*. Thus, various stick-like Geometrid caterpillars do not sit upon the branches, but upon the leaves of their food-plant. In such a situation a stick-like posture would be the reverse of deceptive. Certain of these caterpillars, such as *Ephyra omicronaria*, are at first green in colour. Others are brown, but adopt special attitudes, being twisted into an irregular spiral *Ephyra pendularia*, or into an irregular zigzag, as in *Selenia bilunaria*, so that instead of resembling twigs, they simulate torn or withered fragments of a leaf, or the excrement of birds or snails (496).

Under the present heading we must also include those far-reaching changes seen in many animals like the Eel (*Anguilla anguilla*) and other fishes—as, indeed, in innumerable molluscs and crustaceans—which as pelagic larvæ are transparent and colourless, and as littoral adults opaque and pigmented like their immediate surroundings of weed, rock or sand.

Change in an opposite direction occurs in species like the Flying-fish *Cypsilurus furcatus*, whose young are coloured buff, with the 'wings' marbled in greys, yellows and orange-brown, when as juveniles they shelter among drifting seaweeds; but later, as adults, they assume the typical pelagic uniform of blue-grey and silver.

An interesting example of the same principle is presented by the Opisthobranch Mollusc *Aplysia punctata*, whose colour, varying with age from rose-red to olive green, is correlated with changes in the algal background during its migration from deep to shallow waters (see page 349).

Among mammals and birds the first liveries acquired by the young—whether this happens before or after birth—often differ widely from the full dress of their parents. But it must not be assumed that such differences are necessarily adaptive. Lion cubs have spotted coats, and their tails are ringed. Puma cubs have the face marked with black stripes and spots, while the legs and under parts are spotted. Young Lynxes are liberally spotted with black. Since the kittens of all these animals, as well as of smaller carnivores such as Genets and Civets, Ichneumons and Mongooses, are born in sheltered dens or holes, carefully hidden or guarded by the mother, the spotted pattern can hardly be explained as protective.

The fact that many self-coloured adults have spotted young, while self-coloured young never acquire spots as adults, points to the view that these markings of young carnivores represent a primitive pattern, to be explained on ancestral rather than ecological grounds. What is significant from our point of view is that while the juvenile spotted livery is retained and intensified in Leopards and Jaguars, Servals and Ocelots, in whose wooded surroundings it is turned to useful account, it has been modified as a pattern of stripes in the Tiger, and obliterated in the self-coloured cats of the open country—Lion, Puma and Lynx.

The colour differences between young and adult pigs are hardly to be regarded as adaptive. It is true that the striped young of River Hogs and Wart Hogs haunt grassy surroundings where a striped pattern might tend towards concealment, but as Chalmers Mitchell points out: '. . . the parents guard their young with so great devotion and with so powerful weapons that the little pigs have no need of concealment' (413).

Differences between the young and adult pattern are common among deer. The majority of species have spotted young, and frequently, as in the Red Deer, Roe Deer, Wapiti and Chinese Water Deer, the spotted coat of the fawn is shed in a few months and the spots never reappear. Such white flecks as are worn by fawns which haunt the neighbourhood of trees and lie at rest beneath their shade cannot fail to make them less visible.

With birds, differences of colour and pattern correlated with growth are very striking. The coloration of nestlings is referred to on a later page. There can be little doubt that the disruptive down-patterns worn by newly hatched Rheas, Emus and Cassowaries, by Ducks of many species, by Partridges, Quails and Pheasants, by Gulls and Terns, by Grebes, and by wading birds generally, represent schemes of colour whose function is concealment. And it is to be noted that such cryptic costumes are typical of nidifugous young which run and fend for themselves almost as soon as they leave the egg; while helpless nidicolous young living in sheltered nests are naked and weak at birth and do not subsequently acquire disruptive downy coats. It is interesting to find that this distinction is maintained even between related species. Thus the Sand-Grouse, although related to the pigeons, nest on the ground like game birds, and have precocious young born in an advanced, active condition, and clad in a highly cryptic dress of cream or buff, strongly marked with rich brown or black.

II. CHANGES OF COLOUR CORRELATED WITH THE SEASONS

We have seen in an earlier section that the coloration of successive broods of insects may be correlated with seasonal changes in the surroundings. With various birds and mammals a somewhat similar end is achieved in an entirely different way, involving seasonal changes, not in successive generations of individuals, but in the succeeding dresses worn by one and the same individual.

(1) **Seasonal Change in Snowlands**—The coloration and colour-changes of northern mammals and birds present many puzzling features. The fact that a number of arctic and subarctic species, such as the Ptarmigan, Willow Grouse, Mountain Hare, Prairie Hare, Arctic Fox, Stoat and others undergo a change to white at the approach of winter is known to every one. But this assumption of a cryptic winter dress is by no means universal in the snowlands. In the first place, certain forms such as the Polar Bear, Snowy Owl, Greenland

Falcon and American Polar Hare are white all the year round. On the other hand, others, like Moose, Musk Ox, Glutton, Reindeer, Rabbit and Raven, do not become white during any part of the year even in the coldest parts of their range.

Among those which are subject to seasonal changes, closely allied species may differ considerably in this respect. For instance, the Hudson's Bay Lemming (*Cuniculus torquatus*) assumes a white winter coat, while the Scandinavian Lemming (*Myodes lemmus*) does not (33). In a number of animals the degree of seasonal change varies with latitude and climate. For instance, in the extreme north of its range, the Arctic Fox (*Alopex lagopus*) nearly always discards its bluish-brown summer dress for a pure white winter coat ; but in Iceland, where the winter is less severe, the change to white is exceptional. The same is true of the Stoat (*Mustela erminea*), which in winter regularly turns white in the north of Scotland, but less completely and less frequently in England. Similarly the Weasel (*M. nivalis*) always assumes white in northern Europe, but rarely does so in Great Britain.

The Mountain Hare (*Lepus timidus*) of northern Europe, and its local races in Scotland and Ireland, illustrate the same principle. In Scandinavia it habitually changes into white ; in the Scottish Highlands it generally does so ; but in Ireland and the south of Sweden the grey coat is retained throughout the year. In North America the Prairie Hare (*L. campestris*) and Varying Hare (*L. americanus*) turn white in winter ; the Wood Hare (*L. sylvaticus*), which ranges farther south, retains its summer coloration ; while the northern Polar Hare (*L. arcticus*) remains white all the year round.

There is evidence, in certain cases at any rate, that low temperature is the factor which causes the whitening of the hair (496). On the other hand, there are many facts which this explanation will not meet. In the first place, with certain forms like the Stoat, the change may occur in early autumn, before the onset of cold weather : while, as Dr. Julian Huxley informs me, whitening takes place regularly in Arctic Foxes living in the Zoological Society's Gardens. Such facts do not support the view that the change is due to the direct influence of the climate. Moreover, the fact that some arctic and subarctic animals—both mammals and birds—change in winter while others do not, renders improbable the sufficiency of any such explanation.

On the other hand, the exceptional cases, in which the dark summer coloration is retained throughout the winter, lend indirect support to an adaptive, rather than a climatic, explanation of the phenomena. They are ' the exceptions which prove the rule '—since the outstanding examples, which include the Raven, Sable, Glutton, Pine Marten, Musk Ox, Moose and Reindeer, are animals having no special need for concealment (see p. 151). Moreover, it is significant that those species, like the Polar Bear, Arctic Fox, Snowy Owl, Greenland Falcon, Stoat, Weasel, Willow Grouse, Ptarmigan, and Mountain Hare, which as potential predators or prospective prey may be assumed to need cryptic coloration for purposes of offence and defence, are those which in winter, whether by change or constancy, wear a white uniform.

(2) **Seasonal Change in Deciduous Forest**—We have now to mention briefly a type of colour change in certain respects the very opposite of that considered above. Various inhabitants of forest and savannah in tropical and subtropical countries have their bodies decorated with white spots—such as are worn by the Axis Deer (*Axis axis*) of India, the Bush Buck (*Tragelaphus scriptus sylvaticus*) of Africa, and the Spotted Cavy (*Cuniculus paca*) of South America. In surroundings where shafts from the sun shine through between the leaves and scatter everywhere flecks of sunlight which are bright in contrast to the adjacent shade, such markings distributed over an animal's back and flanks form an important and effective cryptic element.

On the other hand, in colder latitudes, where the leaves fall in autumn, a spotted livery would be the reverse of protective during the winter months. Now it is interesting to find that certain species, such as the European Fallow Deer (*Dama dama*), and the Japanese Deer (*Sika nippon*), which inhabit deciduous forests, undergo a seasonal colour change. During the summer they are decorated with white spots ; but in winter these are lost, and they assume a uniform greyish or brown coloration. In the more tropical climate of Formosa, however, where the forests are evergreen, the latter species is represented by a race whose white spots show a tendency to persist during winter.

When we compare the present seasonal changes with those found among Arctic animals, it will be noted that a similar tendency—namely, to develop white hairs—is correlated with precisely opposite climatic conditions. In the snowlands it is a phenomenon of winter and in the forests of summer occurrence. But in both regions, these opposite methods bring about the same result, namely, cryptic resemblance to a changing environment—resemblance, that is to say, in the one case to fields of snow, and in the other to flecks of sunlight.

III. SLOW ADJUSTABLE COLOUR RESEMBLANCE : MORPHOLOGICAL COLOUR-CHANGE

Many circumstances in the lives of animals place a premium upon the ability to change colour. With more or less sedentary species, different individuals may find themselves facing life in incongruous surroundings. Active animals, on the other hand, are constantly coming into contact with different backgrounds. In neither case can a fixed type of coloration be altogether satisfactory. Varying conditions, whether for different individuals at one time or for one individual at different times, demand variable camouflage ; and it will surprise no one who is at all familiar with the wonderful variety and versatility of nature's adaptive arrangements to discover that this most difficult problem—of matching an animal to a variable or changing background—has been successfully overcome, and this not once, but over and over again by various members of the animal kingdom.

We are concerned in the present section with a type of colour adjustment especially applicable to relatively inactive insects and other creatures which undergo development against a specific background, and which become adjusted to the predominant tones of their surroundings as development proceeds. Such modifications, known as Morphological Colour Changes, tend to be both slow and permanent in effect, in contrast to Physiological Colour Changes which, as we shall see in the following section, may be both rapid and reversible.

(1) **Adjustable Resemblances among Lepidopterous Larvæ and Pupæ**—In a classical series of experiments conducted many years ago, Poulton proved that certain Lepidopterous larvæ and pupæ possess the power of acquiring the coloration of their immediate surroundings (491). He showed with *Vanessa urticæ* and *V. io*, and also *Pieris brassicæ* and *P. rapæ*, that the pupal adjustment was due to extreme sensibility of the larvæ to reflected light when in their final resting position, preparatory to pupation.

A further interesting discovery was that certain larvæ are capable of adaptive adjustment not merely to colour, but also to pattern, in their surroundings. Poulton (502) found that caterpillars of the Scalloped Hazel Moth, *Odontopera bidentata*, which rest by day on twigs and branches, are highly sensitive to various shades of brown and grey commonly associated with the bark of their food plant, but that when the larvæ were exposed to the influence of lichen-covered branches, their brown bark-like bodies assumed green lichen-like markings. Similar results were obtained with young larvæ of the Lappet Moth, *Gastropacha quercifolia.*

(2) **Adjustable Resemblances among Orthoptera**—The resemblance of certain grasshoppers to surroundings of different hues in different localities is well known, and there is strong evidence that such insects react to radiation from their environment, and possess marked powers of individual colour adaptation (514, 207). In 1901 Poulton observed that the grasshopper *Stauroderus bicolor* always matched the reddish-brown earth in Heligoland, but that on a neighbouring sandbank called the Düne grasshoppers of the same species were sand-coloured. Not a single dark example was seen on the Düne, nor one pale specimen on the dark soil. ‘ There is little doubt ’, he writes, ‘ that these results, observed without a single exception in such large numbers, in two localities so near to each other, point to the conclusion that the species possesses the power of adjusting its colours to those of its normal surroundings, although these may differ widely from one another.’

More recent researches by Faure (170) and Hertz and Imms (248) have fully confirmed this prediction, and it is now known that the immature forms of various Acridiidæ possess powers of slow colour adjustment within wide limits, and that this ‘ morphological colour change ’ may lead to remarkable colour resemblances between the insect and its immediate environment. I have referred briefly elsewhere to the very wide range of cryptic colour exhibited by grasshoppers in the Canary Islands. A striking instance has been described by Mrs. H. H. Brindley from the Russian steppes (232). Referring to *Acrida turrita*—a sluggish grass-feeding grasshopper—she says : ‘ In June, while the grass is still fresh and green, the Tryxalids are green, with a silvery bloom shading into purple on the antennæ and margins of the elytra. At this time they are indistinguishable among the blades and purple panicles of the grass. In August, when the herbage is dried and yellow, the grasshoppers still feed in the same spots, but now they are brown and scorched-looking, in the perfect similitude of bits of straw.'

(3) **Adjustable Resemblance of Insects to Areas blackened by Grass Fires**—More remarkable, however, is the case discussed by Poulton (514) of African insects which bear a resemblance to the blackened areas caused by grass fires. A variety of species belonging to several families taken by Bacot, Carpenter and Swynnerton on areas recently blackened by fire, and including a cockroach, a mantis, a cricket, many species of Acridiid grasshoppers, a Pentatomid bug, and a Noctuid larva, all showed more or less of the blackened or charred appearance of their surroundings. For instance, the larvæ, apparently those of *Spodoptera abyssinia*—taken on an island in Lake Victoria by Carpenter—were coloured in longitudinal stripes of coal-black and bright grass-green, a disruptive uniform whose tints harmonized perfectly with those of the fire-blackened stems and new green shoots where they were feeding. The bug *Macrina juvenca*, found under similar conditions by Carpenter in Uganda, was the colour of a partially burnt chip of wood.

Direct evidence that these resemblances are due to individual adjustment, and not to seasonal forms appearing at the time when the grass is burnt, is lacking. But the former explanation is supported by observations by Sjöstedt (575) and is rendered likely by the knowledge that different Orthoptera and Lepidoptera do possess the power of colour-change in conformity with their surroundings.

(4) **Adjustable Resemblance of Spiders to Flowers**—Many other animals, including various Crustacea and Arachnida, exhibit slow reactions of a similar kind. The Crab-spider *Misumena vatia* has a considerable capacity for colour-adaptation to different backgrounds. These spiders have adopted the interesting, and doubtless profitable, habit of lurking among the petals of flowers, where they lie in ambush for insect prey. They exhibit a fair range of coloration, and it is well known that individuals tend to resemble closely the tint of the particular flower inhabited. For instance, Packard (452) found in Maine that in early summer, during June and July, when the greater mass of flowers such as White Fleabane and Ox-eye are white, specimens of *M. vatia* were white also, no yellow individuals being detected. Subsequently, during late July and early August, when the Golden Rod begins to flower, a few yellow specimens made their appearance. But by the middle of the month and through September almost without exception the spiders were pale or deep yellow in colour.

Parallel phenomena were observed by Banks in Virginia, where the white spiders occurring in spring on the white Wake-robin (*Trillium*) afterwards became yellow on the flowers of the Yellow Dog-tooth Violet. In England specimens taken on Heather are usually pink in colour. Kerville (308) and Gabritschevsky (191) have shown experimentally that these resemblances are due to individual colour adjustment, and that the reaction, moreover, is a reversible one. Thus when Kerville transferred a specimen with a yellow abdomen from the yellow corolla of *Ranunculus acris* to the greenish-white *Viola tricolor*, it gradually assumed the colour of its new surroundings; while a white-and-green individual became clear yellow when removed from the white flower of *Calystegia sepium* to the yellow *Chrysanthemum coronarium*. Gabritschevsky found that the immature spiderlings were incapable of assuming white or yellow coloration when raised on papers of these colours; but that after the last moult they became sensitive to reflected yellow or white light—white individuals changing to yellow on a yellow background in from ten to twenty days, while they reassumed their white coloration on a white background after five or six days.

IV. RAPID ADJUSTABLE COLOUR RESEMBLANCE: PHYSIOLOGICAL COLOUR-CHANGE

The type of colour-change now to be considered differs from the last in that the effects produced are both rapid and capable of repetition, being brought about by the rearrangement of pigment granules within specialized cells—the chromatophores. The power of rapid, and sometimes almost instantaneous, adjustment to the colour of the background is one especially suited to active animals which are constantly passing and repassing from one kind of background to another. Its value lies in enabling such animals to depend upon concealment while retaining freedom of movement; and, at its best, it represents undoubtedly the most wonderful automatic cryptic device in existence.

We have to notice in the first place that the mechanism is essentially an attribute of the 'higher' animals. Molluscs, arthropods, and vertebrates represent the three highest lines of evolutionary specialization in the animal kingdom, and it is in these three phyla that chromatic change has been established. Chromatophores are developed in Cephalopoda—the final goal of molluscan evolution; in Crustacea, and exceptionally among insects; and in the three lowest classes of vertebrates—fishes, amphibians, and reptiles. Among mammals and birds chromatophoral activity is of course rendered impracticable, since the skin is usually hidden beneath hair or feathers.

The physiological mechanism responsible for the changes is a complex one, involving reflex activities induced through the sense of sight, control by hormones in the blood, or in some cases being due to the direct action of light on the skin. Parker (455) points out that all the animals concerned have well-developed sense-organs, especially eyes, and that the eye seems to play an important part in initiating the colour response, which is, however, essentially a reflex action rather than a higher nervous response. In general, colour-changes which affect the animal as a whole are due to the action of hormones, while pattern formation, which involves the independent activity of different parts of the body, is under nervous control.

(1) **Semi-permanent Adjustments among Fishes**—Before discussing this type of colour-change, I must refer to another and more permanent type

of adjustment commonly possessed by fishes, which is brought about by a decrease or increase in the number of chromatophores, rather than by the contraction or expansion of their pigment. The latter arrangement might be compared in ourselves to a sudden flushing or pallor, rapid in onset and temporary in duration, due to emotional disturbances such as anger or fear : the former to a gradual darkening or paling of the complexion, progressive in onset and more permanent in duration, due to sunburn or sickness. It is interesting to note that in their effect on an observer these two types of adjustment in fishes are precisely parallel to the two methods by which an artist can deepen the tone of a stippled ink drawing—that is to say, by increasing the *number* of dots in a particular area, or by increasing the *size* of existing dots in the same area.

Adjustments of chromatophore distribution take time to mature, and though reversible, are semi-permanent. Consequently they are suited to, and appear most frequently in, species passing different periods of their lives in different environments. For instance, the production of semi-permanent spots is seen in the Plaice (*Pleuronectes platessa*), whose colour patterns have been studied by Hewer. The young, which normally inhabit inshore sandy grounds, are highly marked and possess numerous white spots which agree well with the surroundings. On the other hand, adults taken from a muddy bottom are mainly greyish-brown, usually without white spots, though these become numerous in specimens kept on whitish pebbly bottoms (255).

Such adjustments of coloration coinciding with the tone, or colour, or pattern of the fishes' environment, are familiar to every naturalist. In certain cases the results produced are very striking. Jordan states that on the coast of California there is a band-shaped Blenny (*Apodichthys flavidus*), which appears in three colour schemes—blood-red, grass-green, and olive-yellow—according to its surroundings. Here the red coloration also is essentially protective, for the region inhabited by such individuals is the zone of red algæ. The Demon Stinger (*Inimicus japonicus*), of Japanese waters, is blackish in colour when taken among lava rocks, but when found among red algæ it wears bright red, broken with a few irregular markings of yellowish-brown (293).

Changes of a similar nature are recorded of certain American Pipe-fishes, which may vary from dark to light green when transferred from tufts of eel-grass to pale weeds ; or from brown to brick-red when taken respectively from mud or from red seaweeds (446). Many other Teleost fishes including Wrasse (*Crenilabrus*), Trout (*Salmo*), Stickleback (*Gasterosteus*), Bullheads (*Cottus*), and Minnows (*Phoxinus*) are likewise subject to a considerable range of variation which is in general correlated with that of their natural surroundings.

Colour-changes in Elasmobranch fishes have received less attention, but it is now known that various species, such as the Dogfish *Mustelus canis* (457), and the Skate *Raja erinacea*, possess a considerable range of variation, and that these changes tend to conform to changes in the environment. Parker carried out experiments with *R. erinacea* which showed the cryptic nature of the adjustment (456). Two individuals, indistinguishable as regards colour, were placed respectively in white-walled and black-walled sea tanks : after eighteen hours the ' white ' fish was light brown, and the ' dark ' one dark brown. They were then transferred, and after nine hours the light skate had become dark. With the other individual the reverse change was slower, but twenty-one hours after transference to the white tank it was itself pinkish-white in colour.

An application of this semi-permanent type of adjustment is seen in the practice of ' conditioning ' Minnows in a can with white sides, so that when subsequently used as bait they appear more conspicuous in the dark waters inhabited by Pike and Perch. As Poulton wrote in 1890 : ' The fisherman knows that he stands an extra chance of catching his fish while the bait remains unadapted to its environment. This experience serves to prove in a practical way that the power of changing the colour is essentially protective ' (496)—a conclusion strikingly confirmed in recent years by Sumner, whose experiments are described at some length on another page.

(2) **Rapid Adjustment in Fishes**—We have now to consider adjustments of a more specialized type. Many fishes—notably certain inhabitants of coral reefs—possess powers of rapid colour-change, which both in range and rapidity far exceed those of chameleons, whose classical achievements pale by comparison. In his detailed study of the colour-changes undergone by different reef fishes from Bermuda on exhibition in the New York Aquarium, Dr. Townsend records ' instantaneous changes ' in twenty-eight tropical species. Some of these, like the Nassau Grouper (*Epinephelus striatus*), can assume six or even eight different liveries, which may be put on and off within a few moments. These colour reactions are frequently to be explained as an emotional response, correlated with excitement, anger, or fear, or with such activities as fighting or feeding. Allowing for this factor, however, there is no doubt that many adjustments are commonly induced by, and correlated with, changes in the background, and are adaptive in the sense that they make for concealment—as has been demonstrated by the work of Sumner (594), Mast (398), Hewer (255), and others.

The remarkable powers of adaptive adjustment in flat-fishes are too well known to merit detailed description here. The Flounder (*Pleuronectes flesus*) is generally greyish-olive in colour, more or less marbled with brown ; but it may be yellow, or almost black. Not only do the most responsive species possess a wide colour range from the palest sandy hues to the deepest brown tones, but they have the singular ability to respond to different degrees of coarseness in their surroundings—taking on a definite pattern which varies, within limits, with the texture of the bottom where they are lying. Sumner's work with the Turbot-like *Rhomboidichthys podas* at Naples, and the Sand-Dab *Lophopsetta maculata* and Flounders *Paralichthys dentatus* and *Pseudopleuronectes americanus* at Woods Hole, provides many striking examples of this phenomenon—the adjustment to the sand or mud or gravel upon which the fishes happen to be resting being often wellnigh perfect from a cryptic standpoint.

The cryptic nature of the colour-changes in reef fishes has been proved by Longley, who was able to evoke different phases at will by leading individuals, with the offer of food, from one characteristic environment to another (337, 339). Rapid cryptic adjustments also follow vertical movements—a number of species readily exchanging their patterned bottom-colours for self-coloured water-uniforms when they leave the bottom to rise through deep water. ' No fish ', says Longley (346), ' may more justly exemplify this class than the great surgeon-fish *Hepatus matoides*, which, when near bottom, may be black except for its tail and particolored yellow pectoral fin, but which 25 feet higher in the water, away from the reef-face, appears in pure pale blue-grey of lowest visibility.' A similar and very interesting example is presented by a species of *Thalassoma* whose alternative colour-phases were originally attributed to two distinct species, *T. nitidus* and *T. nitidissima*—the former wearing a slaty-blue colour scheme, the latter a predominantly yellow one. Longley showed that these phases are correlated with changes in the environment: the blue *nitidus* dress is worn chiefly by fishes swimming well above the bottom, and the yellow *nitidissima* dress by fishes near it. ' Repeatedly schools of 2 dozen or more fishes in the *nitidus* coloration passed over almost instantaneously to the *nitidissima* type when they dashed down to the bottom to feed upon a broken sea-urchin, and underwent the reverse change at once when they returned to their original position ' (347).

Another significant point brought out by Longley's pioneer submarine researches is that particular phases of *pattern* are frequently related to specific activities in a way which accords with the principles of optical illusion (344). For instance, different fishes which have alternate costumes of longitudinal stripes or uniform colour, and of transverse bars, wear the former when in motion (an arrangement which makes for concealment in that it tends to mask forward movement) and the latter when at rest (when bars better serve to break up the contour and surface form against a broken background). Moreover, precisely similar adjustments are found in certain squids, which wear stripes for swimming and bands for resting (345).

Even in cases where the colour-change appears to be primarily an emotional response, its *result* may tend towards concealment. For instance, in one of its several phases the Nassau Grouper wears a boldly banded and mottled pattern of black on a light ground-colour. As may be inferred from Fig. 8, the pattern, with its strong tonal contrasts, its obliterative ocular band, its coincident elements passing from body to fins, and its ruptive design which everywhere breaks across the contour of the body, is highly cryptic if viewed against a background of broken tones. Now Townsend tells us that it is this banded phase which ' is instantly assumed by all specimens when they are frightened and seek hiding-places among the rock-work ' (629).

(3) **Rapid Adjustment in Frogs**—Many of the Anura are capable of more or less rapid colour adjustment, which in certain genera, such as *Xenopus* and *Hyla*, is remarkable for its considerable range from very dark to very light tones. This faculty appears to reach its highest and most perfect form in *Hyla goughi*, from Trinidad. In 1911 Boulenger wrote that the rapid changes in colour which

this species undergoes are probably unparalleled in any other Amphibian (58). Individuals have at their disposal a range of tints varying from dark brown, through reddish-brown and various shades of yellow, to a very pale greyish white.

Yet more striking are the changes recorded for *Phrynobatrachus plicatus* by Ivan T. Sanderson in the Cameroons. One individual, whose head and back were green and brown when captured, became almost black above, except for a stripe along the back which turned terra-cotta, when the frog was taken into a tent; and Sanderson gives the following remarkable range of colours observed in different individuals of this species—' pure white, yellow, gold, orange, brick, various browns, maroon, purple, mauve, pink, sea-green, grass-green and dove-grey ' (551).

Such changes in Amphibia are induced by a great variety of primary factors, including temperature, tactile and visual stimuli, direct action of light on the skin, respiratory disturbances, and so forth, the activation of the chromatophores being effected through the agency of hormones. But whatever their physiological cause, the fact remains that they do tend, in general, to produce colour-harmony with the surroundings. And Gadow (195), referring to the experimental physiologists' observations, says: ' All this sounds very well, but the observations and experiments are such as are usual in physiological laboratories, and the frogs, when observed in their native haunts, or even when kept under proper conditions, do not always behave as the physiologist thinks they should . . . in many cases the creature knows what it is about, and . . . the eye plays a very important part in the decision of what colour is to be produced. The sensory impression received through the skin of the belly is the same, no matter if the board be painted white, black, or green, and how does it then come to pass that the frog adjusts its colour to a nicety to the general hue or tone of its surroundings ? '

(4) **Rapid Adjustment in Lizards**—Among lizards, many species besides chameleons exhibit marked and rapid colour-adjustments, as shown, for instance, by the American Iguanid *Anolis carolinensis*, whose different phases range from dark-brown to pea-green; and by the Asiatic Agamid *Calotes versicolor*, whose habit of playing the harlequin causes it frequently to be misnamed the ' Chameleon ' by Europeans. Certain geckos are also subject to a remarkable range of rapid adjustment. Malcolm Smith says that *Gehyra mutilata* can change colour with considerable rapidity (579), while according to Tytler *Phelsuma andamanense* possesses a colour-range from rich emerald green—which is the costume worn in the sun or strong light, to nearly black—which is that assumed in dark places or subdued light (634). It will be noted that all the above species are, like the chameleons themselves, typically arboreal, and as such (and in contrast to terrestrial forms) rely for safety mainly upon concealment, rather than upon alertness and speed, though colour-changes occur also in various ground lizards, such as *Phrynosoma*.

(5) **Chromatic Response in Cephalopods**—Very remarkable, both for its rapidity and range of action, is the power of colour-response possessed by

cephalopods—the squids, cuttle-fishes and devil-fishes. 'Under excitement a devil-fish may change from an ashen-gray to almost black and back again, and with effects that are described as cloud-like or shadow-like in their delicacy. The endless variety and change that such an animal may show can be compared only with sky and water. In the squids the same colour-play is observable except that it is ordinarily in tints of golden orange, red and brown' (455).

The chromatic organs responsible for these extraordinary effects have been closely studied, in *Loligo*, by Bozler (59). Each is a complex structure, consisting of a highly specialized group of cells: a central element, the chromatophore proper, containing pigment; and a number of innervated muscle fibres radiating from it in the plane of the skin. Contraction of the radial fibres draws out the central cell into an expanded disc, whose contained pigment consequently occupies a much greater area than before. As they relax, the elasticity of the cell membrane causes the chromatophore to regain its original spherical form.

The cephalopod chromatophore is unique for its complexity not only from the structural, but from the functional standpoint. In his valuable review entitled *Chromatophores* Parker states: 'Its functional activities include many of the intricacies of muscle action. In its relation to the central nervous apparatus, it shows a remarkable degree of differentiation, for the whole chromatophoral system may be acted on locally in such a way as to produce the wave-like spread of colour-change so characteristic of these animals. Such an activity would be impossible without a high degree of central nervous specialization whereby a succession of superficial changes may be called forth. In this respect the cephalopod chromatophoral apparatus, peripheral and nervous together, must involve a complexity of communications and of controls such as are present in the modern electric sign over whose surface an ever-changing design may be made to pass' (455).

The peculiar nature of the cephalopod chromatophoral mechanism renders possible the greatest rapidity of colour-change. Solandt and Hill (580) find that the whole transformation in a chromatophore of Sepia, from complete contraction to complete expansion, can take place in two-thirds of a second.

Evidence bearing on the adaptive significance of colour-change in *Sepia officinalis* has recently been brought forward by Holmes, whose observations point to the general conclusion that the assumed patterns have a protective function. He shows that this versatile cuttlefish has at its command an extensive wardrobe, that different dresses are worn under different conditions of background, and that usually the former are adjusted to the latter so as to produce a cryptic effect. For example, when resting against a white background, all the chromatophores contract, until the animal assumes an iridescent whiteness. On a well-illuminated sandy bottom, the exposed dorsal surface bears a mottled pattern of very light and slightly darker browns. In black surroundings the mottled pattern deepens in shade, and the animal becomes very dark in colour. On the other hand, against a dark background containing white objects, a strong disruptive pattern develops with the appearance of a bold white square, or of two white transverse bands, on the back. This disruptive pattern is assumed only when light and dark objects are present simultaneously in the animal's visual field—the reaction in black and white surroundings being entirely distinct from that in surroundings which are either black or white (269).

(6) **Chromatic Response in Crustacea**—Various of the larger Crustacea—amphipods, isopods, decapods—exhibit adaptive colour responses. Such changes may be said, in general, to make for harmony of colour between the animal and its environment—the chromatophores expanding against a dark background and contracting against a light one. Frequently there is adaptation not merely of shade, but of colour also. *Crangon* is stated by Koller (320) to assume an appropriate tint of yellow, orange or red against different surroundings. The chromatic changes in *Hippolyte* have been extensively studied by Keeble and Gamble (198, 199, 304), who found that when young or old prawns were exposed to the influence of white or of black backgrounds, the pigment became for the most part reduced to dots, or disappeared, in the first case; and in the second, maximal quantities of red and yellow pigments developed, giving the prawn a deep reddish tint. Under natural conditions, that is to say, against backgrounds of weed, *H. varians* exhibits close harmony with its surroundings—becoming brown on brown weed, green on *Ulva* or *Zostera*, red on red algæ. Gamble and Keeble found that young transparent specimens became respectively green or brown within forty-eight hours when placed on weed illuminated by direct sunlight (304). The production of sympathetic weed-colours in the shallower zones of the coast is significant, since the life of *Hippolyte* is intimately bound up with the presence of the algæ, among which it lives and feeds: and these authors remark that '. . . of all things which characterize *Hippolyte*, its tenacious immobility on the weed of its choice is the most striking'.

The chromatophoral mechanism of Crustacea appears to be entirely under humoral control. Thus Koller (320) has demonstrated that in shrimps belonging to the genera *Crangon* and *Leander* the eye-stalks produce a substance 'contractin' which on passing into the blood causes pigment in chromatophores of the region supplied to contract; the rostral 'black-organ' producing another substance 'expantin' having an opposite effect. However, the precise mechanism involved must be extremely complex, and as Parker remarks, we are still far from a complete understanding of the operation. In *Crangon*, for instance, the reactions are very varied, for the shrimp can well adapt itself to backgrounds as diverse in colour as white, red, orange, yellow and black.

(7) **Physiological Colour-change in Carausius**—Reversible, or physiological colour-changes are not unknown among insects, for the Phasmid *Carausius* becomes paler or darker in response to a variety of stimuli, including changes of temperature, osmotic changes in the blood, mechanical pressure, humidity, or visual sensations. The colour-responses of these stick insects have recently attracted the attention of several workers, notably Giersberg (207), Janda (286), Pantel and Sinéty (454), and Priebatsch (528). The actual colour-change is effected by a clumping or spreading of pigment granules in the hypodermal

cells, which may therefore be regarded as unspecialized chromatophores. The parallel between *Carausius* and the more specialized condition in various vertebrates and invertebrates with true chromatophores extends to the method of control, in that optical stimuli acting through the insect's eye upon the visual centre of the brain apparently induce the secretion of a hormone into the blood which activates the pigmentary movements.

(8) **Ecological Significance of Chromatic Response**—We see in chromatophoral mechanisms what we find again and again in other classes of adaptive coloration phenomena: namely, a similar final result brought about by the most diverse means. Wide differences exist both in the number and arrangement of the various chromatic elements forming the physical basis for colour-change; and in the physiological method of control.

From a structural standpoint, the various types of chromatic element bear little resemblance. Those of vertebrates are relatively simple, consisting of single cells, each normally carrying a single kind of pigment. The crustacean element consists of a group of cells, or a syncytium, containing pigment of one or more kinds. In cephalopods the complex and unique structure of the chromatophore gives it the status of a simple organ.

From a physiological standpoint, equally striking differences are apparent in the methods of control. Cephalopod chromatic elements are mainly under nervous control, being apparently little influenced by hormones. In Crustacea, on the other hand, the chromatophores are without nervous connexions, and are apparently activated entirely by hormones. Melanophore activity in vertebrates may be either nervous or humoral—being predominantly of the former type in fishes, the latter in amphibians, and influenced by both agencies in reptiles (455).

But the significant fact must be noted that beneath all this diversity of structural equipment and physiological activity there is generally to be traced a common type of external stimulus and a common type of visible result. The primary sensation of background is received through the eyes, which form the essential approach to the chromatophore system. And the final effect is an approximation in colour and tone, and often in pattern, by the organism to its surroundings. It is, in other words, an adaptation to environment leading to reduced visibility.

3. OBLITERATIVE SHADING

Themselves but shadows of a shadow world.
TENNYSON

The second optical principle upon which concealing coloration depends is that of countershading. When an animal or any other solid object is observed out of doors in the open, it will be seen that its upper surface is more brightly illuminated than its under parts, owing to the direction of incident light from the sky. The effect of this top lighting is to lighten the tone of the upper parts, while the lower surfaces, which are in shade, appear to be darkened.

It is owing to the unequal reflection of light from its different surfaces that a solid object of uniform colour presents to the eye the well-known appearance of *light and shade*; and it is almost entirely by this optical appearance of relief —due to light and shade—that we are able to recognize the object as a solid one.

This property of light alone enables us to distinguish at a glance between a disc and a sphere, or between the side of a cube and the side of a cylinder, even when the compared bodies appear to have identical outlines—a circle or square —and in the complete absence of visual clues due to perspective, or stereoscopic effects.

I. THE PRINCIPLE OF CONCEALMENT BY COUNTERSHADING

Shade, then, is a serious matter, and must be taken into account in any serious attempt to reduce visibility—whether by animals in the interspecific struggle for existence, or by man in the international sphere of warfare.

Shade gives the appearance of projection, or of depth, and by means of light and shade alone a solid body can be distinguished *even when it is placed before a background whose colour and texture exactly matches its own.*

This is well illustrated in Plate 7 which shows a white cock standing in the open before a white background, illuminated by ordinary diffused daylight from the sky. Contrary to what might have been expected by any one lacking in artistic perception, the bird appears highly conspicuous, the back looking lighter, and the breast darker, than the background, although in actual fact, back, background, and breast are all pure white. The only parts of the bird's surface which match the shade of the background are those which, like the background itself, are approximately vertical and hence illuminated to the same degree.

Now, short of floodlighting the bird's belly, it would be quite impossible to obliterate the dark tone which betrays it—for we cannot make white whiter than white. But let us suppose for a moment that this bird were coloured instead a uniform brown tone, and were viewed against a background of exactly similar tone. It would then, of course, still look equally conspicuous ; in fact it would appear precisely as in our photograph of the white bird, though in a lower key. But with brush and paint it would be an easy matter for an artist to lighten the undersurfaces and to darken the back with graded tints *so as exactly to counteract the effect of shade and light.* This treatment by countershading, if properly carried out, as in Thayer's famous models, would render the bird almost completely invisible from a short distance away. Now it is this very principle upon which the concealment of many animals in nature depends. The brush of nature has laid down in skin and scale, in fur and feather, darker pigments on the back, grading into lighter pigments on the belly ; and in this way a further important step is taken towards the obliteration of form—a step which prepares the background for the application of the third great optical principle of disruptive coloration, to be considered later.

The theory of concealment by countershading will always be associated with the name of Abbott H. Thayer, who first fully grasped this important principle and applied it widely to problems of animal coloration. In his important discovery he was, however, anticipated in part by Poulton, who fifty years ago clearly showed how the appearance of roundness in the chrysalis of the Purple Emperor Butterfly (*Apatura iris*), was obliterated by the presence of white spots which—in a manner precisely analogous to the stippling of an artist—exactly neutralized the darker tones of its shaded surfaces, by which alone the impression of roundness is conveyed to the eye. ' By this beautiful and simple method,' he wrote, ' a pupa, which is 8·5 mm. from side to side in its thickest part, appears flat, and offers the most remarkable resemblance to a leaf which is a small fraction of 1 mm. in thickness ' (495).

It will be noted that in countershading we have a system of colouring the exact opposite to that upon which an artist depends when painting a picture. A skilled artist is the most wonderful of all illusionists. By means of pigments he can create, upon a flat surface—in addition to impressions of objects in mere colour—the appearance of depth and distance, of light and atmosphere, of roundness and solidity. Now it is remarkable to find that in the countershading of nature the very opposite effect is produced by precisely opposite means. The artist, by the skilful use of light and shade, *creates upon a flat surface the illusionary appearance of roundness :* nature, on the other hand, by the precise use of countershading, *produces upon a rounded surface the illusionary appearance of flatness.*

By countershading surfaces normally directed towards the source of light and counterlightening those normally in shade, using properly *graded* tones, it is thus possible to eliminate the effects of relief, to destroy the appearance of depth and three-dimensional space, and to render an object, whether it be a Hare or a Herring, *optically flat.* When at the same time the animal happens to be seen against surroundings with which it agrees in hue, it will fade into a ghostly elusiveness and become completely invisible from a short distance—

its entire contour and surface blending into the background. In the words of A. H. Thayer, the effect of obliterative gradation of light and shade is ‘ to render the creature’s actual surface unrecognizable as the surface of any object or objects of the immediate foreground, causing it to pass for an empty space through which the background is seen ’ (614).

The ghost-like effect of countershading is perhaps nowhere more perfectly displayed than by various fishes. The Gray Snapper (*Lutianus griseus*), which haunts waters over grey-white sand at Tortugas, is seen in a photograph published by Reighard (538) to be absolutely flattened by the application of this principle, and the fish thus provides a most striking example of general aggressive resemblance. Its prey is the Hard-head (*Atherina laticeps*), a plankton feeder which according to Reighard neither feeds nor shelters in the reefs, but swims over the sand, where it appears almost invisible, especially when seen from below. I quote the following passage from Reighard to indicate the effectiveness of its protective coloration. ‘ Photographs were obtained of this species in its natural environment. Although the photographs were excellent, the fish were so inconspicuous that the loss of contrast in the pictures, inevitable in the process of reproduction, made it inadvisable to make plates from them, as they would have shown practically nothing.’

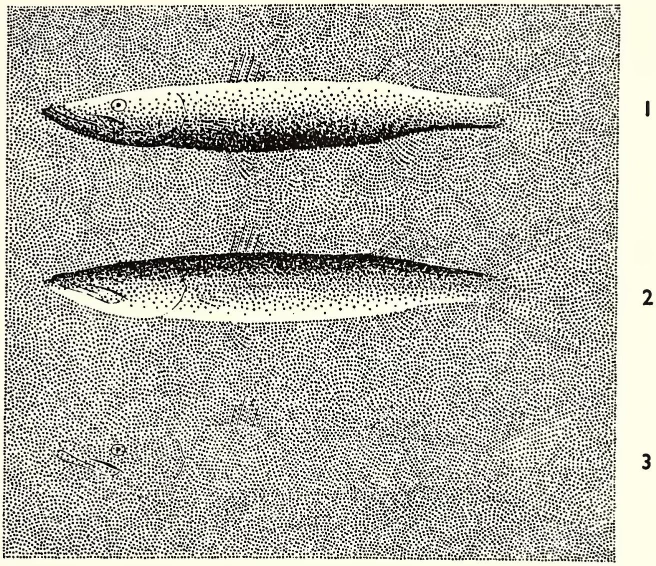

FIG. 1.—Diagrams illustrating Thayer’s principle of obliterative shading : 1 The appearance of light and shade produced by a self-coloured body when illuminated from above ; 2 The appearance of a countershaded body uniformly illuminated ; 3 The combined effect of top-lighting and countershading

The principle is nicely illustrated in the photograph on Plate 7 of a Bush

Buck (*Tragelaphus scriptus*). At a little distance the creature is seen to lose all appearance of solidity, an effect which is in this case enhanced by the white markings on the flanks. These resemble, or at any rate suggest, flecks of sunlight, and, as it were, carry the eye of the observer through the optically flattened surface of the body to the light-flecks that lie beyond.

The coat of the Hare has a similar grading of tone from dark above to light beneath. As she crouches motionless in the field with her long ears pressed down along her back, she is difficult enough to detect; but look at the difference when, having been killed, she lies on her side or back. Now the compensating effect of light and shade on dark and light surfaces is upset; the optical illusion is destroyed; and in death she becomes as conspicuous as in life she was difficult to see.

II. COUNTERSHADING PRODUCED BY BLENDED PATTERNS

Countershading, as considered above, depends upon the employment of graded tones of colour. The view that certain *patterns* found on animals produce the same result when they have become blended with distance was put forward and discussed by J. C. Mottram in 1915 (424). This device depends upon the fact that when a pattern composed of alternate black and white markings—whether of squares or lines or spots—is examined from successively increasing distances, a point will be reached from which the separate markings are no longer visible, but *blend* to form what appears to be a uniform grey half-tone. If in such a pattern the relative proportion of black to white be increased, or decreased, then the resulting tone of grey at blending distance will appear darker, or lighter. In this way it is possible to produce a flat tone of any depth ranging from black to white.

Now it follows that if the proportion of black to white be varied over different parts of the pattern, the effect produced upon the eye at blending distance will be a variegated, or graded, rather than a uniform grey tone. This principle is, of course, one employed by every artist, but nowhere with such effect as in pen drawing. It also forms a basis for printed reproductions in half-tone, which consist entirely of alternate black and white spots whose relative size will give the required pictorial illusion at blending distance. Various methods employed by the artist or printer in producing a graded surface of grey, ranging from black to white, are shown in Fig. 2.

All of the ten designs here shown agree in this—that they present at blending distance a tone graded from darkest above to lightest beneath. But in each case the effect is produced by a different arrangement of white elements. The following changes will be seen to occur in these designs as one proceeds from the solid black area at the top to the solid white area at the bottom: (1) graded change in tone; (2) evenly spaced *horizontal* black bars becoming progressively narrower; (3) evenly spaced *vertical* black bars becoming progressively narrower; (4) vertical black stripes becoming less numerous; (5) and (7) evenly spaced *black* marks becoming progressively *smaller*; (6) and (8) evenly spaced *white* marks becoming progressively *larger*; (9) similar *black* marks becoming more *widely scattered*; (10) similar *white* marks becoming more *densely crowded.*

Mottram has applied this principle to the study of patterns in animals, and points out that the appearance of obliterative shading can be, and is in certain cases, reproduced by means of patterns like some of the above, rather than by the more usual method of graded ground colour as understood by Thayer. As an example he cites Grant's Zebra (*Equus burchelli granti*), whose coloration consists of black stripes on a white ground which lacks countershading, being of the same tone throughout. Upon the back and other surfaces which receive full illumination, the black stripes are wide; but on the belly and under parts which are in shade they are narrow; while between the two extremes they are intermediate in width. This arrangement, which is essentially that seen in Fig. 2, No. 3, produces after blending an appearance similar to that of countershaded patternless animals like the Ass. A similar device is seen in Hardwick's Civet (*Hemigale hardwicki*), which wears a series of broad, dark, saddle-shaped bands across the back, tapering to points on the flanks; and in the patterns of the Banded Duiker (*Cephalophus doriæ*), and the Tasmanian Wolf (*Thylacinus cyanocephalus*). In other cases, as in the Striped Hyæna (*Hyæna hyæna*), there is a tendency for the stripes on the back to increase in number, rather in width, after the fashion of Fig. 2, No. 4.

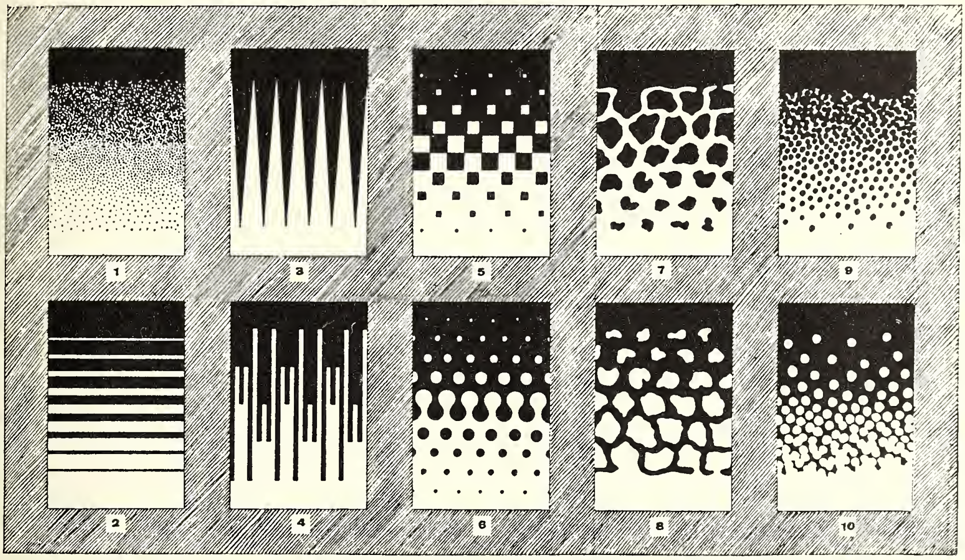

FIG. 2.—Types of pattern which at blending distance produce graded tones similar to those seen in normal countershading

Various other animals exhibit other arrangements which at blending distance produce similar results. For instance, the Cheetah (*Cynælurus jubatus*) presents little countershading; but this deficiency is compensated for by the black spots, which are closer together on the back, and become more widely separated towards the under surfaces—a scheme based upon the arrangement seen in Fig. 2, No. 9. The Fishing Cat (*Felis viverrina*) illustrates the same principle. Here the dorsal stripes break up laterally into spots, which tend to become more widely separated on the flanks beneath. Similar graded effects are seen in the arrangement of spots in the Serval (*Felis serval*).

In the Leopard Cat (*Felis bengalensis*), and in the Pale Genet (*Genetta tigrina*) and related species, the same countershaded effect is produced at blending distance by dark markings which are larger on the back and become progressively smaller on the flanks, disappearing altogether on the under surfaces, as in Fig. 2, No. 7.

A similar result may be achieved by a great variety of other patterns. In the Guineafowl (*Numida meleagris*), for instance, the spots are light upon a dark background, instead of dark upon a light one; but here, in accordance with the same optical principle, they are small on the back, and become larger towards the ventral surface, as in Fig. 2, No. 8. One essential feature all these patterns have in common—namely, the decreasing area of dark, and increasing area of light colour as one passes from the dorsal to the ventral aspect. And by this means they each produce, when at sufficient distance for blending, the appearance of countershading.

III. THE FUNCTION OF OBLITERATIVE SHADING IN ANIMALS

Countershading is a fundamental principle of animal coloration, and is of wide occurrence in nature. It has been evolved alike in many unrelated groups of animals; by the hunter and the hunted; in the sea and on land. It tones the canvas on which are painted the Leopard's spots, the Tiger's stripes, and the patterns of smaller Carnivora such as Serval and Ocelot, Civet and Genet, Jackal and Hyæna. It is the dress almost universally worn by rodents, including the Vizcacha, Jerboas, Gerbils, Cavies, Agoutis, Hares, and many others. It is the essential uniform adopted by Conies, Asses, Antelopes, Deer, and other groups of ungulates. It is repeated extensively among the marsupials, as seen in the coloration of the Tasmanian Wolf, Opossums, Wallabies, and others. It forms a background to reveal the beautiful and subtle picture-patterns worn by Wheatears, Warblers, Pipits, Woodcock, Bustards, and innumerable other birds. It provides a basic livery for the great majority of snakes, lizards, and amphibians. Among insects it reaches a fine state of perfection in different caterpillars and grasshoppers. And the same is true of cephalopods like *Sepia*, where, as Holmes has recently shown, countershading may even be adjusted to suit different inclinations of the body.

It is, however, in rivers, and in the surface waters of the sea, that countershading reaches its maximum development and significance. Among active pelagic fishes belonging to many unrelated groups, and in different sea snakes (*Hydrophidæ*) and Cetaceans, this arrangement of pigment typically forms the foundation colour-scheme. In most oceanic forms, like the Blue Shark (*Car-*

charinus lamia), Mackerel Shark (*Isurus oxyrhynchus*), Yellow-finned Albacore (*Neothunnus albacora*), Tunny (*Thunnus thynnus*), Barracuda (*Sphyræna barracuda*), Tarpon (*Megalops atlanticus*), Flying-fish (*Exocœtus volitans*), Hake (*Merluccius vulgaris*), Herring (*Clupea harengus*), and Dolphin (*Delphinus delphis*), concealment is effected by countershading in uniform hues of blue, green or grey, more or less undecorated by a pattern. But others, like the Mackerel (*Scomber scombrus*), Spanish Mackerel (*Scomberomorus maculatus*), Sergeant Fish (*Rachycentron canadum*), Pilot-fish (*Naucrates ductor*), and certain Sea Snakes such as *Enhydrina valakadien*, have patterns of bars, blotches, stripes or spots superimposed upon a background of obliterative shading. In the variegated and brightly coloured surroundings of coral reefs obliterative shading likewise forms the essential background upon which patterns, themselves countershaded, are commonly superimposed. 'Countershading,' says Longley, 'appears almost universally upon reef fishes, and its absence, or relative deficiency, seems to be definitely correlated with some unusual habit or peculiar form' (340). Again, in inland waters the same phenomenon is of almost general occurrence, as in the Trout (*Salmo trutta*), Dace (*Leuciscus leuciscus*), Roach (*L. rutilus*), Perch (*Perca fluviatilis*), Bream (*Abramis brama*), Pike (*Esox lucius*), and many other fresh-water species.

Of singular interest in this connexion are certain transparent or semi-transparent fishes in which the principle of countershading is extended even to certain opaque *internal* organs. Thus Longley states that *Coralliozetus cardonæ* of the Tortugas reefs has the trunk musculature almost transparent; but the brown and yellow of the normal externally pigmented head extends backwards in a relatively elaborate pattern, with countershading such as normally appears upon external surfaces, but worn on the peritoneum (349).

What is the effect of such colour-schemes, and what is their value? The answer to the first question is perfectly clear. That they confer upon their owners a degree of invisibility is a fact which cannot be reasonably disputed—a fact that is in no sense a scientific discovery, but one that must have been familiar to fishermen and sailors from time immemorial. What does not appear to have been recognized before Thayer made his important contributions to the subject are the principles upon which the inconspicuousness of these fishes depends. When viewed from the side such forms are rendered unsubstantial in appearance by countershading, as already explained. Under favourable circumstances they are made to melt perfectly into their watery surrounding background. But the dark back and silver belly so characteristic of surface-swimming ocean fishes, and of many fresh-water forms, also evidently reduce visibility in another way—that is, when the creatures are viewed by enemies or prey from above, or from beneath. The back will be difficult to recognize, for it is effaced against the deep colour of the ocean which itself appears from above dark-grey, or leaden, or deep-blue; or it may be against the muddy or olive tones of the river bottom; and it is interesting to note that the dorsal colour appears frequently to be in close harmony with the dominant note in the environment—the blackish-brown in the Herring (*Clupea harengus*) is practically invisible from above in boreal waters; the Barracuda (*Sphyræna barracuda*) from Atlantic Coasts of tropical America has its upper parts clad in dark green; the Flying-fish (*Exocœtus volitans*), the Pilot-fish (*Naucrates ductor*), and the young of *Scombresox*, wear the bright blue coloration almost peculiar to tropical surface-dwelling pelagic forms; while in the muddier, more opaque waters of rivers the metallic shades worn by marine forms are replaced by the familiar olivaceous and brownish tones displayed on the upper parts of numerous fresh-water fishes such as River Trout, Pike, and Perch. When, on the other hand, such forms are seen from beneath, the eye of an observer would recognize with equal difficulty the silvery sheen of the belly, whose iridescent surface displays the nearest possible approach to the bright surrounding background of sky, or surface film.

As regards the second question—the value in nature of obliterative coloration is a matter which still requires further observation and experimental proof. In cases such as those described above, the coloration appears to be adapted intimately to the conditions of life; and there has been a tendency for many writers to accept, on *a priori* grounds, the assumption that concealment is valuable to the fish, either as a means of escaping capture or of approaching prey; and this uncritical attitude has led others to doubt, or reject, any explanation of countershading in terms of adaptation. Further consideration of this important matter will be deferred until a later chapter, when the evidence will be discussed. Further (indirect) evidence is afforded by certain facts now to be considered.

IV. THE RELATION BETWEEN COUNTERSHADING AND THE CONDITIONS OF LIFE

So general is the application of Thayer's principle in the coloration of vertebrates, and especially of fishes, that exceptions are relatively few, and in these the lack of countershading can usually be ascribed to some peculiarity of form or of habit—for instance: where the body is already flattened structurally and therefore only requires incipient countershading; or where it is seen under conditions of lighting which do not normally cause strong relief; or where, again, the normal attitude of the species is an abnormal one for the group. Under any of these circumstances strong countershading would be either redundant or harmful.

(1) **Countershading in Relation to Form**—Some modification is found in the distribution of ground-pigment in several unrelated genera of deep-bodied, laterally compressed forms, such as *Zeus* (Zeidæ), *Chætodipterus* (Ilarchidæ), *Scatophagus* (Scatophagidæ), *Chætodon* (Chætodontidæ), *Platax* (Platacidæ), *Zanclus* (Zanclidæ), and *Pterophyllum* (Cichlidæ). These have their sides nearly vertical and presenting to an observer but slight convex curvature. With fish of this type strong countershading would defeat its own end, and it is significant that such forms are only slightly countershaded.

(2) **Countershading in Relation to Environment**—Countershading is found in various degrees of strength, and may be related to the conditions of illumination—and hence to an animal's appearance to an observer—in different surroundings. For instance, various fishes like the Glass-eyed Snapper (*Pria-*

canthus cruentatus), which dwell habitually in dim light, are only slightly countershaded (340). Again, the contrast between upper and under surfaces is slight in desert animals, which gain something from the light reflected upwards from the sand. The contrast is also slight for another reason in animals whose home is the interior of shady forests, where the light is diffused and dim and where consequently the differences between the illumination of upper and lower parts is less marked. In the deep waters of the sea, fishes and other animals living beyond the limit of light-penetration lack countershading altogether. On the other hand, contrast between the dorsal and ventral tones reaches its maximum in surface-swimming fishes, and in land animals which live on dark ground under an open sky, as in many deer, antelopes, and rodents of the open plains.

(3) **Countershading in Relation to Habits**—Among fishes which lack countershading, the following apparent exceptions to Thayer's principle prove on examination to be as significant as the examples which support it. The Remora or Shark Sucker (*Echeneis naucrates*) is in the habit of attaching itself by the sucker on top of its head to different parts of large fishes. It may consequently have any side uppermost, and, as pointed out by Longley, the lack of countershading is correlated with the fact that the fish maintains no constant position with reference to the source of light (340). The same author mentions the case of *Fierasfer*, which spends most of its time in retreat within the cloaca of large Sea Cucumbers (Holothuroidea) on the reef flats, and which, like many cave animals, not only lacks countershading, but has lost its external pigment. This state of affairs is reproduced in a colourless crab (*Pinnotheres*) occurring in the mantle cavity of the oyster. Finally, countershading, like colour-pattern, is typically absent from deep-sea forms living in the everlasting gloom of the abyss.

(4) **Countershading in Relation to Attitude**—More remarkable as exceptions, however, are different animals which have the countershading inverted, the back being light and the belly dark in tone. Such reversal of tones is found in the Nile Cat-fish (*Synodontis batensoda*), which has the singular habit of swimming with the belly upwards—' an attitude taken up by no other fish unless it be sick or dead ' (446). In the pelagic snail *Glaucus atlanticus* inverted coloration is likewise correlated with inverted habits. The same arrangement occurs in different spiders, like members of the family Linyphiidæ, which suspend themselves in the web with the ventral surfaces uppermost. It is of great interest to notice that the same reversal of countershading is widespread among caterpillars, like those of *Automeris io* and *Tropæa luna*, which habitually feed or rest upside-down.

A beautiful example of this arrangement is furnished by the larva of the Eyed Hawk-moth (*Smerinthus ocellatus*). When resting among the leaves of sallow, the food plant, they do so with the back inclined in an inverted position, often hanging back with only the hinder pairs of claspers applied to the stem. In this position the underparts are fully illuminated from above, while the back is in shade. The caterpillars are beautifully countershaded, being pale apple-green on the back grading over the sides to dark greyish sage-green beneath.

This inverted countershading, correlated with the inverted attitude, effaces the larva so effectively that all appearance of solidity is destroyed. The illusion is completed by the superimposed design representing the effect of light and shade on lateral leaf-veins. So effective is the result, that in searching for such larvæ one finds the partly eaten leaves a far easier clue to its possible whereabouts than the presence of the larva itself, which may be as readily discovered with the hand as with the eye.

But such things have to be experienced in the field to be appreciated. In an attempt to record the optical conditions for the benefit of those who have not known these animals in the wild state, I have sketched (Fig. 3) the appearance of one resting on a stem of its food plant in two positions—that on the left, with the back downwards as in nature; that on the right with the back upwards, an attitude quite foreign to its instincts. The latter shows the insect in bold relief, which is exaggerated since the effect of countershading is added to that of illumination, and its solidity stands out in conspicuous contrast to the flat leaves. In the former, a wonderful appearance of flatness is produced. That this sketch does represent the phenomena in these respects is clearly proved by the two photographs on Plate 8 of a larva taken out of doors under an open sky, under conditions identical as regards exposure, stop, plate, and lighting; *the only* difference between them being that of orientation—the larva having been turned

FIG. 3.—Larva of Eyed Hawk-moth. Left: Natural (e.g. 'up-side-down') resting attitude, showing the obliterative effect of inverted countershading. Right: Unnatural (e.g. 'right-way-up') position, showing strong relief and solid appearance

over for the second exposure through about 180 degrees, so that it is illuminated from the opposite direction.

Many striking examples of countershading are described in Süffert's detailed study of adaptive coloration in Lepidopterous larvæ and pupæ (593). Thus, he has shown that sometimes, when the normal attitude of rest is *perpendicular*, as with the larva and pupa of the Purple Emperor (*Apatura iris*), the countershading is likewise in the long axis of the body: the former, which rests head uppermost, is most deeply shaded anteriorly; but in the latter, which hangs head downwards, the countershading is also reversed.

Süffert has further demonstrated that in certain cases, as with the caterpillar of the Clouded Yellow (*Colias edusa*), the appropriate attitude in relation to the direction of light is taken up as a response to the light itself. Thus, when subjected to light reflected *upwards* from a mirror, the insect takes its stand beneath, rather than above, the stem of its food plant. Experiments with Brimstone (*Gonepteryx rhamni*) larvæ showed that the response is due to the perception of light by dermal sense organs in the general body-surface.

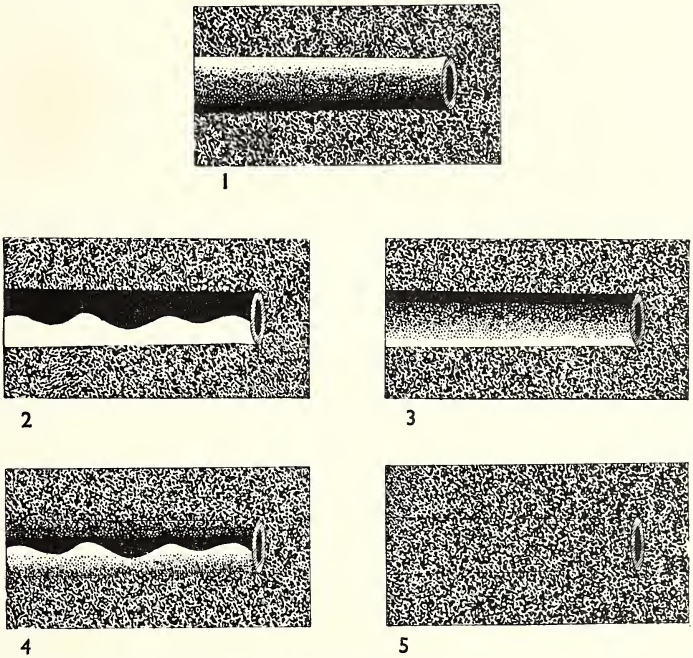

FIG. 4.—The principle of obliterating shading as applied to guns: 1 The appearance due to top lighting; 2 and 3 The appearance due to obliterative paint; 4 and 5 The appearance due to a combination of top-lighting and obliterative paint. It will be noted that 2 and 4 show the incorrect method of applying paint; 3 and 5 the correct method

The same author also describes a type of countershading in which two regions of the body—separated by a pale contrasted element—are countershaded independently. This optical device renders the body as two flat surfaces converging at an angle. It is seen, for instance, in the larva—and with especial effect in the pupa—of *Colias edusa.* We may note here that the same two-surface effect forms the basis of the remarkable leaf-like coloration of the toad *Bufo superciliaris*, described on page 321.

In conclusion, some passing reference may be made here to those cases of inverted coloration which are *not* correlated with an up-side-down attitude. Under such circumstances the pigmentation will enhance, rather than efface, the animal's relief, thus tending to make it more, rather than less, conspicuous. It is significant that where this arrangement occurs, as, for instance, in the Skunks, Zorillas, and Badgers, there is often good reason to believe (as will be shown in a later chapter) that self-effacement is unnecessary, but that, on the contrary, self-advertisement is advantageous to the species.

(5) **Applied Aspects of Countershading**—Among the more perfect protective and aggressive adaptations of animals, few are without some special application to the art of war. And in this respect countershading is no exception. The conditions of light which affect the appearance of a caterpillar or a snake are the same as those which cause a gun or torpedo-tube to stand out conspicuously *even against a background covered with exactly the same paint.* Hence it is essential that such rounded objects be treated with paint properly graded in tone so as to counteract the effects of relief.

Photographs recently published in the press of ' camouflaged ' coastal-defence guns reveal a complete failure to apply the relevant system of coloration. On the contrary, the scheme favoured by the authorities is one which entirely misses the mark, as may be seen by reference to the accompanying diagram (Fig. 4).

During the early months of the Great War failure to apprehend the same principle led to a blunder which doubtless caused the loss of very many lives. I refer, of course, to the service cap with which our men went into action—a cap whose attributes as a reflector of light seemed especially designed (by the reversal of this principle) to present the sniper and machine-gunner with a conspicuous target.

The case of aircraft is in some respects analogous to that of surface-swimming fishes like the Mackerel. Such creatures, being dark blue on the back and silvery-white on the belly, are relatively difficult to detect whether viewed against a background of water from above or of sky from beneath. Aircraft operating by day present an analogous case, and should be coloured on similar lines : the most brilliant white underneath—the colour which most nearly approaches the bright background of sky ; and some darker tone above—calculated to harmonize with the ground when viewed from overhead. For special duty at night bombers should be treated with an absolutely matt black paint—the deepest black obtainable. A machine so painted would on a clear night become totally invisible from the ground, and would reflect downwards relatively few rays if caught in the beam of a searchlight.

4. DISRUPTIVE COLORATION

> Neither is there any creature that is not manifest in his sight: but all things are naked and opened unto the eyes of him with whom we have to do.
>
> HEBREWS IV. 13

We now come to what is perhaps the most interesting, and certainly the most important, set of principles relating to concealment—namely, the type of camouflage familiar to most people from its war-time uses under the quite inappropriate term 'dazzle',[1] and properly known as Disruptive Coloration.

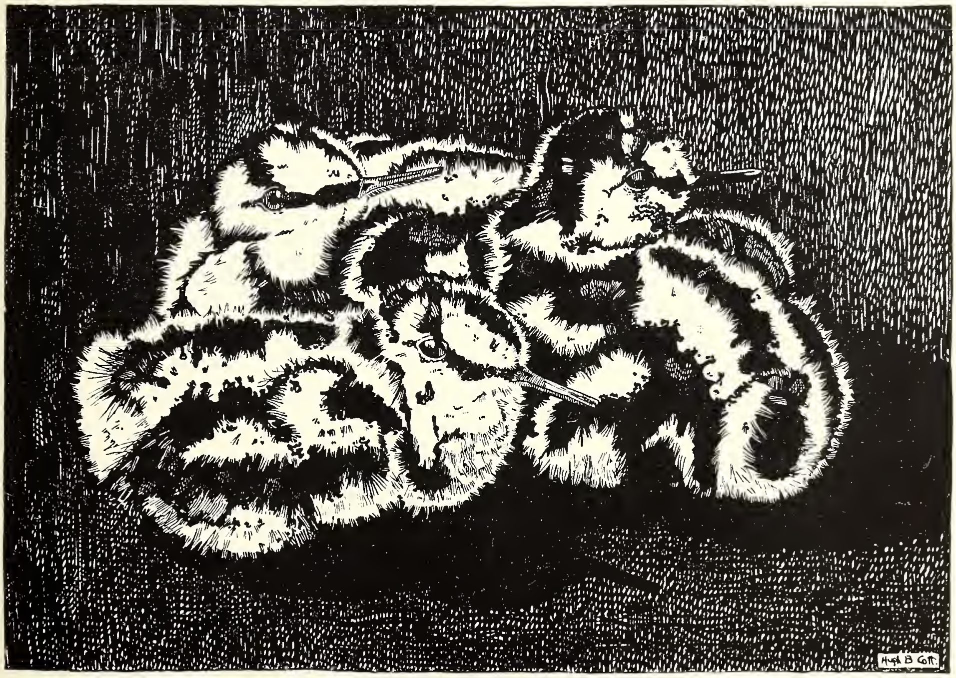

FIG. 5.—Young Woodcock

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[1] The word 'dazzle', which came into popular use during the War in connexion with camouflage painting, is an American term applied by Thayer in his work on Concealing Coloration to disruptive colouring in animals. It is based on the American slang 'razzle-dazzle', which has a meaning—expressive of active confusion—quite different from the correct English use for partial blinding by brilliant lights.

It will be clear from what has already been said that under ideal conditions, colour-resemblance combined with countershading would suffice to render an animal absolutely invisible against a plain background, even at a short distance. But in nature, as in war, conditions are rarely ideal, and they never remain so—for they change. Most animals, like most machines, are active, and their movements bring them before a constantly varying background, which is itself rarely uniform in colour and pattern. Moreover, the light which falls upon them itself varies constantly in colour, intensity, and incidence.

Even allowing, therefore, for the most efficient colour-harmony and countershading, we still have to reckon with the fact that a uniformly coloured animal presents to the eye a continuous patch or area in the visual field, standing out more or less conspicuously against darker, or lighter, or differently coloured surrounding objects. It is this *continuity of surface, bounded by a specific contour or outline*, which chiefly enables us to recognize any object with whose shape we are familiar. Thus for effective concealment, *it is essential that the tell-tale appearance of form should be destroyed.* The difficulty of doing this is met, often with extraordinary success, by the application of optical principles involving the use of *patterns.*

I. THE FUNCTION OF DISRUPTIVE COLORATION

When a pickpocket intends to relieve you of your watch or wallet, he, or his confederate, takes care to distract your attention from what he proposes to do by creating a diversion. He draws your eyes from what is really happening to what seems to be happening. Now the patterns worn by many animals such as Giraffes and Jaguars, Anacondas and Iguanas, Pipits and Plovers, and various Grass-frogs, Grasshoppers, Moths, and Mantids, operate in a somewhat analogous way. The function of a disruptive pattern is to prevent, or to delay as long as possible, the first recognition of an object by sight. Its success depends not only upon optical principles, but upon a psychological factor. When the surface of a fish, or of a factory, is covered with irregular patches of contrasted colours and tones, *these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them.* The patterns themselves may be conspicuous enough, but since they contradict the form on which they are superimposed, they concentrate attention upon themselves, and pass for part of the general environment, in the same way that the pickpocket's tactics of bluff pass for a commonplace incident.

Even the simplest disruptive patterns tend to hinder recognition and so to make for concealment. In its most elementary state, the principle is well shown in the coloration of certain tropical frogs and toads. For example, the East African *Rana adspersa*—a large frog whose general colour-scheme is a patchwork of subdued earthy-browns and olive-greens—wears on its back a conspicuous yellow stripe extending from the snout right along the middle of the back (Plate 9). So far from drawing attention to the animal, however, the effect of this stripe is the very reverse. In the first place, the yellow line—which, of course, in itself bears no resemblance whatever to its wearer, but rather suggests to the casual glance a twig or blade of grass—stands out from the back and catches the observer's eye. Secondly, by providing a strong incident of colour, it serves to flatten by contrast the less-defined half-tones by which the real form of the frog is differentiated from its surroundings. In the third place, it serves to bisect the form of the frog, so that the eye of an enemy is actually presented with a configuration of two half-frogs—which look very different from one whole one—and as likely as not the brain behind the eye will fail to join them together in recognition.

An analogous arrangement is found in countless animals of different kinds: cases which come to mind are the light dorsal stripes of different grasshoppers (Figs. 26, 27); and among birds the buff back-streaks of the Jack Snipe, the light head-stripes of the Common Snipe, those on the mantle of the Woodcock, and on the wings of the Stone-Curlew. An extremely interesting case which beautifully illustrates the principle in its simplest form is that of the flower-like mantis *Hymenopus bicornis*, observed in the Malay Peninsula by Annandale (7). Pale pink and white in colour, this remarkable insect has its body optically broken into two pieces by a bold transverse bar of deep sage-green on the thorax. When seen on an inflorescence of *Melastoma polyanthum*, Annandale states that the effect of the bar is to divide the insect into two parts which appear to have no connexion with one another on the inflorescence, a fact which seems significant when it is realized that the complete insect is ordinarily larger than the expanse of a single flower.

Whether or not the body is optically broken up by strongly accentuated patches of conspicuous local colour, such as those considered above, it is usual for the disruptive scheme to extend as an irregular patchwork of cryptic tones over the body-surface generally, or over such parts of it as are normally exposed to view. Beautiful examples of general disruptive coloration are afforded by the buff and black eggs of the Lapwing (Plate 18), and by the South American *Ceratophrys cornuta* (Plate 9), with its wonderful camouflage scheme of gold and green and brown.

II. THE COLOURS OF DISRUPTIVE PATTERNS: DIFFERENTIAL BLENDING

The success in nature of the various devices, which may be lumped together under the general heading of disruptive coloration, depends upon a number of optical principles which we must now examine a little more closely. Provided an animal is seen against a broken background, it is probably true to say that any pattern of darker or lighter colours and tones will tend to hinder recognition by destroying to a greater or less degree its apparent form. But it must not be imagined that to effect concealment any pattern will do, or that any colours will do, or that any arrangement of tonal contrasts will do. In order to achieve effective results, the colours, tonal contrasts, and patterns employed must conform to definite optical principles. A little investigation shows that certain colours, certain degrees of contrast, and certain arrangements of design are more effective than others for purposes of effacement; and it is a fact of the greatest interest and significance that the particular disruptive devices which on theoretical grounds appear best for this purpose are those which occur on the bodies of innumerable animals which rely for safety, or for success in hunting, upon remaining incognito.

In the first place, the effect of a disruptive pattern is greatly strengthened when some of its components closely match the background, while others differ strongly from it. Under these conditions, *by the contrast of some tones and the blending of others, certain portions of the object fade out completely while others stand out emphatically.* And it is to be noted that the shape of the latter—which alone can be distinguished—is such that their real identity cannot be determined.

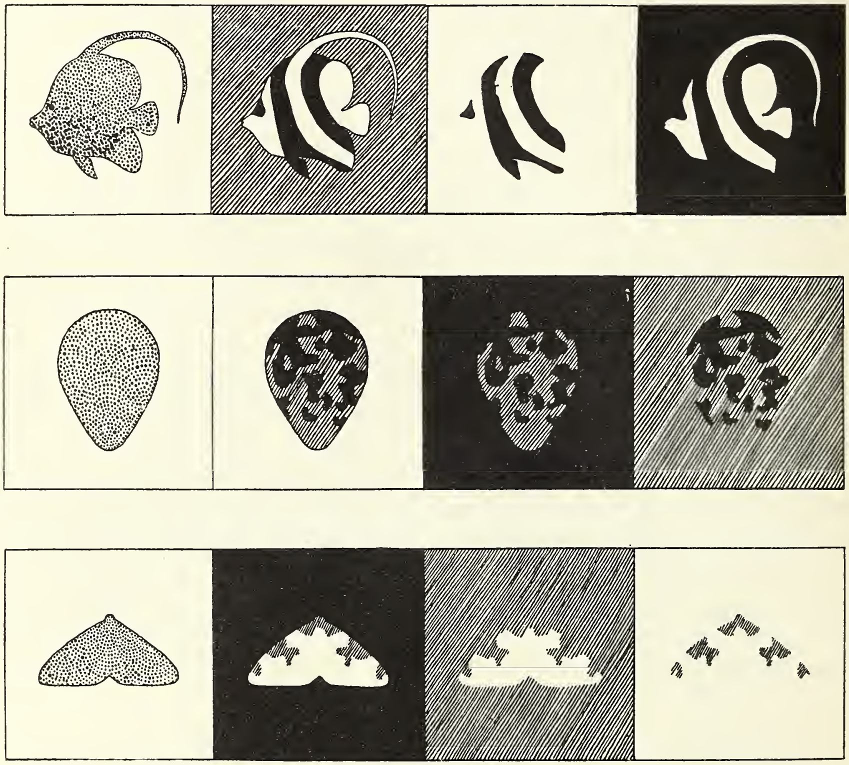

FIG. 6.—Diagrams illustrating the principle of differential blending

The principle is illustrated by the simple diagrams shown in Fig. 6, where a series of forms—a fish, an egg, and a moth—are represented against different backgrounds. Seen as self-coloured objects without any pattern, as in the left-hand figure of each series, these forms are easily recognizable. If dressed in a disruptive pattern they become less distinguishable, even when seen, as in the second figure of each series, before a background against which each stands out clearly. But when, as in the third and fourth, the background matches and absorbs one element of the colour-scheme, the difficulty is much increased, and the effect on the eye of an observer is such as greatly to delay, or even altogether to prevent, recognition. The photographs of the Garden Carpet Moth (Plate 10) and Oak Beauty Moth (Plate 11) illustrate this principle of Differential Blending in operation.

We have to realize, consequently, that the actual range of some of the colours employed should in general be such as occur typically in an animal's environment. This theoretical point is sufficiently obvious. Many instances of its application in nature amongst all kinds of animals have been given in other parts of this book and are familiar ground to every field naturalist. We need therefore only mention here once again the type of criticism which claims that cryptic animals are often seen against backgrounds against which their colour-scheme fails to harmonize; and that by searching it would be possible to find a background against which any animal would appear more or less concealed. Such critics entirely fail to grasp the vital fact that the backgrounds which different cryptic animals match are typically those where they normally rest, or in which they pass those periods of their lives when concealment is most necessary—for instance, the diurnal resting-places of nocturnal moths, and the nesting-sites of ground-breeding birds. Plenty of evidence for this will be found on another page. No colour-scheme whatever could hide a Woodcock as it flies on migration over the sea, but at such times it relies not upon concealing coloration, but upon speed or the cover of darkness. On the other hand, during the weeks when it incubates and nurses its treasures in the woods, invisibility is vital, and the colours which it wears are precisely those best adapted for concealment in the surroundings in which it elects to carry out these parental duties.

III. THE TONES OF DISRUPTIVE PATTERNS: MAXIMUM DISRUPTIVE CONTRAST

Next we have to bear in mind the part played by tone, as opposed to colour, in patterns whose function is to break up continuity of surface. We have seen that the effect of a disruptive pattern is to break up what is really a continuous surface into what appears to be a number of discontinuous surfaces. These tend to be interpreted by the eye as separate objects—none of which suggests, but all of which contradict, the shape of the body on which they are superimposed.

Now this illusory appearance—this contradiction of the true form—is greatly intensified by the use of *strongly contrasted tones*. In general, very light markings on a dark object, and very dark markings on a light one, will be most effective. The principle is similar to that which makes an open network curtain effective as a screen in preventing a casual passer-by from seeing into the interior of a room.

When any one glances at such a window, his gaze falls upon, *and is arrested by*, the curtain, whose excessive brightness in contrast to the relatively dark room interior prevents him from noticing what lies beyond it. Now it is not to be imagined that such a curtain intercepts the view, after the manner of an opaque screen. Details in the room beyond are openly exposed to view—although they cannot be seen clearly. That the curtain acts in this way, merely dazzling and distracting the eye, and not, like an opaque screen, by actually intercepting vision, can easily be proved by dyeing it black, when it at once becomes almost useless as an optical barrier against an observer outside. But it will now tend to prevent those inside the room from seeing out. This reversal of effect is due to the same cause which renders a white curtain effective in the ordinary way, namely, *to the contrast in tone between the curtain and the rest of the visual field behind it*—in this case, as presented by a black screen silhouetted against the brightly illuminated view outside. From what has been said, it follows that while a *white* curtain is effective *by day* against observation from outside, though at the same time it allows those in the room to see out; *at night*, when the room is artificially illuminated and it is dark outside, a *black* curtain is what is needed for the same purpose.

I have referred to the present matter because it introduces on grounds familiar to every one an important principle upon which the concealment of different animals depends, and which we may conveniently refer to as the principle of Maximum Disruptive Contrast. The greater the contrast in tone between adjacent elements in an animal's pattern, the greater will be its disruptive function. Broadly speaking (and provided the design used conforms to the nature of the environment), we may say that white marks on dark animals living in dark surroundings (such as forests) and black marks on light animals living in light surroundings (such as deserts) will be those most effective in breaking up the continuity of their surface, and in masking by contrast tell-tale half-tones of surface structures and modelling; and they are, in fact, the type of markings commonly found in these environments. To produce their greatest effect, these distracting marks need to be used sparingly in relation to the total area of the body, or they may fail in their function—which is to prevent recognition by forcibly drawing the attention of an observer to themselves, so that the cryptic parts of the animal wearing them pass unnoticed.

The simplified diagrams in Fig. 7 illustrate the value and effectiveness of maximum disruptive contrasts better than any verbal description. In each series of diagrams *the corresponding figures are shaded to exactly the same tone*, which is one approximating to that of the background—this being black in the first, white in the second, and half-tone in the third set. The second figure of each horizontal series carries a superimposed pattern—white in the dark figure, black in the light figure, and black and white in the one of medium tone.

On looking at these drawings from a little distance, it will be seen that the conspicuous patches operate most efficiently in distracting attention from the form of the animals wearing them. By sheer force of their brightness, or blackness, or contrasts, they dominate the picture presented to the eye, apparently destroying form *by levelling out the lesser contrasts between the animals themselves and their respective monochrome backgrounds.*

The third figure of each series illustrates the effect of broken surroundings in further blending and confusing the picture. In nature, it is, of course, this last which most nearly represents the impression presented to the eye of an observer. Any one who looks at the right-hand column *before* seeing the figures on the left will appreciate the value of these optical devices in delaying first recognition.

The principle is one with many applications to modern warfare. In the Great War it was utilized by the Germans when they introduced strongly marked incidents of white or black tone to conceal the fainter contrasts of tone made by the sloping sides of overhead camouflage-screens, or roofing, as seen from the air. The same principle has, of course, a special application in any attempt to reduce the visibility of large objects of all kinds, such as ships, tanks, buildings, and aerodromes. The essential function of dazzle painting is to break up continuity of surface by means of violently contrasting *tones*, rather than by mere differences of *tint*. The latter are relatively unimportant: the former are all-important.

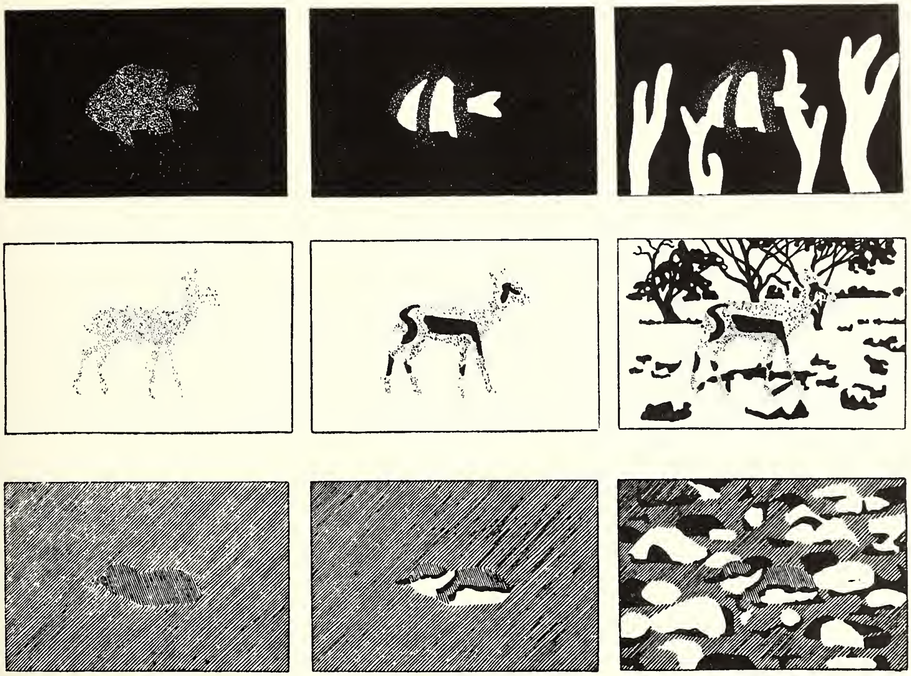

FIG. 7.—Diagrams illustrating the principle of maximum disruptive contrast, and showing the distractive effect upon the eye of patterns which contrast as violently as possible with the tone of their background

Various recent attempts to camouflage tanks, armoured cars, and the roofs of buildings with paint reveal an almost complete failure by those responsible to grasp the essential factor in the disguise of surface continuity and of contour. Such work must be carried out with courage and confidence, for at close range objects properly treated will appear glaringly conspicuous. But they are not painted for deception at close range, but at ranges at which big gun actions and bombing raids are likely to be attempted. And at these distances differences of tint—mere blotches of brown and green and grey like those commonly used for ' camouflaging ' army vehicles—blend and thus nullify the effect and render the work practically valueless.

In nature vigorous disruptive contrasts are frequently seen at work, and their wonderful effectiveness in hindering recognition needs to be experienced in the field to be appreciated fully. Beautiful examples are seen in the *white* markings of the beetle *Lithinus nigrocristatus* (Plate 43) ; of newly hatched Little Grebes and Jaçanas ; of tree frogs such as *Hyla leucophyllata* (Fig. 20) from the Amazon and *Megalixalus fornasinii* (Fig. 19) from the Zambesi ; in the disruptive phases of many reef-fishes like *Epinephelus striatus* (Fig. 8) ; and of bottom-living fishes—*Lophius piscatorius*, and cuttlefishes—*Sepia officinalis* : and on the other hand, in the *black* gorget of the Ringed Plover and the black cheek and breast markings of the Turnstone, in both cases associated with, and contrasted against, patches of white. Both of the last-mentioned birds are splendidly camouflaged when seen in their native haunts—the former especially against a pattern of pebbles, the latter among the tide wrack on rocky shores. The extraordinary efficiency of such strongly contrasted markings is very well shown in Plate 19, which illustrates the appearance of newly hatched Woodcock chicks in their natural woodland surroundings.

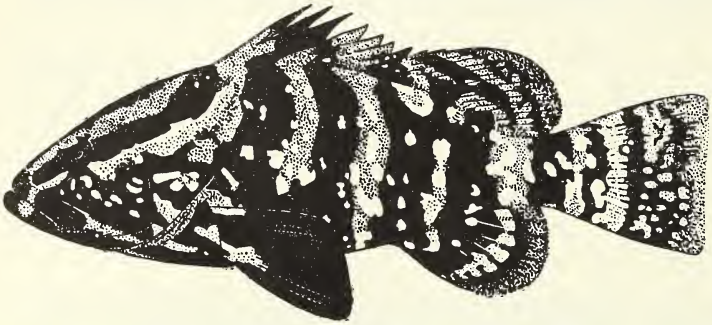

FIG. 8.—Nassau Grouper (*Epinephelus striatus*). Heavily banded phase (*Drawn from a photograph by* TOWNSEND)

A striking application of the curtain principle is found in the white silken bands with which various spiders decorate their cartwheel snares. In this case, however, the function of the conspicuous design (which might be compared to the patch of whitewash with which the builder marks a newly fitted window-pane) is not to conceal something beyond the web, but to protect something upon it, namely, the spider itself. These devices have been the subject of much careful and detailed field observation, by Major Hingston (265). The points to be noted here are : firstly, that the snare is almost invisible owing to the thinness and transparency of its lines ; and secondly, that the spider is therefore the only thing visible in an undecorated snare. Thus the white zigzag or spiral will be a source of distraction to any enemy hunting by sight. This is what Hingston calls a ' dispersing device '. ' The enemy, when it flutters in front of the web, is attracted and confused by this wavy spiral and drawn away from the spider's seat.' In order that it may serve this end, the distracting band should be as conspicuous as possible, and it is significant that in the webs of different spiders, such as *Cyclosa filiobliqua*, it forms a most striking feature.

IV. THE RELATION BETWEEN ADJACENT ELEMENTS IN THE PATTERN

In the foregoing pages I have attempted to show that the success of a disruptive design depends upon the obliteration of form by means of superimposed patterns. Various objects included in the visual field are presented to the eye in such a way that they appear to be more or less clearly segregated as separate patches or masses, differing from one another in colour, tone, shape, size, and texture. When therefore any single object like an animal bears upon its surface a superimposed pattern of contrasted colours and tones, these serve to mask its real form, which is replaced by an apparent but unreal series of separate forms. *These forms tend to be interpreted as representing a number of different objects*—none of which suggests, by its shape or arrangement, the body which bears them.

This illusory appearance is an objective underlying all types of disruptive coloration. We have seen that the disruptive effect of a pattern depends, among other factors, upon the range of tones employed. Now a further important factor depends upon their mutual distribution upon the body. To make the point clear, it will be helpful to inquire first what are the visual characteristics of single objects of simple form—as opposed to complex forms seen in the aggregate. Look at a rounded cloud, illuminated from the side, and poised alone in azure space. It has a light and a shadowed side. At one margin—that directed towards the sun—it is an intensely pure white, or ochreous, or warm rose in hue, according to circumstances. At the other, it is a soft neutral grey, or a dark, cold, slaty purple. At no point on the cloud can you make out abrupt changes of colour or tone, *except at its edge.* The passage from light to dark tones, and from warm to cold hues, is *gradual, and delicately graded.* Gentle gradations of tone, easy transitions of colour—these are characteristic of simple rounded surfaces, and by them the eye records and the brain perceives their form.

Compare with this a complex system of cumulus. Here sudden transitions of tint and shade are everywhere apparent at the billowing contours of each formation—where the mountain ranges of vapour are seen piled up one behind another, and where the margins of the nearer masses overlap or eclipse the surface of those beyond. Now what we have said of clouds applies to almost any objects seen in the aggregate, except that the more solid they are, the more irregular they are, and the more varied they are, the more contrasted, confused and complex will be the configuration or pattern presented to the eye. The passages of colour will be harsher, less delicate, and more abrupt ; the shadows harder and deeper ; the high lights brighter by contrast.

Such effects meet the observant eye everywhere in nature—the golden gleam of sunlight reflected from a curving grass-blade strikes out boldly from the surrounding gloom of shaded herbage and from the yet darker interstices of intense shadow : the fallen leaf, sodden and glistening on the forest floor, has its highest light just where the edge arches over the black tunnel of shade beneath it: grey lichen tufts clothing the tree trunk with a delicate veil break the bark into a thousand irregular and varied masses of light, shade, and shadow. The same thing is seen in the broken surroundings of a desert, a rocky coast-line, or a shingle beach; in the varied foliage patterns of leaves and lianas; in the traceries of twigs or of corals—indeed in the varied patterns presented by different objects anywhere and everywhere.

What I have attempted to stress here is that a broken visual pattern made up of *sudden transitions of colour*, *sharply contrasted passages of tone*, and of *irregular shapes of all kinds*, are features typically associated in the mind—as a result of visual experience—with the appearance of objects in the aggregate, rather than of single objects of simple form. It therefore follows that the most effective disruptive patterns will be those which present these appearances to the observer's eye. In particular, the maximum effect will be produced *when the tones of greatest contrast*—that is to say, those representing the highest lights and deepest shades—*occur adjacent to one another in the pattern*; and *when the transition from one to the other is sharply defined, without intermediate gradations or half-tones*—which would at once tend to detract from the apparent discontinuity of surface.

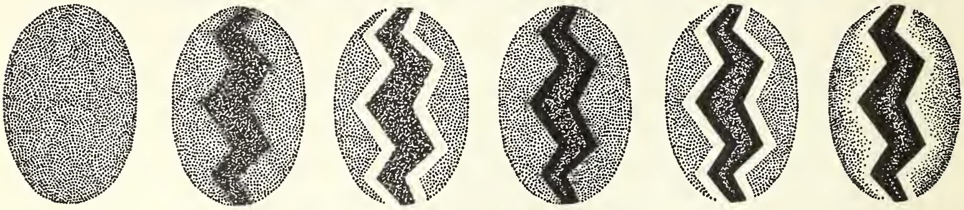

FIG. 9.—Stages in the construction of a disruptive pattern, showing the effect of strong contrasts in tone between adjacent elements in the pattern

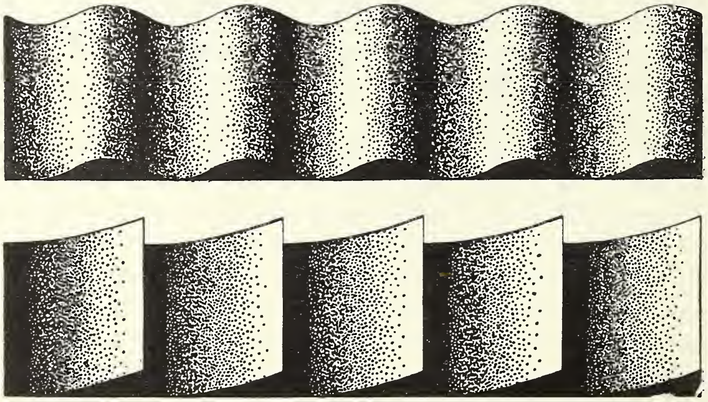

FIG. 10.—Showing the disruptive effect of adjacent contrasted tones (lower diagram); as compared with contrasts which are separated by half-tones (upper diagram)

These principles are clearly illustrated in Figs. 9 and 10. The first shows the way in which a disruptive pattern of the kind with which we are dealing can be built up in progressive stages, each of which tends to be an improvement on its predecessor, and culminating in a very striking disruptive effect whose essential feature is the apposition of black patches contrasted with white ones. The second diagram illustrates the inferior effect produced when the brightest and blackest areas, instead of being adjacent, are separated by graded half-tones.

Now it may be suggested that these are theoretical considerations far removed from questions of animal coloration. Theoretical they are. Yet a little investigation shows that the underlying principles are made use of in the cryptic colour-schemes of innumerable animals. The fact is that in group after group we find disruptive patterns incorporating these very optical devices. Since, so far as I am aware, this is the first time attention has been drawn to the subject, it may be worth while to consider a few examples in greater detail.

Speaking generally, the coloration found among snakes is decidedly cryptic—largely, no doubt, owing to the need for concealment from their prey. While in some, such as the green *Oxybelis fulgidus* and the sandy *Cerastes cerastes*, this result is achieved solely by colour-harmony and countershading, in very many the deceptive appearance is perfected by the addition of a bold disruptive pattern. The value of such superimposed designs in breaking up the elongated serpentine form is obvious, and it is perhaps especially necessary for large-bodied snakes, whether constrictors like *Python molurus* or sluggish venomous species like *Bitis gabonica.* When we examine these patterns it is very interesting to notice that in snakes belonging to widely different families, and inhabiting totally dissimilar surroundings, the optical device under consideration is incorporated in the pattern. Although the designs used show almost infinite variety in the form, colour and arrangement of their component parts, over and over again we see that the lightest element in the pattern is opposed to, and off-sets by contrast, the deepest tones. The diagram (Fig. 11) shows the arrangement in a number of species. Here, for the sake of simplicity, the intermediate or half-tones have been represented by shading, while the deepest and lightest elements are shown respectively by black and white—but it must be remembered that the actual colours used are the cryptic tones of the environment, the ‘ white ’ parts, for instance, being actually light brown, buff, ochre, or pale green according to circumstances.

This principle of *adjacent contrast* is especially marked in head disguises. For instance, *Constrictor constrictor* (Plate 24) wears a light patch on the upper jaw immediately below the bold dark patch associated with the eye. Similar contrasts are presented by head markings in *Python regius*, *Oxybelis acuminatus* (Fig. 32), *Bitis gabonica* (Plate 25), *Bothrops jararacussu*, *Crotalus confluentus*, and many others. In all these the details of the head-mask differ widely, but all agree in the strong contrast effects of adjacent tones. Doubtless some day an analysis of these patterns in terms of embryology and physiology will be forthcoming: but what we are concerned with here is their ecological significance—namely, that the nature of the patterns is such as to employ the very principles by which concealment can be most effectively attained.

If we turn to other groups we find the same pictures repeated over and over again—in the scaly suits of lizards and fishes, in the skins of frogs and toads, in the feathered costumes of birds and the fur coats of mammals, as well as in innumerable insects and other invertebrates belonging to different orders. It would serve no useful purpose to describe these in detail here. Before leaving the subject, however, I wish to draw attention to a few striking cases among various groups.

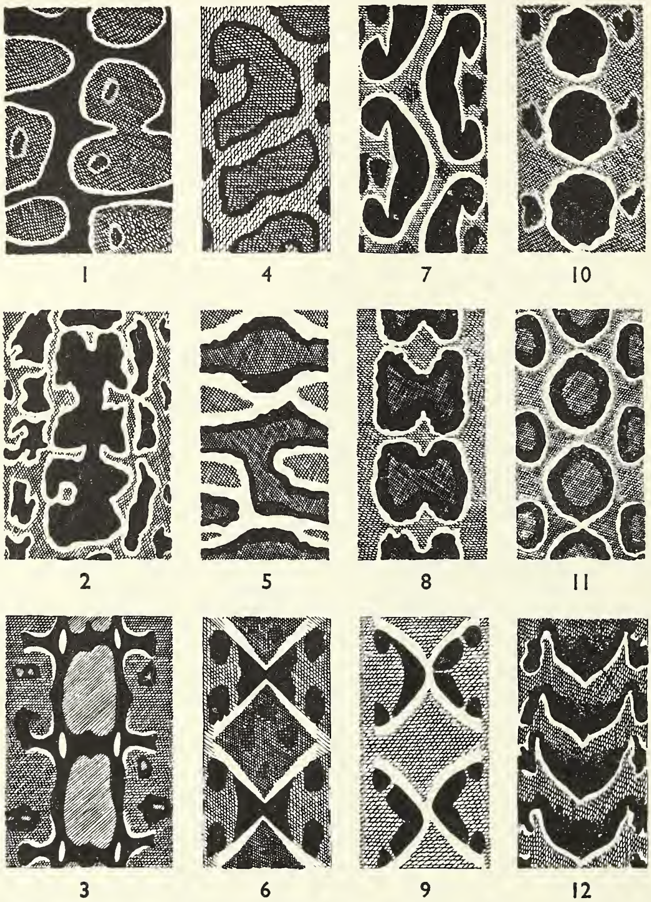

FIG. 11.—Diagrams of the disruptive patterns of various snakes: 1 *Python regius*; 2 *Python molurus*; 3 *Constrictor constrictor*; 4 *Ophibolus doliatus triangulus*; 5 *Natrix fasciata*; 6 *Bothrops atrox*; 7 *Bothrops alternatus*; 8 *Crotalus confluentus*; 9 *Bothrops jararaca*; 10 *Causus rhombeatus*; 11 *Vipera russellii*; 12 *Bitis arietans*

Many frogs, belonging to widely separated families, have the side of the head boldly painted with black or dusky blotches of irregular shape, which serve, as I shall show later, to camouflage the eye. Now it is a very common characteristic for such species to have the upper or lower adjacent areas pale in hue, or white. In fact, the pattern reproduces, so far as its contrast effects are concerned, that occurring in snakes. This is beautifully seen in wild specimens of the Common Frog (*Rana temporaria*), where the value of this arrangement for concealment under natural conditions is well demonstrated in the photograph reproduced on Plate 24. Other examples are furnished by *Rana oxyrhynchus*, *R. stenocephala*, *R. sphenocephala*, *Cardioglossa leucomystax*, *and C. gracilis* (Figs. 12 and 31).

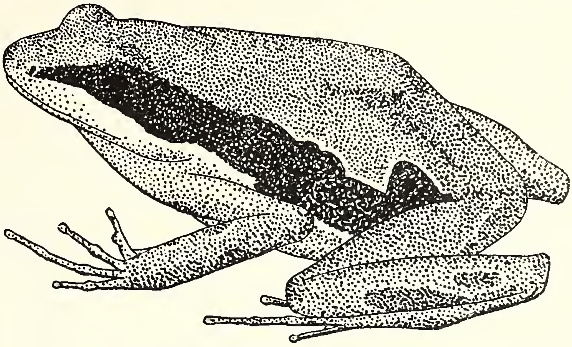

FIG. 12.—*Cardioglossa gracilis*

Many fishes show the same thing, dark ocular bands, be they longitudinal, diagonal or vertical, being bordered with areas of the lightest tone, which by contrast enforce and exaggerate the deeply pigmented parts. And, of course, the arrangement is not confined to the head. It may occur on any part of the body, and frequently it also extends on to the fins and tail. Among examples which we have figured the reader is referred to the disguise of *Eques lanceolatus* (Fig. 13), *Chætodon capistratus* (Fig. 76), and *Epinephelus striatus* (Fig. 8).

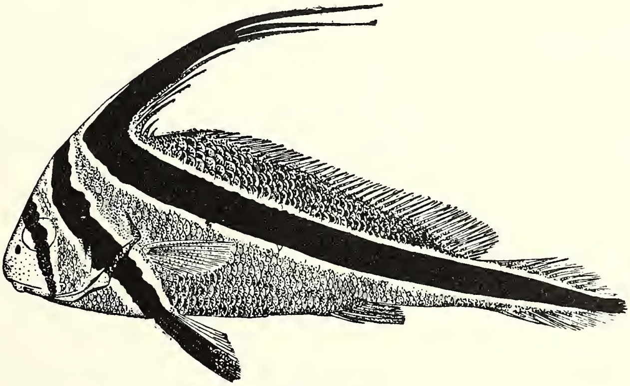

FIG. 13.—*Eques lanceolatus*

Similar disruptive effects are seen in many lizards, such as *Mabuia doriæ* and *Gymnodactylus albofasciatus*—the former wearing a dark lateral stripe in a light setting ; the latter a series of light transverse bars bordered with dark pigment.

Among birds, the Turnstone and the Ringed Plover provide striking examples of the same principle. As already mentioned, both of these species have on the head, throat, and neck a series of strongly contrasted black and white markings, whose function can best be appreciated by observing the actual appearance of these delightful species in nature—especially when brooding. Similar contrast effects are found in the Reeve, Cream-coloured Courser, Stone-Curlew, Bittern, Quail, and many other birds.

The principle is illustrated even better by the newly hatched young of the Ringed Plover. The coloration of these tiny down-clad chicks incorporates in a wonderful way the three fundamental principles of colour-resemblance, countershading, and maximum disruptive contrast. As regards the last, it will be noticed (Plate 13) that the chick has its form optically broken into two pieces by a collar passing through the eyes and round the back of the head. This does not consist merely of a dark band breaking up the intermediate tone of the head and back. On the contrary, this narrow black band is accentuated by another band of white immediately behind it, and it is the combination of the two bands, one black and one white, and both in contrast to the general tone of the upper parts, which produces so deceptive an appearance. With some individuals this effect is repeated at the back of the body—a black mark on the flank dividing the greyish upper parts from the white down of the belly (Fig. 14).

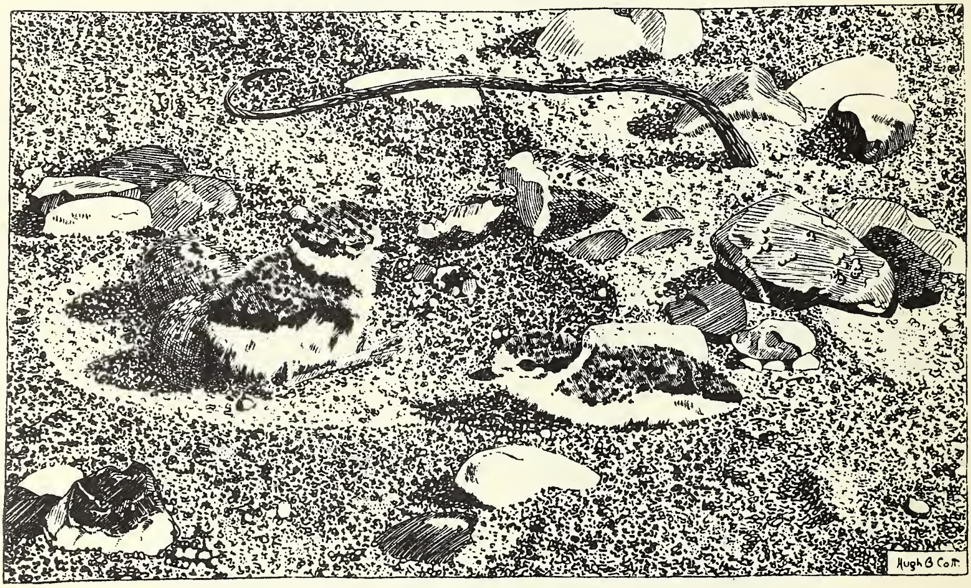

FIG. 14.—Nest of Ringed Plover, with eggs and newly-hatched young

Various other nidifugous chicks, like those of the Golden Plover, Oyster-Catcher, Snipe, and Sandpiper, illustrate the same point. In every case the essential function of the pattern is *to prevent recognition by breaking up visible form.* In effect, these down-clad babes have rejected the injunction ' Rend your hearts and not your garments '. Instead, by rending their garments they have gone a long way towards saving their hearts from the claws and beaks of Peregrines, Lesser Black-backed Gulls, and other blood-thirsty robbers. How well they have succeeded will be best understood by those who have attempted to locate newly hatched young of birds like the Woodcock, Snipe or Oyster-Catcher. Indeed, if we except the insects, chicks such as these provide some of the most perfect and admirable examples of camouflage in the whole realm of nature.

Among mammals such complex patterns are less frequently found. However, it may be worth noticing that adjacent contrast effects of the type we are considering occur in a number of cases. For instance, the Brazilian Anteater (*Myrmecophaga jubata*) has the side of its head and body decorated with a characteristic black patch which is bounded above and below by a band distinctly paler than the general tone of the body. On the other hand, the grey-haired Three-toed Sloth (*Bradypus tridactylus*) has its back broken with a bright orange-coloured patch, which is bordered with a zone of dense black. Here the relation between the dark and light masses has been reversed, but its effect is the same and undoubtedly tends to give concealment amidst the broken surroundings of the forest foliage. Two other mammals which appear to illustrate the same principle in a striking manner (though I cannot speak from any field acquaintance with them) are the Patagonian Cavy (*Dolichotis patachonica*) and the Vizcacha (*Lagostomus trichodactylus*) (Fig. 37).

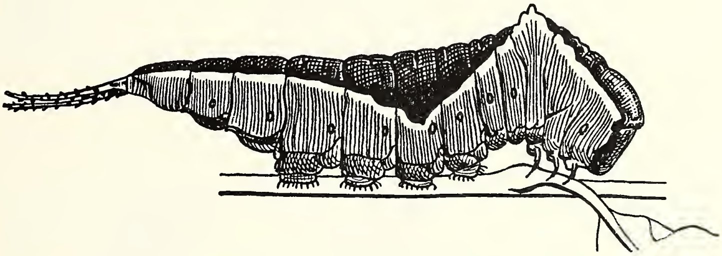

FIG. 15.—Larva of Puss Moth (*Cerura vinula*)

Finally, it must be mentioned that the same phenomenon is of wide occurrence among invertebrate animals which depend upon concealment for safety. It is well seen in the Puss Moth larva (Fig. 15), whose dark saddle of brownish-purple is bordered by a narrow pale margin. This accentuates the disruptive dorsal patch, so that when the caterpillar is seen on its food plant, the misleading superimposed pattern is noticed in preference to the real form of the insect.

V. CONSTRUCTIVE SHADING AND PICTORIAL RELIEF

The principles and examples described above lead imperceptibly to a very subtle and singular type of optical illusion which is of great importance to our subject. The phenomena treated under the heading of Maximum Disruptive Contrast, though extremely effective in breaking up surface continuity, do so in a crude way. At best, flat patches of contrasted tones serve to throw the surface into a number of flat optical planes which to the eye strongly suggest discontinuity. But if, in addition to violent contrast between contiguous elements in the pattern, the individual patches of colour are themselves *graded* in tone, then at once we introduce a new factor—namely, the false appearance of relief. This illusion of surface modelling, in combination with the disruptive principle, is a brilliant achievement of organic evolution. But it is one to which little attention has been paid by biologists, since Darwin's detailed analysis of the pattern of the Argus Pheasant (136). In display the male exhibits a wonderful series of ocelli on the secondary wing feathers. Each ocellus consists of an intensely black circular ring, enclosing a space shaded so as exactly to resemble a ball illuminated from above—the high-light being represented by a patch of pure white, shading downwards through pale leaden tints into yellowish and brown tones which deepen gradually towards the lower part of the ball. A curious detail in this illusion is produced by the position of the white ' high-light ' : in the inner feathers, which are held perpendicularly, the white marks are uppermost and distal in position ; but in the outer feathers, which are held almost horizontally, the white markings have shifted laterally, so that in spite of their different orientation the ocelli still appear as balls illuminated from above.

Dr. A. D. Imms has recently brought to my notice a paper by Schwanwitsch (560) on the so-called stereoeffect of cryptic colour-patterns. By stereoscopic methods, and by sculptured models, Schwanwitsch has reconstructed and interpreted the wing-patterns of various butterflies in terms of series of elevated and depressed areas, with here and there cast shadows. His methods undoubtedly open up a very promising line of investigation, but I do not follow him in his interpretation of different tones on a flat wing as representing different surfaces lying in the same plane but at different levels. Omitting the question of cast shadows, and considering only the illusion caused by light and shade, contrasted tones on a flat surface (Fig. 16, No. 1) are the optical equivalent in relief of surfaces differently inclined towards the source of light (No. 2) rather than of surfaces seen at various levels in one plane (No. 3) as shown in his figures. In other words, the optical effect is not one of stepped surfaces, but of sloping surfaces.

Nor does the matter end here. One of the most significant illusory effects produced by individual elements in the disruptive patterns of animals is an arrangement whereby curved, rather than angular relief, is suggested. This results from tones which are graded, as opposed to those just considered, which are uniform. A flat surface of graded tone (Fig. 16, No. 4) is the optical counterpart of a curved surface of uniform colour (Nos. 5 and 6).

In fact, we are dealing here with optical effects which are analogous to those reproduced by the artist when representing three-dimensional chiaroscuro on a flat surface. And it is on flat surfaces, like the wings of butterflies and moths, that nature has achieved some of her most wonderful results. Thus regarded, these patterns are seen to be pictures. But they are not necessarily pictures of particular objects. In general, pictorial relief, like flat disruption, is an arbitrary form of illusion and the function in either case is to grip the attention of an observer and to distract his eye away from what matters—the real form of the animal—and thus to delay or altogether prevent recognition.

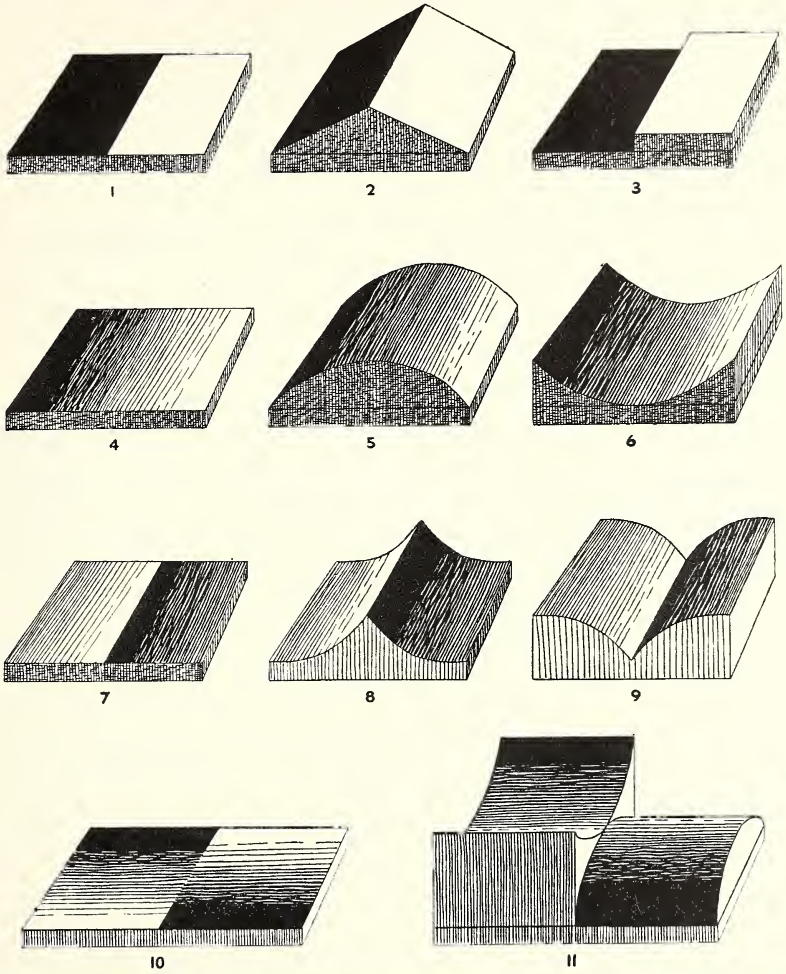

FIG. 16.—Diagrams illustrating correspondence between pictorial relief on a flat surface, and light and shade on a modelled surface

Now the system we are considering reaches its most striking expression when two contiguous patches in the pattern—one being light and one dark—are both graded in such a way that *the pale tint becomes yet lighter and the dark shade deeper as each leads up to the line of contact with its fellow.* Such an effect, and its equivalent in terms of relief, is illustrated in Fig. 16, Nos. 7, 8, 9.

A further development of the last principle is illustrated in Fig. 16, No. 10, in which adjacent elements in the pattern have their tones graded from dark to light in opposite directions. The equivalent of this arrangement in relief is shown in No. 11. I have no doubt that ' dazzle ' patterns based upon this arrangement of tones could be most effectively employed in war-time camouflage, both on land and at sea, and will prove worthy of the careful consideration of those who are concerned with practical aspects of visual concealment.

My reason for giving these somewhat laboured explanations of phenomena familiar enough to the artist, though perhaps scarcely appreciated by the layman, is that this principle—whereby different tones *diverge yet further from one another in shade as they approach one another in space*—is one applied in the most beautiful and effective fashion in the markings of different animals.

Effects of this kind are seen in the toad *Bufo superciliaris* (Plate 37) ; in grasshoppers such as *Leptacris monteiroi* (Fig. 29) ; and in the wings of many Lepidoptera. In the last group such effects are typically associated with the underside of the hind wings in butterflies—such as *Vanessa urticæ*, *Satyrus semele* and *Epinephele ianira* (see Fig. 17) ; and with the upperside of the fore wings in various moths—such as *Thyatira batis.*

Its application could hardly be better illustrated than it is by the British Grayling Butterfly (*Satyrus semele*). These insects, which frequent waste lands and commons, are in the habit of resting with closed wings on the bare ground. On alighting they habitually shut back the fore wings with a slight, sudden movement, so that these come to rest between the hinder pair. In this position only the costal margin and the tip of the fore wing is exposed, and this area conforms with the hind wings, which are remarkable for their cryptic design of white, grey, buff, and dark brown, which blends in the most extraordinary way with the ground. At the same time, the butterflies frequently orientate their wings to the sun, so that no tell-tale shadow is cast by them ; or they may combine with this the cryptic instinct of tilting over to one side in an attitude which shows off the ground picture on the wings to greater advantage. So closely does the pattern simulate the surrounding grey peaty soil and patches of fractured flint variously reflecting and absorbing light from different surfaces, that the insect seems, on alighting, to sink into the background like water into sand. If one be observed to settle a few yards away, or just out of sight behind a near-by clump of heather or patch of gorse, it is often impossible on reaching the spot to discover its exact whereabouts before disturbing it—even when the butterfly is resting in full view on open ground and its place of rest known within a foot or two (see Plate 31).

The principle of pictorial relief is not only applicable to flat surfaces of animals. It may be extended and applied almost without limit to various forms, simple and complex. For while it is true that constructive shading operates essentially by throwing a flat surface into optical relief, it may also serve *to add false relief to a surface already curved.* Many beautiful examples are seen in the cryptic patterns of snakes and caterpillars, and here again I shall attempt to make my meaning clear by the use of diagrams, which may be compared with the simpler examples already given in dealing with the wings of Lepidoptera.

As a final illustration of this beautiful principle we may consider the pattern of the Phalangid *Phalangium opilio.* Here once more we find that the wonderfully deceptive appearance, when seen against broken surroundings, is essentially due to the special arrangement of darker and lighter tones in the body design. An irregularly shaped dark dorsal stripe is seen, at any rate in many specimens, to become distinctly darker towards its edges, where it terminates quite abruptly against the light-grey area of the flank; and, as though to perfect the arrangement, where the lateral area approaches the dorsal stripe it fades to a bright cream tint. As a result, the very darkest and very lightest parts in the design are contiguous. They meet, moreover, along a line which is itself highly irregular in shape. On theoretical grounds the pattern thus approaches a state of perfection. The effectiveness of the principle in application is well shown in the photograph (Plate 43) of the animal in its natural surroundings, where it is seen that the compact, rotund form of the body, which would at once be conspicuous if it wore no patterned livery, appears to have been replaced by a series of irregular sculptured shapes—none of which in any way suggest a phalangid, but which, on the contrary, are repeated over and over again in the broken background of lichen-covered bark.

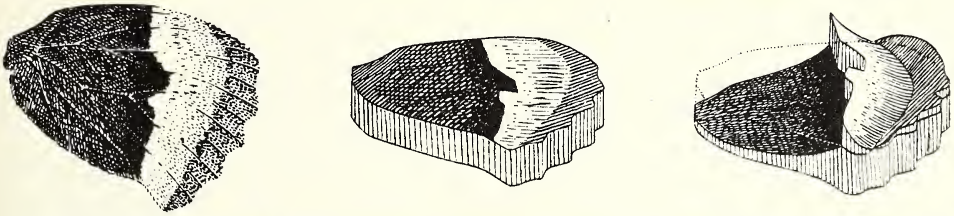
FIG. 17.—Diagram showing disruptive coloration in terms of pictorial relief, based upon the underside pattern of the hind wing in *Epinephele ianira,* the Meadow Brown Butterfly

In conclusion, then, I have attempted to describe here an optical principle which is distinct from, and goes further than, disruptive coloration in the ordinary sense. I have emphasized that we are dealing not merely with the illusion of discontinuity caused by flat contrast; not merely with the illusion of shadows caused by stepped planes; but with the subtle illusion of surface sculpture combined with these, and *caused by constructive shading of a type which is the very opposite of obliterative shading.* In the latter, as we have seen, a rounded surface is rendered optically flat: in the former, a continuous surface is presented to the eye not only broken (as by contrast), or stepped (as by false shadows), but made up of separate surfaces variously curved and sculptured.

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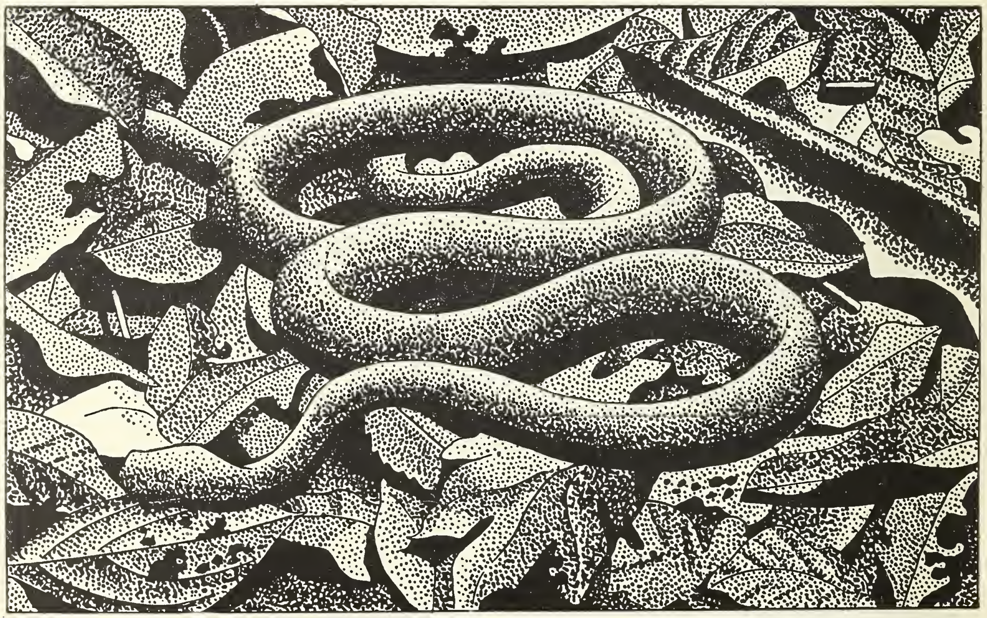

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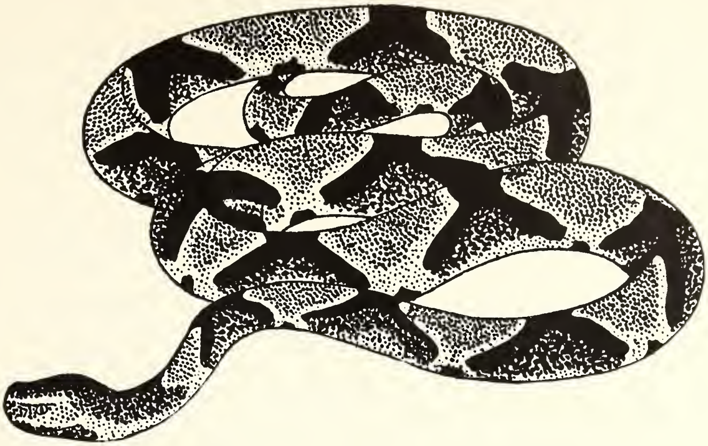
FIG. 18.—Comparative diagrams showing the effectiveness of disruptive contrast and pictorial relief, based upon the pattern of the Copperhead Snake (*Agkistrodon mokasen*). Pale and dark brown in colour, the pattern of the coiled snake strongly suggests the configuration of fallen leaves on the floor of the forests and plantations which it frequents



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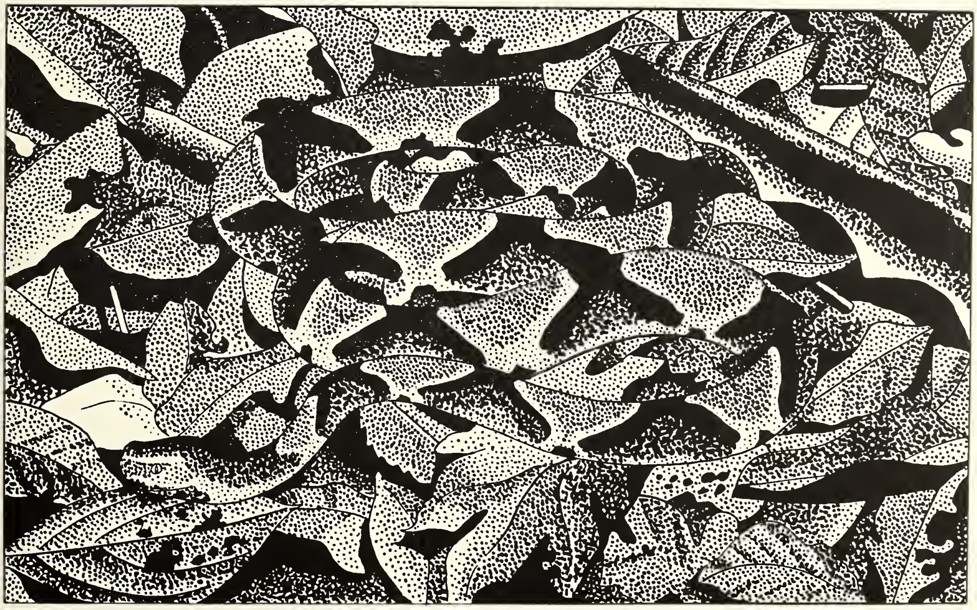

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FIG. 18 *contd.*—1 The snake as it would appear if self-coloured and illuminated from above; 2 The Copperhead, seen against a uniform background; 3 The self-coloured snake in natural surroundings; 4 The Copperhead in natural surroundings

5. COINCIDENT DISRUPTIVE COLORATION

Where order in variety we see
And where, though all things differ, all agree.
POPE

There remains to be examined a further expression of the disruptive principle which is of the very greatest interest. Such patterns as we have so far considered are successful because they appear *to break up the continuous surface of the body*. Now this optical device is carried even further in the case of many animals where the pattern appears *to join together separate parts of the body*. If this can be done—and as we shall see, it has been successfully accomplished in a wide range of totally unrelated organisms—the chances of recognition must obviously be further reduced.

I. CONCEALMENT OF THE APPENDAGES

One of the main factors leading to the recognition, by the eye, of a particular object, such as an animal in nature, is the familiar appearance presented by the component parts of the body—for instance, legs, fins, wings, mouth or eyes. Such organs, if caught sight of, will tend to spoil and betray the whole colour-scheme. This is a vital point that has not been overlooked by nature in the cryptic disguises worn by different animals—though as a fundamental principle of wide application in nature it has hitherto been largely overlooked by zoologists and students of animal coloration.

My attention was first directed to the problem when collecting tree-frogs in Portuguese East Africa. One of the commonest species in the valley of the Lower Zambesi, where I happened to be working, is a little frog known as *Megalixalus fornasinii*. This creature bears on its back a mid-dorsal stripe of brown, tapering to a point in front, and extending backwards to the end of the body. Between this stripe and a similarly coloured stripe on the side of the body there lies an area of brilliant silvery-white. A stripe of the same colour occurs on the inner side of the hind limb between the knee and ankle joints. Now *it is only when the pattern is considered in relation to the frog's normal attitude of rest that its remarkable nature becomes apparent*. The characteristic resting position, like that of most tree-frogs, is with the limbs folded closely in to the sides. At such times the fore-feet are hidden, like those of a cat crouching before the fire, beneath the chin; and the hind limbs are drawn up with the thigh pressed against the belly and concealed beneath the lower segment of the leg, which is closely applied to the flank, while the foot is tucked away beneath the body (Fig. 19). It will be seen that *in this position the silvery stripe on the exposed part of the hind limb exactly coincides with, and forms an extension of, the similar stripe on each side of the back.* At the same time, the dark lateral stripes extending backwards from the nostrils are continued along the outer forearm and leg, while these are themselves so disposed that elbow meets knee. Meanwhile the eyes, at other times so bright and conspicuous, sink from view into their orbits and are covered by the lower lid, so that neither they nor the limbs attract attention. The attitude and very striking colour-scheme thus combine to produce an extraordinary effect (Plate 21), whose deceptive appearance depends upon the breaking up of the entire form into two strongly contrasted areas of brown and white. Considered separately, neither part resembles part of a frog. Together in nature the white configuration alone is conspicuous. This stands out and distracts the observer's attention from the true form and contour of the body and appendages on which it is superimposed, and, like a veil obliterating the features of its wearer, effectively masks its identity.

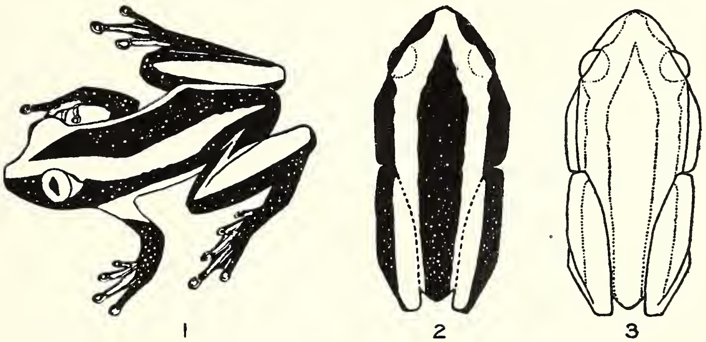

FIG. 19.—*Megalixalus fornasinii.* Drawn from photographs of living specimens, to illustrate the principle of coincident disruptive coloration, which operates when the frog assumes its natural attitude of rest

(1) **Coincident Disruptive Patterns in the Anura**—The principle so beautifully exemplified in the coloration of *M. fornasinii* is one which finds extensive use in nature, and for which, in a paper read before Section D of the British Association, 1935 (114), I suggested the term Coincident Disruptive Coloration. Since various members of the Anura well illustrate a variety of ways in which this principle may be applied, I propose to consider briefly here a few further cases.

In the first place, it is interesting to notice that, as may be seen from Fig. 20, the misleading design worn by *M. fornasinii* is very closely reproduced on the body of *Hyla leucophyllata*, a South American tree-frog belonging to an entirely different family. When I first saw this Hylid frog, which occurs at Pará, I quite failed to appreciate the disruptive significance of its pattern, and it was not until I had taken, two years later, its Polypedatid counterpart near Caia that I grasped the apparent explanation.

Even if these were isolated cases, the exhibited correlation between posture and pattern is sufficiently remarkable, and could hardly be dismissed as insignificant. However, subsequent investigation showed that coincident patterns of one kind or another occur frequently in the group, and widely among other groups of animals also. In the two instances just considered the pattern extends from the back on to the hind limb—the markings in each case being longitudinal in direction. In many, and probably the majority of Anura, the hind legs are marked, not with longitudinal stripes, but with transverse bands of dark and light tones. And in different species, these disruptive elements are so disposed, that when the leg is folded up at rest, one or more of the markings or sets of markings accurately coincides with and continues the pattern of an adjacent segment. Such an arrangement is illustrated in Fig. 21.

What is the effect of this coincidence? We have already seen that the disruptive value of a pattern lies in its tendency to hide the real form of an animal by suggesting a false form to the eye. So long as the false configuration is recognized in preference to the real one, concealment will be effected. Now the result of coincident disruptive coloration is greatly *to accentuate and strengthen the superimposed configuration*, *and to weaken by contrast the real one.* In the present example, for instance, the pattern does not merely break up the apparent form of the leg segments into a number of isolated patches: on the contrary, by the union of corresponding patches, it builds up an entirely new configuration, cutting right across the existing structures and thus creating the additional illusion of continuity where in fact none exists. In this sense, indeed, the principles of disruptive, and of coincident disruptive, coloration are quite opposed—the first working by the optical destruction of what is present, the second by the optical construction of what is not present. *For while disruptive patterns appear to break up what is really a continuous surface*, *coincident patterns seem to unite what are actually discontinuous surfaces.*

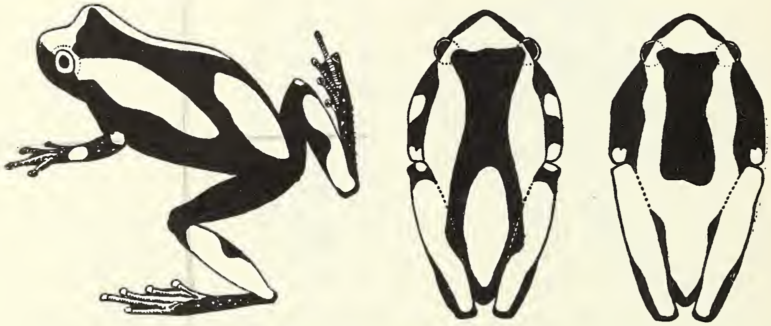

FIG. 20.—*Hyla leucophyllata.* A South American Hylid tree-frog with a pattern similar to that of the East African Polypedatid *M. fornasinii*

That this coincidence of markings across different segments of the leg is not a mere accidental effect, unconnected with the function of concealment, is indicated by several classes of evidence, namely, (1) the statistical examination of large numbers of individuals belonging to a single species; (2) the detailed agreement of the pattern in special cases; (3) the wide occurrence of the phenomena in many genera and families of the Anura; (4) the extensive application of the same principle to other parts of the body in this group, especially in relation to the eye and adjacent areas; (5) the development of parallel or analogous patterns among many other groups of unrelated animals, and in connexion with a very wide range of anatomical structures.

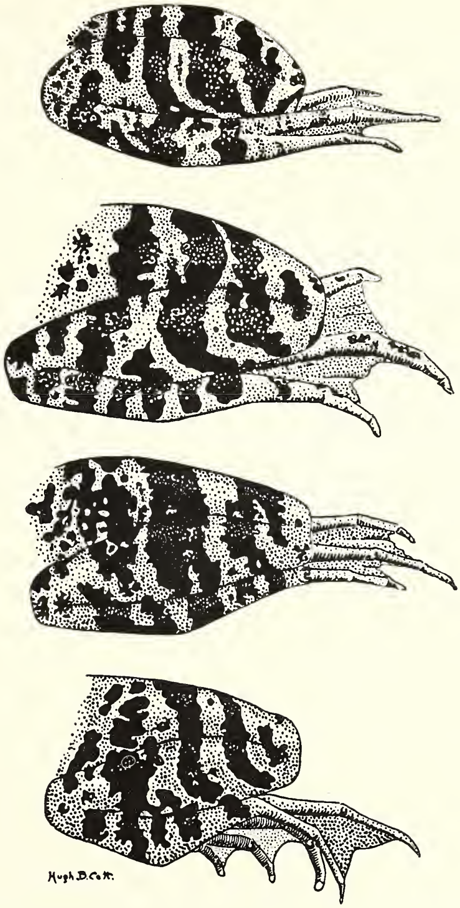

FIG. 21.—Hind limbs of the Common Frog (*Rana temporaria*), showing coincident disruptive pattern

When we examine certain species which have the leg decorated with a somewhat complex pattern of stripes differing from one another in width, tone, and colour, the likelihood of chance providing the coincident effect becomes exceedingly remote. The correlation between pattern and posture exhibited, for instance, by *Edalorhina buckleyi* (Plate 23), seems especially remarkable and significant when we realize that the disruptive patches of colour are entirely independent of, and literally cut across, underlying structural features. This fact will become clearer with the following considerations. The arrangement of pattern in a frog's leg falls into three separate series—the first on the thigh, the second on the segment between knee and heel, and the third on the tarsal region and foot. In order that these three series may register as one when the leg is folded at rest, it is not merely necessary that the intervals between the dark and light elements should correspond on each segment: but also that *the sequence of the middle series should be reversed.* That is to say, if the markings on the respective segments are numbered *in their apparent order on the folded leg*, so as to read like I II III IV V, 1 2 3 4 5, i ii iii iv v; then *the anatomical order on the extended leg* will be I II III IV V, 5 4 3 2 1, i ii iii iv v. Such effects, as seen in *Edalorhina buckleyi* and *Eupemphix nattereri* (Plate 46), find a ready explanation in terms of camouflage, and it is difficult to conceive of any other satisfactory explanation of them.

As already mentioned, coincident leg-patterns of various kinds are of wide occurrence in the Anura. This is not the place, however, to discuss the matter further. A number of examples are illustrated on Plates 21, 23, 46; while the cosmopolitan nature of this particular phenomenon will be indicated by the following examples belonging to different families: Discoglossidæ—*Discoglossus pictus* (Sardinia); Pelobatidæ—*Batrachopsis megalopyga* (New Guinea); Bufonidæ—*Leptodactylus mystacinus* (Uruguay), *Ceratophrys ornata* (Paraguay), *Hylodes ventrimaculatus* (Ecuador), *Bufo valliceps* (Nicaragua), *B. ockendeni* (Peru) and *B. typhonius* (Brazil); Hylidæ—*Ceratohyla proboscidea* (Columbia), *Amphignathodon guëntheri* (Ecuador), *Hyla rosenbergii* (Ecuador), *H. venulosa* (Brazil) and *Nototrema angustifrons* (Ecuador); Ranidæ—*Rana temporaria* (Europe), *R. adspersa* (East Africa); Polypedatidæ—*Rhacophorus fasciatus* (Sarawak), *Mantella baroni* (Madagascar) and *Kassina senegalensis* (East Africa); Brevicipitidæ—*Microhyla picta* (China) and *Ramanella montana* (India).

(2) **Coincident Disruptive Patterns in Reptiles and Fishes**—Patterns of the kind we have been considering are, of course, only applicable to parts of the body which come together in the attitude of rest. This is characteristic of the leg segments in Anura. Among other groups of animals, where coincident disruptive patterns occur, we should naturally expect them to be associated with other parts of the body, since—with the exception of a few creatures such as grasshoppers (which as we shall see frequently exhibit colour-schemes parallel to those found among frogs)—the leg posture does not well lend itself to this treatment.

Among snakes and lizards, a part frequently dealt with in an analogous way is the mouth. Various members of both sub-orders have the head adorned by a disruptive pattern which extends uninterruptedly from the face and upper jaw across the mouth to the lower jaw. Beautiful examples of this arrangement in snakes are presented by the East African *Vipera superciliaris*, where a conspicuous series of dark and light stripes coincide across the whole of the mouth opening (Plate 22); and by the West African *Bitis gabonica*, certain specimens of which have the bold triangular cheek-patch continued on to the side of the lower jaw.

With lizards a parallel arrangement is found, as, for instance, in the Agamids *Moloch horridus* and *Shinisaurus crocodilurus* (Plate 22); and in the Iguanid *Corythophanes cristatus*, a wonderfully bark-like form whose facial mask doubtless helps the cryptic disguise.

With fishes the same principle finds expression in the relation between fins and body. Various arrangements are those seen in such species as *Dascyllus aruanus* (Fig. 22) from the Philippines, *Eques lanceolatus* (Fig. 13) from Florida, *Chætodon unimaculatus* from Jamaica, and *Pterogobius daimio* from Japan—in which the disruptive disguise extends without break from the body on to the dorsal, anal, pelvic or caudal fins.

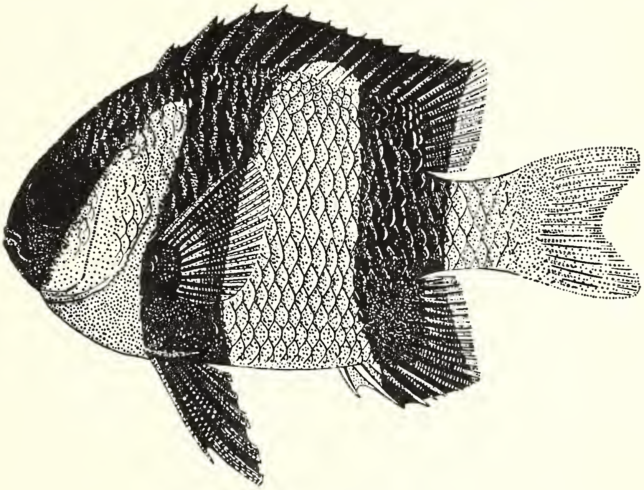

FIG. 22.—*Dascyllus aruanus*

More remarkable, however, are cases like that of *Heniochus macrolepidotus* (Fig. 23), from the Seychelles, where one band in the body pattern forms an apparent extension of the narrow elongated dorsal fin. If seen against a suitable background, the disruptive effect of this costume must be very striking—*for the central white band will appear to be produced as a continuous configuration far beyond the contour of the fish itself.* Such an effect cannot fail greatly to increase the difficulty of recognition.

(3) **Coincident Disruptive Patterns in Lepidoptera**—Insects provide many instances of coincident coloration—which reaches its highest state of perfection in the orders Lepidoptera and Orthoptera. With moths such as Scorched Carpet Moth (*Ligdia adustata*), which rest with the fore wings overlapping the hind wings and meeting behind along the axis of the body, the union of the

markings on one wing with the corresponding markings on the other is not particularly significant, in that this is the inevitable result of symmetry—although the effect is such as to strengthen the disruptive scheme, just as it is in cases where the coincidence of pattern is less easily to be accounted for. I shall refer here especially to the arrangement whereby the corresponding elements in the patterns, both of butterflies and moths, are seen to run without apparent break from the fore wing to the hind wing when the insect is in its normal attitude of rest.

Examples of the principle in its simplest state are furnished by a number of butterflies, where the general coloration beneath the hind wing is repeated along the costal margin and apex of the fore wing (which is the part exposed to view at rest), while the remainder of the fore wing wears a different, and frequently more conspicuous picture. This state of affairs is very well shown in the Orange-tip (*Euchloë cardamines*). As pointed out by Beddard (33), the scattered green spots on the under surface of the hind wings might have been intended for a rough sketch of the small flowerets of an umbelliferous plant—its favourite resort—so close is their mutual resemblance. Now this cryptic pattern is repeated beneath the fore wing over an area precisely corresponding

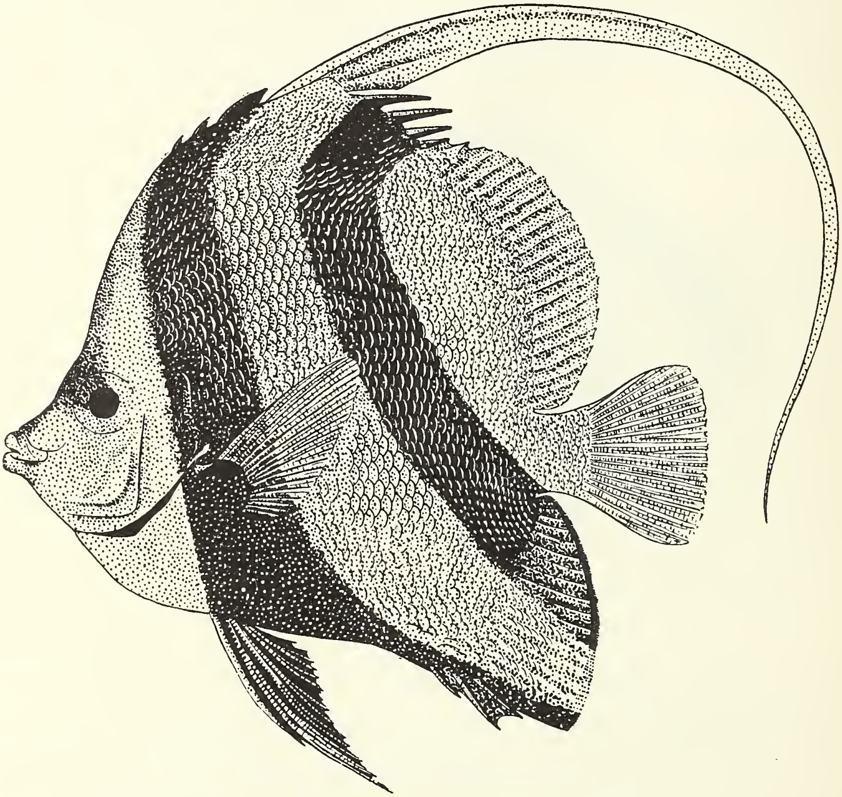

FIG. 23.—*Heniochus macrolepidotus*

with that which remains exposed beyond the margin of the hind wing in the normal attitude of rest.

A most singular example of the same kind is seen in the beautiful South African *Eronia cleodora*, a conspicuous black and white butterfly whose underside *cryptic* surfaces of yellow, irregularly marked with grey and darker shades, strikingly suggest the yellow, blotched and perforated leaves of the shrub *Isoglossa woodii* upon which it was observed to rest by Dixey and Longstaff (150). An excellent plate in colour published by these authors well illustrates the highly effective cryptic appearance of the butterfly under such circumstances.

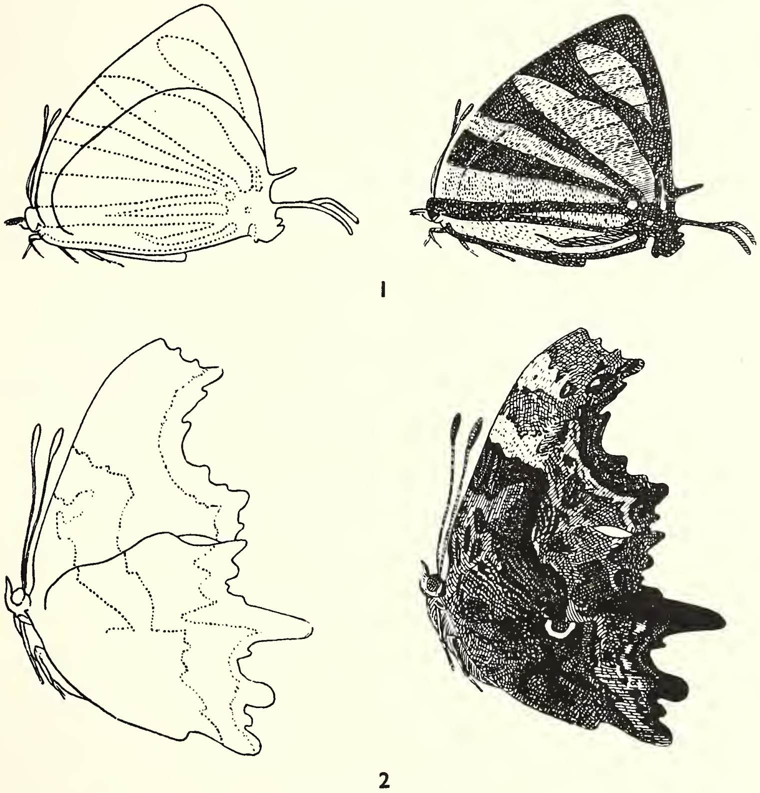

FIG. 24.—1 *Thecla phaleros*, illustrating the use of a coincident pattern in conjunction with deflective characters. (*After* T. MORTENSEN.)

2 *Polygonia c-album*, illustrating the use of a coincident pattern combined with a camouflaged contour

More exact and specialized are the underside patterns of *Polygonia c-album* (Fig. 24), *Kallima paralekta* and other butterflies where definite elements in the pattern are repeated, line for line and tone for tone, across the gap between the wings as seen in their position of rest. A very beautiful example, and one whose pattern is believed to have special directive significance (p. 368), is furnished by *Thecla phaleros*. To cite a final example, one of the most perfect is the Indian *Yoma sabina*.

Unlike the previous example, which wears a strongly contrasted and somewhat crude pattern of light and dark converging stripes (Fig. 24), this butterfly has a delicately figured design, which may be compared to an artist's painting in that *an illusory appearance of form, relief, and depth is suggested on a flat surface. The result presented to an observer is thus the very opposite of that produced by countershading, which, as we have seen, causes a solid object to appear flat.* Each of these effects is, of course, calculated to hinder recognition, for each disguises the real form and substitutes to the eye something quite different. But the point to which I would draw attention here is the remarkable conformity between the picture carried on the fore and hind wings respectively. Every change of hue, and difference of pattern, and gradation of tone is carried across from one wing to the other, *so that a single cryptic configuration is revealed upon what are really two separate surfaces*, like an advertisement extended across two sheets of paper.

With moths analogous appearances are produced across the *upper* surfaces of the wings. Species which rest with the four wings spread out flat frequently have markings forming a continuous series right across the full expanse. In all such cases it is of great interest to note *the close correlation between the disposition of the pattern and the mutual position of the wings in the resting insect.* Two examples will suffice to make this point clear. The Blood-vein Moth (*Timandra amata*) has the upper surfaces of its wings broken by two narrow darkish lines, both of which coincide across the four wings (Plate 26). The moth rests in a characteristic attitude with the wings spread flat, the front pair slightly overlapping the hind pair. The normal degree of overlap is precisely allowed for in the position of the lines on the fore and hind wing respectively. These markings cross the wing margin diagonally: therefore if the overlap is increased, or decreased, the lines no longer register. But in the living insect they do so perfectly, or at any rate sufficiently well to give the impression of a continuous uninterrupted set of markings.

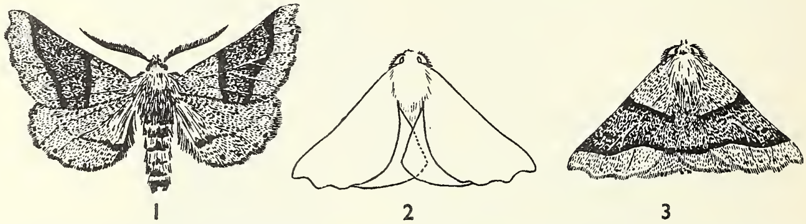

FIG. 25.—Scalloped Oak (*Crocallis elinguaria*). Diagrams showing the coincident disruptive pattern: 1 Wings opened to show the arrangement of the disruptive elements; 2 Diagram showing the position of the wings in the natural attitude of rest; 3 Appearance of the moth at rest

In the Scalloped Oak Moth (*Crocallis elinguaria*) the normal resting attitude differs in that the fore wings are folded back so as to leave only the inner part of the hind wings exposed to view. In this case the disruptive pattern is carried mainly on the fore wings, but it continues (with less definition) across the inner exposed part of the hind wings (Fig. 25). Thus the living insect has its surface broken by a continuous band, whose colour-scheme conforms to the principle of maximum disruptive contrast which we have already considered. When, however, the covered part of the hind wing is examined, it is found to be almost devoid of any pattern. In other words, *the pattern occurs only over the area where it can be seen, and in a position where it can produce a particular optical effect.* Several other British species, such as the Barred Umber (*Numeria pulveraria*), illustrate the same principle.

(4) **Coincident Disruptive Patterns in Orthoptera**—We may conclude the present brief survey of coincident body markings by examining the very perfect development of this system of camouflage among various Orthoptera. In its simplest form, the principle is well shown by grasshoppers which bear on the back or sides a pattern of lighter and darker longitudinal stripes. For instance, the nymph of an acridian common in the New Forest is an earthy-brown insect whose form is apparently divided down the back by a pale buff stripe just the colour of dried grass. That this stripe pays no respect to incidents of anatomy in its straight course down the whole length of the body may be seen by the way in which it traverses head, thoracic and abdominal segments, and especially in its course over the wing buds, dividing them longitudinally into an upper light and a lower dark region in perfect alignment with the coloration of adjacent areas. In July, when the insects may be found among sun-dried grass and baked earth which are the two things which their own colour-scheme exactly matches, the disruptive effect is wonderful. I have endeavoured to reproduce this in a somewhat diagrammatic figure (Fig. 26). In its wingless condition, *Aptoceras fasciata*, from Uganda, exhibits a simple arrangement of similar type. Here the colours are dark green and ochre, the light components taking the form of a pair of yellow lines extending from the eye over the head and thorax to the end of the abdomen.

Among larger grasshoppers, two very perfect examples of coincident dorsal stripes are seen in the Brazilian *Agriacris trilineata* (Fig. 27), a green species wearing a clearly marked mid-dorsal stripe of buff; and in *Prionolopha serrata* (Fig. 27), also from Brazil, whose general green uniform is divided by two straw-coloured stripes. Both species have the light stripes continuing without break from the pronotum on to and along the upper margin of the elytron. In *P. serrata*, which occurs at Pará, the effect is peculiarly suggestive of variegated grasses, for the pronotum is extended upwards and backwards into a blade-like keel, round the sides of which pass the stripes already mentioned, to unite behind on the tegmina as a single pale dorsal streak. A third example, illustrating a further step in the elaboration of coincident patterns, must be introduced here. *Calliptanus italicus* is a dark-brown grasshopper which, like *P. serrata*, bears two dorso-lateral straw-coloured stripes. In the present case, however, the disruptive elements do not converge behind the pronotum, but continue backwards along the tegmina as independent stripes. The disposition and

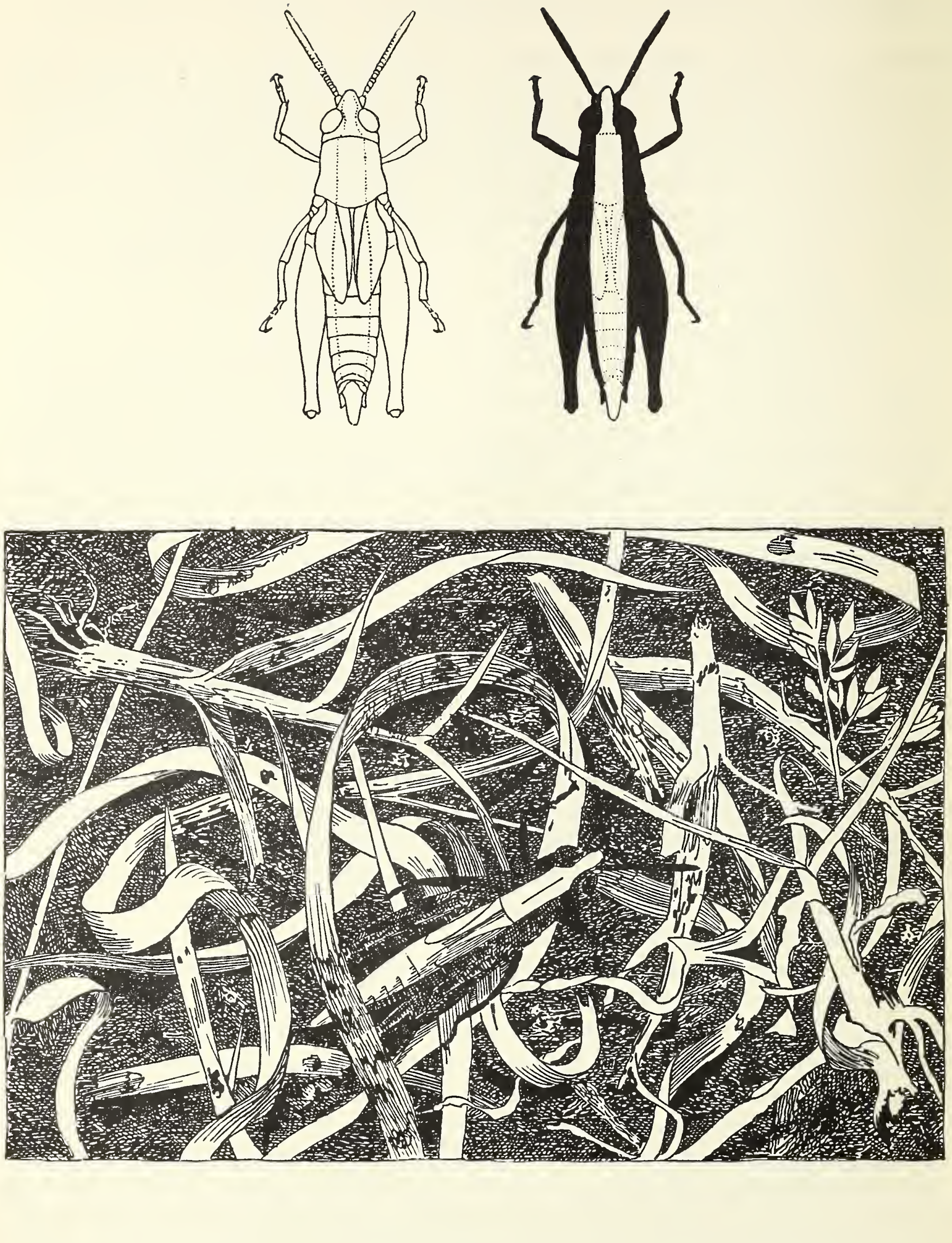

FIG. 26.—*Chorthippus parallelus*, showing the relation of the coincident pattern to its morphological background; and its disruptive effect against uniform and broken surroundings

significance of these markings can be better appreciated when the tegmina are separated, as in Fig. 27, which shows how the coincident effect is arrived at. It will be noticed that the inner margin of each tegmen bears a patch of dark pigment, so placed as to extend backwards the bold sepia patch on the head and thorax. Outside this the light stripes, dividing each tegmen longitudinally, extend unbroken (in the resting attitude) from one end of the insect to the other.

With grasshoppers, as with frogs, it is the relatively enormous hind limbs (whose great development is, of course, correlated with the leaping habit) which are especially apt to lead to recognition. Accordingly, and in view of what can be, and has been, achieved in the Anura, it is perhaps not surprising to find coincident patterns widely employed here also. Such patterns, worn on the exposed parts of the femur, bear a significant and often very exact relation to those worn on adjacent parts. Still more interesting is the fact that the coincident elements may be transverse or longitudinal, in relation to the type of country inhabited—the latter being the common arrangement among grass-haunting species; the former among those living on stony ground; but whether they run across or along the body, the hind limb has received appropriate attention. It is incorporated in and forms part of the general design. Thus it is disguised and more or less lost to view beneath a bold super-imposed pattern which extends, regardless of anatomical features, over the form of the insect as a whole, and which flattens out by contrast the lesser incidents of tone between parts anatomically distinct.

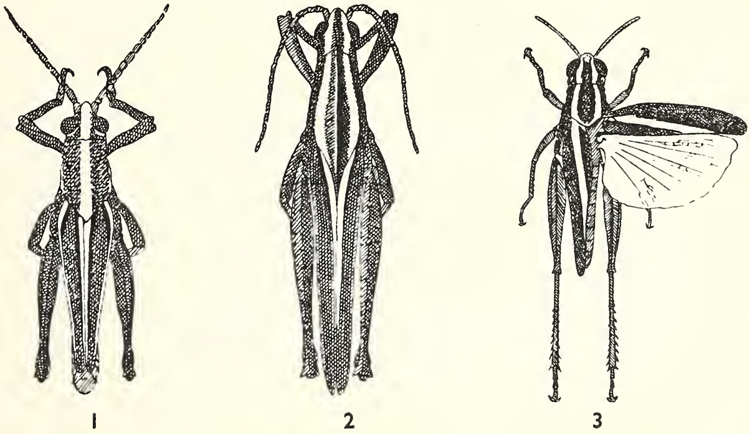

FIG. 27.—Coincident patterns among grasshoppers: 1 *Agriacris trilineata*; 2 *Prionolopha serrata*; 3 *Calliptanus italicus*

Of the transverse type we have excellent examples in the European blue-winged *Œdipoda cœrulescens* and the Mexican species *Hadrotettix trifasciatus*, where dark bars on the femora agree in position with corresponding bars on the tegmina—an arrangement which finds its parallel in the Bufonid frog *Hylodes longirostris*, from Ecuador, in the Brevicipitid *Caluella brooksii*, and in the Polypedatid tree-frog *Rhacophorus fasciatus*, from Sarawak (Fig. 28). In such cases the degree of coincidence is subject to variation. Sometimes the continuity of pattern is perfect; sometimes it is less accurate. It may, however, be pointed out here that the optical effect does not depend upon anything approaching a mathematically exact fit at the edges of the corresponding marks. So long as the coincidence is fairly close, the appearance of general continuity will be maintained, and with wide bars of the type we are here considering there is considerable latitude for variation without prejudice to the disruptive function.

Finally, a few words about the longitudinal type of leg pattern which is especially adapted to grassy surroundings, as opposed to the banded design, which breaks the insect transversely and is more appropriate to forms inhabiting stony places. Considered from the aspect of camouflage, the striped system is in certain respects the more perfect and remarkable of the two, both as regards the means adopted and the end achieved. This is seen firstly in the greater absolute length of separate elements in the design; secondly, in the increased number of different organs or parts traversed; and thirdly, in the more accurate registration and alignment of corresponding tones on different surfaces.

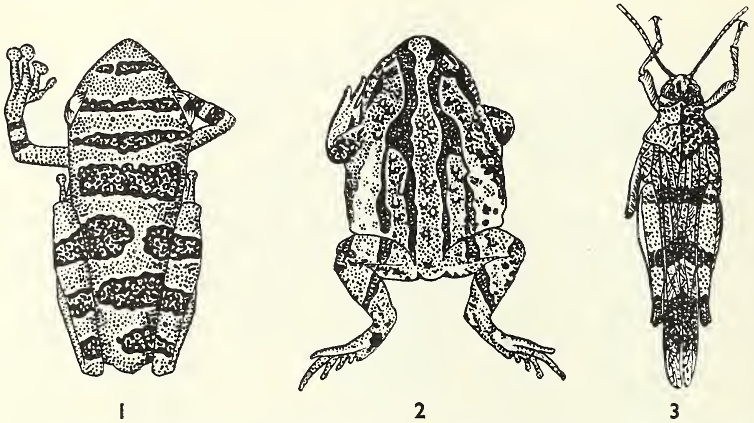

FIG. 28.—Coincident disruptive patterns: 1 *Rhacophorus fasciatus*; 2 *Caluella brooksii* (*after* BRONGERSMA); 3 *Œdipoda cœrulescens*

Leptacris monteiroi, from Nigeria, is a buff-coloured grasshopper whose more or less uniform hue is abruptly broken by a clearly defined cream-coloured stripe on the side. This stripe, as will be seen in Fig. 29, ends in front beneath the eye, and extends over the side of the head and thorax to the base of the hind leg, where it continues without break along the lower side of the femur, while immediately above it the femur is light brown in agreement with contiguous areas of the body. The first two pairs of legs, unlike the third, lie beneath the light stripe, and lack any white markings. The disruptive effect of this white stripe is reinforced by the deeper tones along its upper and lower margins. The contrast thus produced serves to flatten out and draw attention away from the lesser gradations of tone by which it is possible to distinguish different parts of the body from one another and the insect as a whole from its surroundings.

Mesopsis brevicauda, from Tanganyika, has what is essentially the same device, though here the body is divided longitudinally into an upper dark and a lower light part. The lower limit of the dark dorsal area in this case passes just above the femur and is accurately continued backwards as the darkened lower border of the tegmen (Fig. 29). In the case of the African *Oraistes punctipennis* and the Australian *Gesonia mundata*, to which we must refer again presently, parallel conditions are found in the leg region, the former having the hind femur divided longitudinally into an upper dark and a lower light area (Fig. 29); the latter having the dark lateral stripe above the femur and continued backwards along the full lateral aspect of the tegmina.

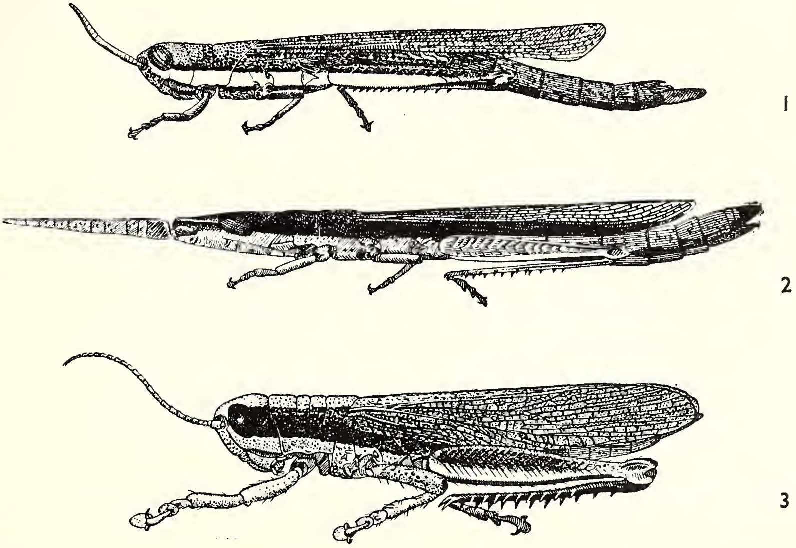

FIG. 29.—Coincident disruptive patterns: 1 *Leptacris monteiroi*; 2 *Mesopsis brevicauda*; 3 *Oraistes punctipennis*

A beautiful example of the principle here dealt with has been described by Nicholson, whose photograph of *Betixa*, in Australia, well illustrates the correlation between the disposition of the markings on the body and the attitude of the insect in life. Pattern and posture combine in the present case to show a bold disruptive line of white extending straight and unbroken from the head, over the thorax, and along the femur. Commenting on the striking appearance thus produced, the author states: 'the perfect continuity of this line on such a heterogeneous basis is strong presumptive evidence that continuity and straightness have been produced as such' (440).

II. CONCEALMENT OF THE EYE

A singular application of this principle is seen in the camouflage of the eye itself—that most difficult of all organs to conceal. Few natural objects possess greater inherent conspicuousness than the vertebrate eye. This characteristic is due mainly to its sharply defined, rounded form. Of all shapes a round disc is the most striking and easily seen and recognized—hence the use of the ‘ bull's-eye ’ for target practice. Its power of attracting attention to itself in preference to other objects in the visual field is shown in Fig. 30. Here we have a number of forms arranged in an artificial configuration, differing individually in shape and size. And among these, it is not the largest which is first noticed ; but the round eye-spot—which is actually one of the smaller areas in the configuration.

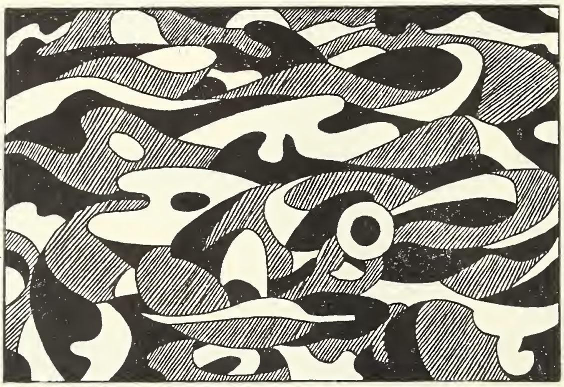

FIG. 30.—Diagram illustrating the inherent conspicuousness of an eye-spot, which attracts attention to itself in preference to a variety of other, and even larger, objects in the visual field

Yet it stands out from everything else, and rivets the attention. In view of the above considerations, it is clear that no scheme of camouflage will be completely effective which does not mask or modify the appearance of the eye ; and it is interesting to note how this end has been attained in different animals.

(1) **Cryptic Coloration of the Iris**—In the first place, we find that with various animals the difficulty is met without having recourse to disruptive patterns. In certain nocturnal geckos and tree-frogs, for instance, and in snakes like the Horned Viper, the pupil when contracted in daylight becomes a mere slit, and *the iris is of a tint which matches the rest of the head.* In such cases we have, in fact, a special use of the principle of colour-resemblance applied to the eye in relation to the animal, rather than to the animal in relation to its surroundings—though, of course, it frequently happens that the local and the larger effects are combined.

A further step is taken by animals which have *the general pattern of the body reproduced on the iris and on the membrane investing the eye.* Longley (347) has described a good example of this in *Petrometopon cruentatus*, a fish which is marked with dark-brown spots, which are smaller above and larger below the eye. The arrangement is closely reproduced on the conjunctiva, the spots on its dorsal and ventral area agreeing respectively in size with those nearest them on the head. Longley points out that the pattern even extends to parts of the conjunctiva normally hidden, but which come into view when the eye is rolled. In this way, movement of the eye is not betrayed by the appearance of coloration out of harmony with the general scheme.

In the absence of anything better, a pattern of spots on the head will tend to diminish the conspicuous appearance of the pupil, which, as we shall see, is the part requiring special attention. This is essentially the device adopted in newly hatched young of Partridges and of various gulls and terns (see Plate 20), which have the crown, forehead and cheeks liberally flecked with dark spots approximately the size of the eye, which consequently becomes lost as one spot among many in the general pattern.

(2) **The Nature and Function of Disruptive Eye Masks**—It is, however, with the employment of coincident disruptive patterns for eye-camouflage that we are especially concerned here. Many fishes, frogs, snakes, birds, and mammals have large rounded black pupils which conform to this very shape most likely to catch an observer's eye. However effectively such animals may be camouflaged in other respects, unless the eye receives special treatment, it will prejudice the success of the whole colour-scheme. It is therefore very interesting, though not surprising, to find that nature—the supreme camouflage artist—has dealt in great detail with this problem, which is evidently one of urgent importance. We must now examine the system devised for this purpose.

In its essentials, the method adopted invokes the optical principle of coincident disruptive coloration which we have already discussed. If an eye, and *particularly its staring black pupil*, can be made to appear another shape, then it will cease to resemble an eye. In theory, such an illusion could be created by covering the eye, or its pupil, with a black mask of irregular shape—so designed as to blend with and seem part of the pattern which surrounds it. Now that is essentially the system devised in nature.

By way of example, we may begin by referring to the photograph on Plate 24 of the Common Frog, where it will be seen that a blackened area, level above with the top of the pupil, extends over the iris and continues over the skin on the side of the head as a continuous dark patch of colour. This effectively masks the eye and also the head in which the eye is set, for it looks like an interstice between grasses, the effect being intensified by the strongly contrasted adjacent light streak bordering the lip.

Animals belonging to many widely separate families and orders have the eyes camouflaged in precise detail. Although the underlying principle is everywhere the same, the incidents of the picture vary widely in different cases. Sometimes an irregular dark disruptive area includes the whole orbit. Sometimes the upper margin of an elongated patch of dark pigment crosses the iris exactly on a level with the top of the pupil. Or conversely it may extend beneath to the pupil's lower limit. Or again, the eye may be crossed by a stripe exactly the width of the pupil itself. In other cases similar effects are produced in vertical bars instead of horizontal stripes; or in diagonal markings or irregular shapes varying greatly in size and distribution. *The one consistent feature in all this diversity is the significant relation between that unmitigated black spot—the pupil—and the dark element which serves to absorb it.*

Another striking point is the recurrence of the above variations in group after group of animals. They are exhibited in wonderful perfection and diversity by fishes. The same devices reappear in one form or another on the iris and contiguous structures of snakes and lizards. They are displayed by different frogs and newts. The same essential effects are seen once more in the feather masks of various birds, and in the tracts of dark hair associated with the eye in different mammals. And they are repeated again on the chitinous covering of grasshoppers and various other insects. Consequently, as we shall see, the phenomena present some very remarkable cases of convergence.

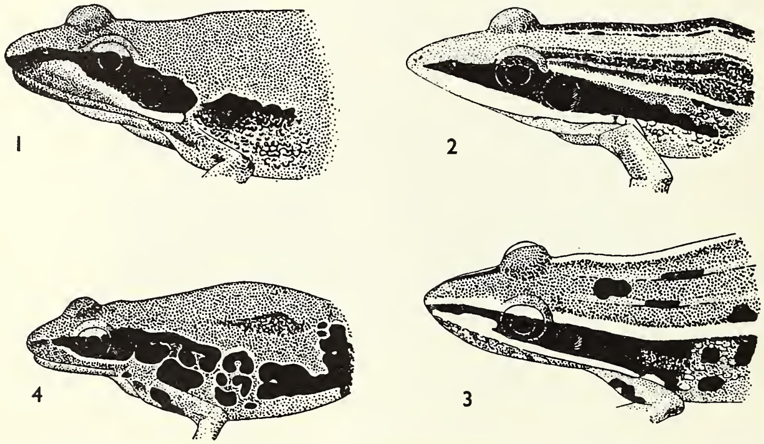

FIG. 31.—Disruptive ocular stripes: 1 *Rana oxyrhynchus*; 2 *R. stenocephala*; 3 *R. sphenocephala*; 4 *Cardioglossa leucomystax*

(3) **Eye-masking Patterns in Fishes**—It would be altogether outside our present purpose to attempt any detailed survey of these devices. I shall here merely point out some of the chief types of pattern met with in different groups. In many cases the animals have been figured, so that the essential points can be seen at a glance and the various types readily compared. One of the most perfect examples of eye camouflage with which I am acquainted can frequently be seen to advantage in the aquarium of the Zoological Society of London. I refer to the Short-nosed Garfish (*Lepidosteus platystomus*). The head and anterior part of the body is a uniform sandy colour. Against so light a background the round jet-black pupil would stand out as a highly conspicuous target unless specially camouflaged, and it is interesting to see in how apparently

simple and effective a way this has been done. The iris agrees with the head in colour, so that the edge of the orbit blends fairly well with the head. But in front of, and behind, the pupil it is crossed by a jet-black ribbon of pigment, just the width of the pupil. The stripe so formed across the front of the eyeball continues forwards on to the snout and backwards on to the operculum, and in each direction it gradually fades until it becomes lost in the general body colour (Fig. 32). It is on the eye itself that its tone is blackest and its contour sharpest. Considered as a camouflage scheme, its effect is twofold. In the first place, the stripe altogether conceals the pupil, which in well-marked specimens is quite invisible from a distance of a few inches. In the second place, the strong, black, clearly defined mark flattens by contrast the fainter tell-tale half-tones—for instance, where the eyeball joins the head—and so not only conceals the pupil, but tends to hide the eye as a whole. The aggressive signi-

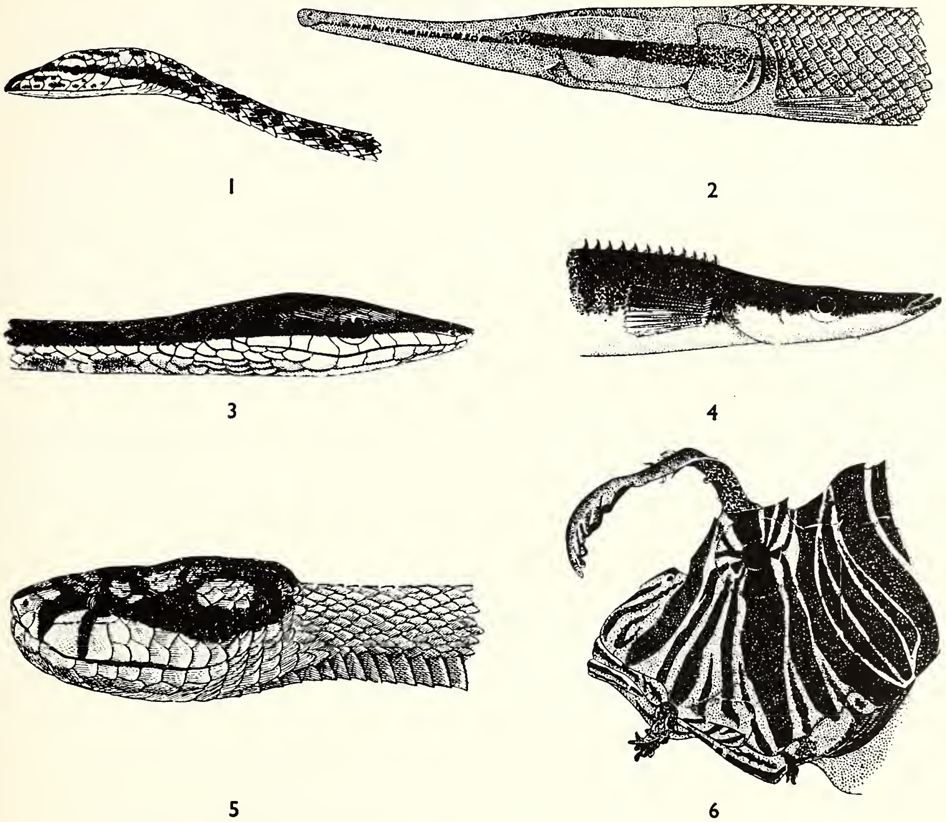

FIG. 32.—Types of coincident disruptive eye-mask in various fishes and snakes: 1 *Dryophis fasciolatus*; 2 *Lepidosteus platystomus*; 3 *Oxybelis acuminatus*; 4 *Gasterosteus spinachia*; 5 *Lachesis trigonocephalus*; 6 *Pterois volitans*

ficance of this admirable arrangement can be readily appreciated in view of the fishes' predaceous habits.

When examining such a pattern, we must not allow its apparent simplicity to mask its underlying complexity. In point of fact, these ocular designs seem ever more remarkable the more closely they are studied. We have firstly to realize that, as pointed out by Longley (348), what appears to an observer as a single straight stripe, consists in reality of a series of pigmented areas based upon, or involving, seven distinct anatomical units—three on each side of the pupil, namely, the skin of the head, the conjunctiva and the iris ; and the pupil itself, where the dark interior of the eyeball takes up the pattern and forms the central link in the series. And further, that the effect produced demands mutual agreement over this heterogeneous basis as regards colour, width, orientation, and coincidence of the pigmented areas. Yet so consistently are the various details presented to the observer that the illusion is complete. Not only is the eye concealed, but also its movements within the orbit are hidden.

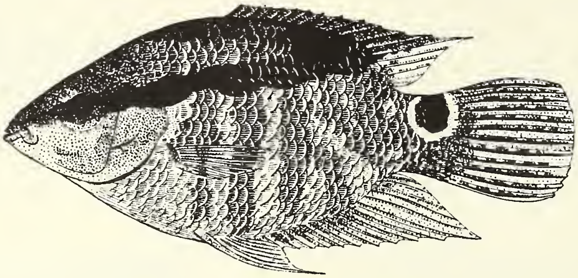

FIG. 33.—*Cichlasoma festivum*

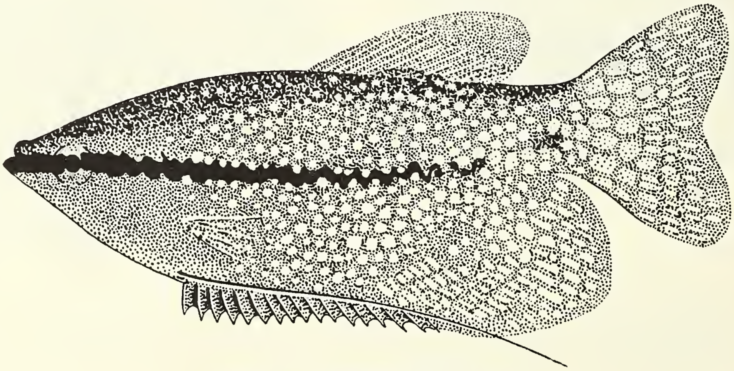

FIG. 34.—*Trichogaster leeri*

Horizontal ocular stripes the width of the pupil occur in a number of other species, such as *Trichogaster leeri* (Fig. 34) and *Upeneus martinicus*. In others, such as *Chætodon capistratus* (Fig. 76), *C. bennetti*, and *Eques lanceolatus* (Fig. 13), the disruptive element takes the form of a vertical band. Or the eye mask may be oblique, as in *Cichlasoma festivum* (Fig. 33) and *Chilodactylus gibbosus.* Frequently it has an irregular form, as in *Heniochus macrolepidotus* (Fig. 23); in other cases it embraces the whole orbit, as in *Pristipoma virginicum* (Fig. 35) and *Dascyllus aruanus* (Fig. 22); in others again it consists of a number of isolated markings, as in *Antennarius notophthalmus* (Fig. 77) and *Monocirrhus polyacanthus* (Fig. 63); in others, like *Pterois volitans*, a complex pattern converging on the pupil (Fig. 32).

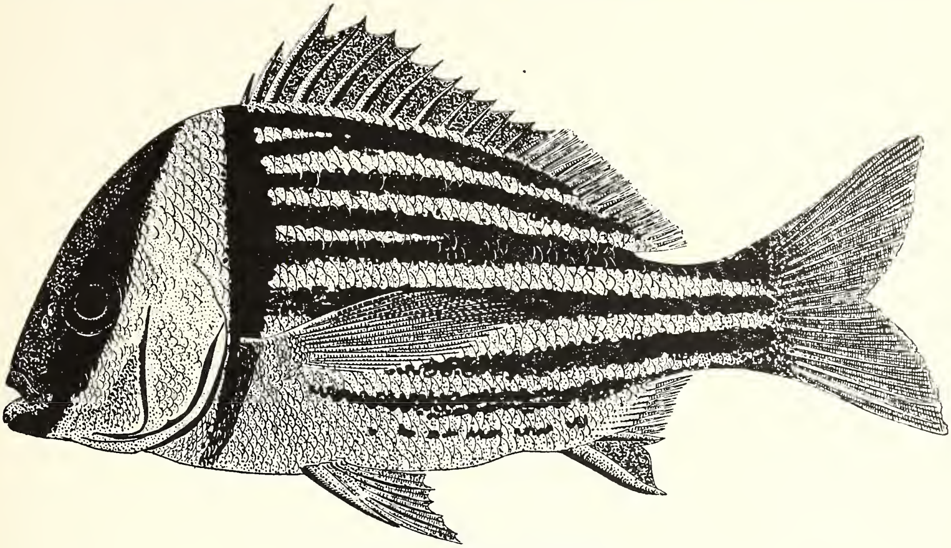

FIG. 35.—*Pristipoma virginicum*

(4) **Camouflage of the Eye in other Classes of Vertebrates**—Snakes present many extremely perfect examples of the principle. The following are a few examples: *Oxybelis argenteus*, *Philodryas olfersii* and *Dryophis fasciolatus* bear a horizontal disruptive patch on the side of the head approximately the width of the horizontal pupil. *Oxybelis acuminatus* (Fig. 32) and *Thelotornis kirtlandii* have the horizontal mask terminating below on a level with the bottom of the pupil, which is precisely the arrangement found in a number of fishes such as *Gasterosteus spinachia* (Fig. 32). More commonly, however, the converse figure

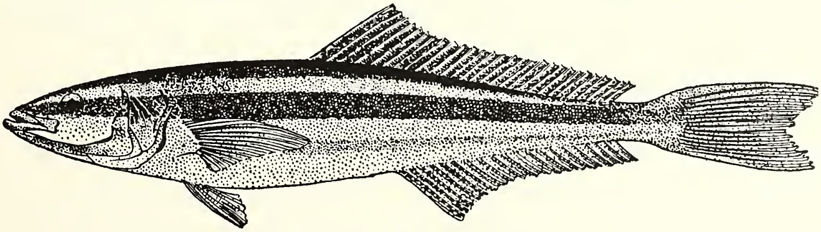

FIG. 36.—*Elacate nigra*

is adopted, the dark mask crossing the lower part of the eye and terminating above on a level with the top of the pupil. A very clean-cut and perfect example of this device is seen in *Constrictor constrictor* (Plate 24); and in a large number of other forms, such as *Python molurus*, *Gastropyxis smaragdina*, *Agkistrodon blomhoffi*, and *Vipera russellii*, this type of pattern constitutes an effective blind, which is a reproduction of the arrangement found in certain fishes such as *Elacate nigra* (Fig. 36). Other species have the eye treated in a variety of ways, one of the most effective involving the use of large patches of dark tone spread over the entire orbit, as seen, for instance, in *Vipera superciliaris* (Plate 22), *Trimeresurus gramineus*, and *Crotalus confluentus*.

Among lizards these eye effects are less perfect and elaborate, possibly owing to the possession of eyelids which somewhat complicate matters. It is certainly significant that the most specialized, clearly marked and precise instances of eye camouflage occur in creatures that are lidless—namely, fishes, snakes, and grasshoppers. Nevertheless we may point out in passing that many lizards, such as *Hemidactylus richardsoni* (Fig. 67), *Physignathus lesueurii*, *Anolis equestris*, *Mabuia quinquetæniata* and *Rhampholeon spectrum* exhibit the illusory effects already mentioned in other groups. With frogs, the usual arrangement, where such devices are found, consists of a dark patch, variously shaped but usually placed more or less horizontally on the side of the head and terminating above on a level with the top of the pupil. A number of examples are figured on page 84.

More or less well-defined ocular bands or stripes occur widely among birds, as seen, for example, in the Nuthatch, Snipe, Whimbrel, Woodcock, Ringed Plover, and Turnstone. It is significant that with many nidifugous young, bold and characteristic disruptive markings are typically associated with the eye in such a way as to mask its outline. Young Great Crested Grebes, Woodcock, Sandpipers, and Common Tern all wear ocular masks of one kind or another, and the device is beautifully illustrated by the Ringed Plover chick (Fig. 14), whose main disruptive incident includes the eye in its sweep. Among mammals, what appear to be markings of similar significance occur in a number of forms, such as the Gemsbok (Plate 25), Sable Antelope, Grant's Gazelle, and the Vizcacha (Fig. 37).

(5) **Eye Obliteration in Grasshoppers**—A striking parallel to the devices we have been considering is afforded by different grasshoppers. *Diponthus bivittatus*, from Brazil, is a green insect whose brown eyes contrast with the general body colour. Here, then, we have a feature likely to attract attention and lead to recognition. When, however, we come to examine the grasshopper among broken surroundings, we find the eyes are scarcely noticeable. They are, in fact, well obliterated by two broad brown stripes. Just the width of the eye, each of these stripes runs from that organ backwards across the head, extending unbroken over the thorax on to the wings. In effect it is as though an artist, when drawing the insect, had accidentally smudged the eye while still wet and drawn a trail of ink or paint right along his figure.

Such a colour-scheme would be sufficiently remarkable even if it were an isolated case. But the same arrangement, with slight modifications according to circumstances, is one which occurs frequently in the group. For instance, it is reproduced in several other Brazilian species, such as *Oxybleptella sagitta.* Similar ocular stripes are well marked in *Adimantus brachypterus*, from Paraguay, in *Oxya minor*, from Tanganyika, in *Oraistes punctipennis* (Fig. 29), from West Africa, and in *Gesonia mundata*, from Australia. The two last-named afford beautiful examples of eye-obliterating pattern. But the case of *O. punctipennis* is especially noteworthy. In this insect we have combined a number of optical devices worthy of the closest attention. Firstly, the coloration, both as regards the tints used and the pattern displayed, are in general harmony with grass and ground herbage. Secondly, the broad dark lateral stripe effectively conceals the eye, with which it agrees in width and tone, and the femur, which is bisected by its lower margin into a green upper and a yellow lower half—altogether a remarkable instance of coincident disruptive coloration. Thirdly, beneath the dark lateral stripe a strongly contrasted incident is introduced by the bright yellow adjacent area—thus flattening by comparison the less violently graded

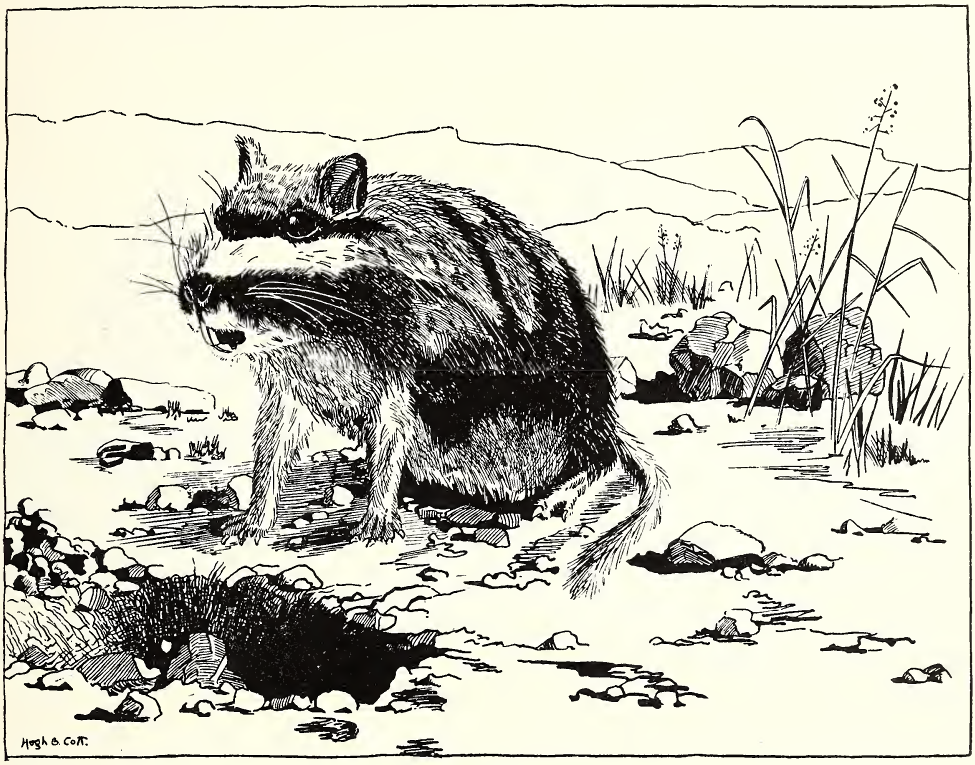

FIG. 37.—Vizcacha

tones between the various parts of the body, and between the margins of the body and its natural surroundings.

(6) **Eyelids as Camouflage Screens**—Finally, the same end is attained in an entirely different way by various cryptic vertebrates which instinctively close, or nearly close, the eyes when in danger of being seen by an enemy. As a result the eye is concealed, not by virtue of its own coloration, but by that of the lids whose scales or feathers carry the tints of the head over the orbit. This habit is well developed by certain large-eyed nocturnal birds, notably the Frogmouths (*Podargus*) and Nightjars (*Caprimulgus*, *Nyctibius*), which either rest by day with almost closed lids, or else shut the lids when danger threatens. Further reference to this interesting habit is made on pages 120 and 136.

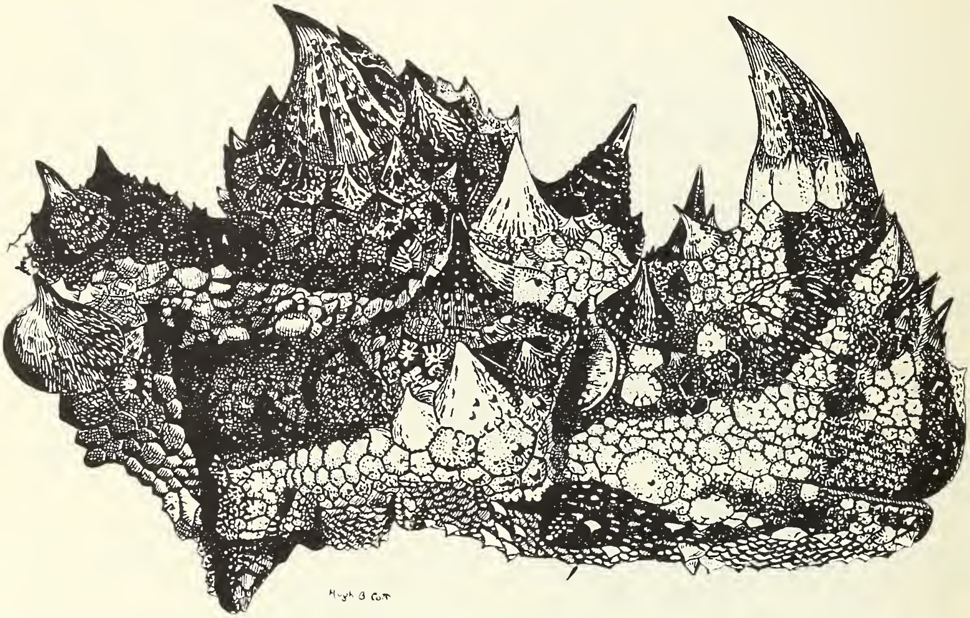

FIG. 38.—Head of *Moloch horridus*

Various lizards make use of the same tactics. For instance, Darwin describes seeing in Patagonia the lizard *Proctotretus multimaculatus*, ‘ which, when frightened, flattened its body, closed its eyes, and then from its mottled tints was hardly distinguishable from the surrounding sand ’ (136). Although it must not be imagined that there is anything deliberate or conscious in the performance of so simple an action, ***in its effect on the observer*** we have here a device forming the very foundation of applied camouflage—seen in the analogous use of overhead screens whose function is to hide vulnerable targets from the reader of aerial photographs. The accompanying drawing (Fig. 38) of the head of *Moloch horridus* shows the eye closed and its position camouflaged by a coincident disruptive pattern which passes across the slit of the eye from the upper to the lower lid.

Under this heading we may also include a device—analogous in function though totally different in nature—occurring among insects, to which attention has been drawn by Poulton (496). The Herald Moth (*Gonoptera libatrix*), which is active in England in the autumn and winter, bears somewhat appropriately a fairly close resemblance to a withered and fungus-spotted leaf. ' The bright eyes of the moth might expose the deception, but they are covered during rest by a tuft of hair which springs from the base of the antennæ. When the moth is about to fly the antennæ are brought forward, and the same action raises the tufts and uncovers the eyes.'

(7) **Applied Aspects of Coincident Coloration**—Once again it is quite evident that we have in coincident patterns an optical device which may be applied with considerable effect in any attempt to reduce the visibility of large objects as seen from the air, or of ships at sea. The essential point here is that elements in the disruptive pattern must be carried boldly without interruption across adjacent surfaces, such as the hull and upper works of a ship, or in the case of buildings, from the roof to adjacent ground topography. A good deal of what has been said has a very special bearing upon the concealment from relatively great altitudes of landing-grounds and aeroplane hangars.

III. THE BEARING OF COINCIDENT DISRUPTIVE COLORATION ON THE THEORY OF CONCEALING COLORATION

The arrangement of disruptive patterns, both in relation to the several parts of the body, and to an animal's environment, provides important indirect evidence of their biological function. Various attempts have been made, especially by Tylor (633), to interpret markings on an anatomical basis. Defining his ' Law of Structure ', Tylor writes : ' Coloration, especially when diversified, follows the chief lines of structure, and changes at points, such as the joints, where function changes.' He attempts to show that this principle applies widely, almost universally, in the animal kingdom. For instance, he suggests that the facial pattern in the Tiger is determined by the paths of underlying nerves ; that the patterns of snakes are related to underlying skeletal structures—the vertebræ and ribs ; and that the markings of birds, cuttlefishes, caterpillars, and many other animals depend upon the same principle.

Other workers have subsequently drawn attention to the apparent relationship between colour and structure. In three species of European newts, Linden (333) found that a pattern of stripes, which developed even before hatching, was apparently correlated with the development of the main blood-vessels beneath the skin. McCook (380) accounts for the markings of various spiders in a similar way.

That pattern must have some structural foundation, in the sense that every picture has one, is obvious. But that it always or usually has any such basis in the sense intended by Tylor—that is to say, that it is the outward and visible expression of internal anatomical features—a sort of superficial chart of underlying muscles or nerves, blood-vessels or bones—is not generally true. Indeed, it is often the *very reverse of the truth.* For the plain fact is that *such patterns as we have been considering run out of all relation to, and frequently cut right across, the distribution of deeper structures.*

Frequently, as we have seen, they bridge the gulf between upper and lower jaws ; or step over the pupil from one side of the iris to the other ; or cross the slit of the eye from lid to lid ; or span the space between the folded segments of the leg. Not only do they frequently pass without let or hindrance across different neighbouring structures, but coincide without interruption across adjacent but morphologically separate parts of the body. What possible basis in gross anatomy, it may be asked, can any such patterns possess ?

Then over and over again we find patterns differing as widely as possible from one another in closely related animals—members of the same genus or family ; or differing in corresponding parts or segments of the same individual. Among these we have outstanding examples in the coloration of snakes and cats and caterpillars. Many snakes, like *Vipera russellii* and *Bitis gabonica*, exhibit patterns whose dorsal elements are, as it were, out of gear with those on the flanks, the two sets of markings bearing to one another a relation somewhat like those on the fixed and movable scales of a vernier. It is obviously impossible to relate both sets to a common series of underlying segments.

If the markings of a Tiger are due to the distribution of its gross anatomy, then how can almost the same anatomy give rise to those of the Cheetah, Puma, Leopard, and Ocelot ? Or if among Sphingid larvæ the diagonal lines of *Smerinthus ocellatus* are built upon an anatomical basis, then what forms the basis for the longitudinal stripes of *Hyloicus pinastri*, or the vertical bars of the aposematic *Isognathus swainsoni* ?

Again, the markings on the eggs of birds, and on the legs of frogs, quite contradict basic details of anatomy, while, as every naturalist knows, they are frequently closely correlated in a very special way with the coloration of their natural surroundings. Moreover, how can we refer the pattern on a butterfly's wing, or on a bird's feather, to structure ? Such pictures as they present to the eye are laid down like a mosaic on numerous minute separate elements, and seem to be scarcely more dependent upon anatomical features than is the pattern of a mosaic pavement upon its underlying foundation, or the colours of a picture upon the threads of its canvas background.

Further, in certain groups, notably fishes and cuttlefishes, the same individual can put on several entirely different dresses in as many moments. If any one of these represents the distribution of underlying structural features, then what do the others represent ? And conversely, as I have already shown, we repeatedly find similar patterns exhibited by animals morphologically and systematically as distinct as a grasshopper is from a grass snake, or a moth from a gecko.

It amounts to this. If disruptive patterns are in any general way dependent upon underlying structural features, then we are driven to the impossible conclusion that such characters are more closely correlated with external appearance than with internal function. I want to insist in the strongest manner that the distribution of coincident disruptive markings lies in the province of the ecologist rather than of the anatomist; and that their explanation depends less upon inward structure than upon outward appearance. This complete subordination of structural elements to the illusory appearance which is built upon them is a highly remarkable phenomenon, and one in complete agreement with the principles of concealment; and it provides a striking body of indirect evidence that such patterns have been developed in reference to the visual perception of other animals, and to the need for escaping observation in a state of nature.

IV. CONCEALMENT OF THE CONTOUR

Disruptive patterns may be applied to the surfaces of solid bodies for two fundamental purposes—namely, for the *disguise of surface*, and *for the obliteration of contour*. Hitherto we have examined the deceptive appearance produced in the surface form of different animals by disruptive patterns—which break up the continuous modelling of the body; and by coincident patterns—which unite discontinuous parts of the body. We have been concerned essentially with the *concealment of surface form*.

But what of the edge of this surface—that is to say, the contour of the animal? It is, of course, true to say that no outlines occur in nature. Yet every solid object has a boundary, which divides the space where it is from the space where it is not. And while this boundary occupies no room itself, yet it has a recognizable form, and it is, indeed, one of the most important factors enabling one to recognize any familiar body. It therefore follows that *camouflage of the contour* —like that of the limbs, eyes and other structures already dealt with—will demand special attention in any satisfactory scheme of camouflage.

(1) **Disruptive Marginal Patterns**—Pattern can be used to break up a continuous contour, just as it can to break up a continuous surface. Theoretical aspects of the subject have been carefully studied by J. C. Mottram (424). Broadly speaking, it may be said that outline obliteration is induced when contrasted elements in the pattern are interrupted at, or near, the margin. (Conversely, the contour is accentuated when the pattern conforms to its border.) The essential point is that for purposes of concealment, the pattern must cut across rather than run along the contour.

This principle is illustrated in the simple diagrams shown in Fig. 39. In each of the six designs here shown, half of the patterned area is white, and half black. When these are examined from successively increasing distances, a point will be found for each where the black and white patterns blend to form an even grey tone, intermediate between black and white. At about this blending distance the figures will be lost to sight against the grey tone of the background. But this point will not be the same for each design: it will be farther away for that on the left of each pair—in which the lines of the pattern conform to the margin; and nearer for the corresponding diagram on the right—in which the pattern is interrupted along the margin.

In nature, interrupted patterns breaking against the contour are found in many classes of animals, and undoubtedly play their part in the problem of camouflage by masking the margin of the body or appendages. The same principle has, of course, a wide war-time application in the disruptive painting of ships, tanks, hangars, and other objectives. Well-known examples are furnished by the Giraffe and Zebra, whose patterns of dark and light patches or stripes everywhere cut across the outline. Under certain conditions, that is to say, in full sunlight and in open country, the Zebra may be a conspicuous enough object. But in the dusk, when he is liable to be attacked, and in country affording thin cover, he is one of the least easily recognized game animals. White, who claims a wide experience with these animals, and states that he has seen 'thousands upon thousands' of zebra against different backgrounds, writes that: 'At any rate, in the thin cover described he is the most invisible of animals. The stripes of white and black so confuse him with the cover that he is absolutely unseen at the most absurd ranges. Time after time not only did Cuninghame and myself fail to make them out even as close as forty and fifty yards, but Kongoni confessed himself baffled. And of the many keen-eyed savages with whom I have had to do, Kongoni can see farthest and best. A switch of the tail, or the actual movement of the head, was time and again our first warning. This same

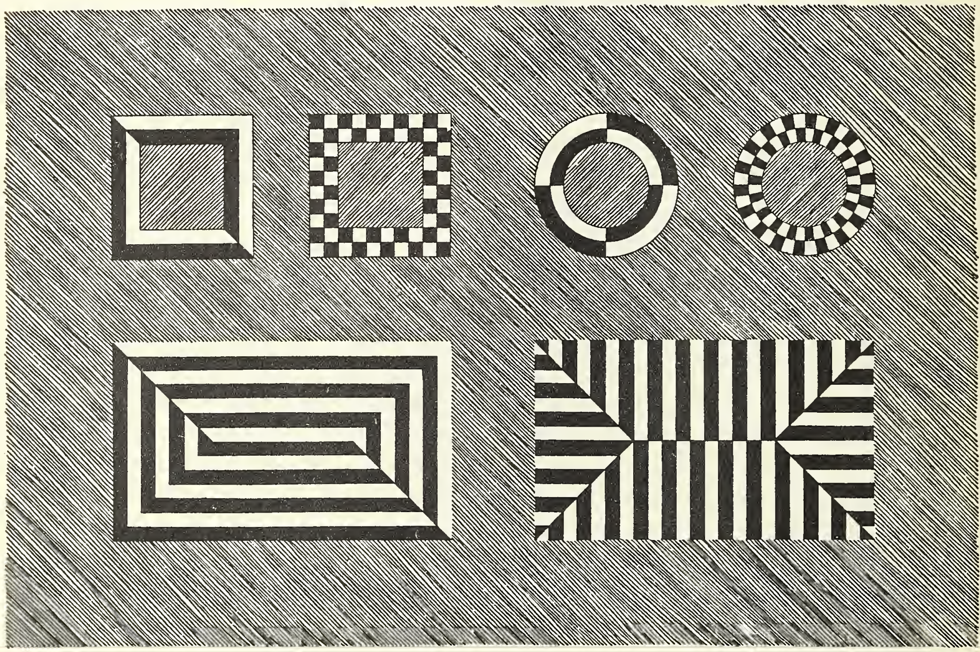

FIG. 39.—Paired diagrams illustrating the use of disruptive patterns for the obliteration of contour. (For explanation see text)

cover was open enough so that we could see topi or wildebeeste up to 200 yards' (666).

Some years ago Professor A. C. Hardy drew my attention to a curious optical illusion which may have some bearing on this subject. When a pair of patterns such as those in the lower part of Fig. 39 are compared, it will be seen that the 'zebra' type of pattern appears to be larger than its counterpart; and the suggestion has been made that in altering the zebra's apparent size—and therefore distance—the stripes may cause a predator to misjudge its leap.

The obliterative effect of a Giraffe's colour-scheme has been commented upon by Vaughan Kirby. He writes: 'But once they have made up their minds to go, they wait to ask no questions, but screw up their tails and go straight away. And the ghostly manner of their disappearance is most remarkable. I have often been riding up to them, when some other object has drawn my attention off for a few moments; glance again, and they are gone! Not merely gone to a distance though still in sight, but gone utterly, vanished like a mist-wreath at sunrise. Indeed, strange as it may seem, few animals are so easily lost sight of, if once the attention is taken from them . . .' (311).

FIG. 40.—Application of the principle illustrated in Fig. 39

Many instances of the principle occur among birds, lizards, snakes, frogs, and fishes, and among different classes of invertebrates. Among butterflies, for instance, the device finds expression in the checkered or banded marginal configuration worn on the underside of the wings, and especially on the tell-tale costal region and apex of the fore wing, which, as already mentioned, is frequently the only part exposed in the resting attitude. This is well seen in the Painted Lady (*Pyrameis cardui*) (Plate 31), Small Tortoiseshell (*Vanessa urticæ*), Grayling (*Satyrus semele*) and Speckled Wood (*Pararge egeria*).

A number of moths have the outer margin of the fore wing decorated in accordance with the same principle. Among bark-resting species like the

Merveille du Jour (*Agriopis aprilina*), Scarce Merveille du Jour (*Diphtera orion*), and the Frosted Green (*Polyploca ridens*) such patterns are especially effective and undoubtedly increase the difficulty of detection by breaking the regularity of wing contour.

Mention should be made here of the 'zebra-pattern' often assumed by the cuttlefish *Sepia officinalis.* In this phase the central region of the back, dark brown in colour, is surrounded by a broad border over which somewhat irregular dark and light bands radiate outwards (269). The disruptive effect thus produced is not less remarkable for the fact that, unlike that of the zebra, it is a temporary manifestation of the complex chromatophoral mechanism.

We may here note in passing the very interesting fact—which will be illustrated on a later page—that the converse fundamental principle is made use of, with precisely opposite effect, in cases where conspicuousness, rather than concealment, is aimed at; and in which the pattern runs along, rather than across, the contour. This advertising appearance is reflected in the brightly coloured hind wings of moths exhibiting flash coloration, as seen, for instance, in *Catocala electa*, *Triphæna pronuba*, and *Isognathus scyron.* The same device is reproduced among grasshoppers like *Œdipoda miniata*, and bugs like *Fulgora spinolæ*, where the membranous hind wings likewise exhibit flash coloration during flight.

Moreover, a similar optical effect is seen in the advertising coloration of many aposematic animals. Thus in Skunks, Zorillas, Salamanders, and in various Danaid and Heliconiid butterflies and many other forms the pattern conforms to the contour of the body or depicts the margin of the wings.

(2) **Irregular Marginal Form**—There are certain inherent characteristics of the outline in many animals which greatly facilitate recognition by sight—namely, regularity of form, repetition of detail, and symmetry. It follows that any device which destroys or subdues these qualities will increase the difficulty of detection. Among many of the most perfectly camouflaged animals, this problem has been met by the modification of the contour itself. In fact, we see in this connexion two complementary methods of concealment in use among animals. In some cases, like those already mentioned, the outline is obscured by an interrupted marginal pattern: in others, to be considered here, it is effaced by an irregular marginal form. The first method depends mainly upon optical illusion; the second upon structural modification.

The device is beautifully illustrated by the Comma butterfly (*Polygonia c-album*) (Fig. 24), whose outer wing margins are highly irregular, and give the resting insect a very cryptic appearance in nature. The same effect is seen in many moths, such as *Gonoptera libatrix*, *Selenia lunaria*, and *Phlogophora meticulosa.* A very remarkable example is *Draconia rusina* (Plate 39). This insect not only has the border of the wings deeply and irregularly indentated, as though they had been eaten away or accidentally broken, but shows patches simulating a partly skeletonized leaf with great fidelity. Even more remarkable is the dry, skeletonized, lifeless appearance of the bug *Pephricus fragilis*, where the process has gone so far that the insect cannot properly be said to possess a contour at all. Deceptive modifications of a similar kind occur in the leaf-like grasshoppers *Systella rafflesii* (Acridiidæ) and *Tanusia picta* (Tettigoniidæ), in which the tegmina seem to have been partly eaten or broken away.

These and many similar cases of irregular contour belong more properly to phenomena classified under the heading of Special Resemblance, to be considered on a later page—for they intergrade with modifications representing definite features of the environment. The arrangement thus has a *general obliterative* and a *special deceptive* function. As further examples of the principle it is only necessary to cite here the wonderfully effective weed-like screen or fringe round the jaws of the Angler Fish (*Lophius piscatorius*); the bark-like expansions on the tail of the bark gecko *Phyllurus platurus*; the foliaceous expansions on the limbs of the mantis *Gongylus gongyloides*; the deeply serrated margins of the body in the extremely depressed bark-like bug *Dysodius lunatus* (Fig. 41); and the thorn-like spines on such stick insects as *Acanthoclonia sævissimus.*

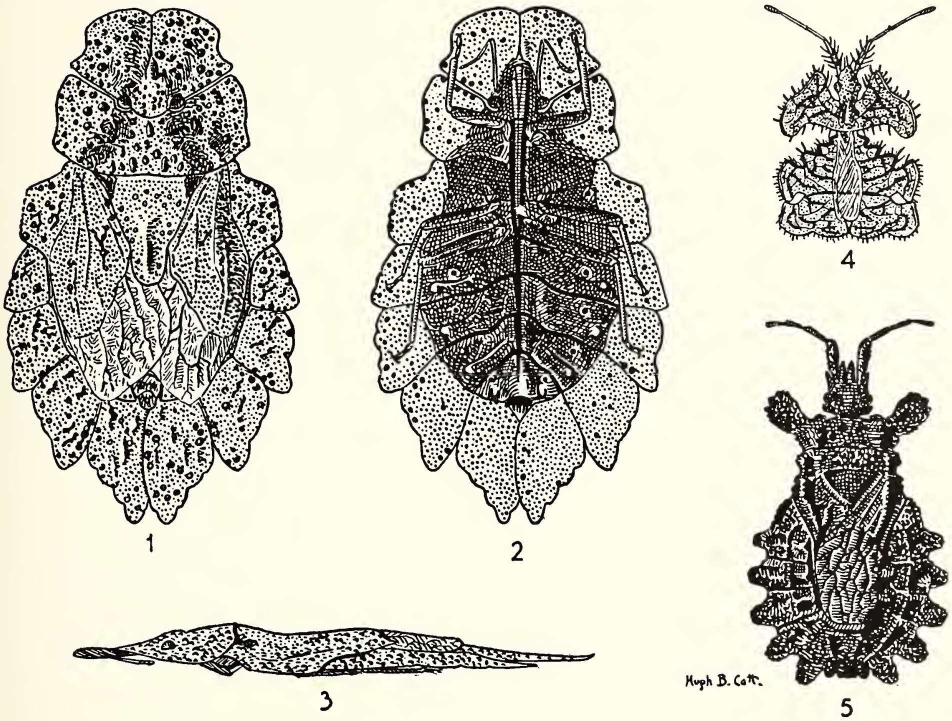

FIG. 41.—Special cryptic resemblance in bark-like Heteropterous bugs: 1, 2 and 3 Dorsal, ventral and lateral views of *Phlœa subquadrata*; 4 *Craspedum phyllomorphum*; 5 *Dysodius lunatus*

V. BACKGROUND PICTURING : THE RELATION BETWEEN PATTERN, ATTITUDE AND ENVIRONMENT

We now come to another aspect of disruptive coloration particularly applicable to animals which habitually rest upon fairly constant surroundings. We have seen that in its crudest and most generalized condition a cryptic pattern serves to break up an animal's form into a number of more or less contrasted patches of colour whose shapes are arbitrary. While the shapes of these patches entirely fail to suggest to the eye the form of the body on which they are superimposed, they do not necessarily suggest anything else in particular. As far as concealment is concerned, this probably does not much matter in very broken surroundings, so long as the shapes employed destroy the original form and outline without being in themselves unduly conspicuous. However, a further step towards invisibility is taken when the disruptive design more or less closely resembles the particular environment against which it is normally seen—as happens, for instance, in the case of many moths, birds, and fishes. Such animals reproduce on their bodies a detailed picturing of the normal habitat-background—of bark or lichen, of grass or heather, of coral or seaweed, and thus, when motionless, become extremely difficult to detect.

In war, as in nature, such methods are especially applicable to fixed objects such as observation posts, or to those likely to be viewed against a typical configuration. Such colour-schemes differ from the disruptive type, in being *realistic*, or *scenic*, rather than *abstract*, or *arbitrary*. By their use it is possible, not merely to disguise an object's form, but *to obliterate the break which it causes in its background, and so to render it invisible.*

I do not propose to discuss this type of coloration here, for the whole subject has been repeatedly treated by various writers, and has received detailed treatment by Thayer in his monograph on ' Concealing Coloration in the Animal Kingdom '. There are, however, one or two points of great significance and interest to which I must refer in this connexion.

Firstly, in a particular type of environment the same type of disruptive picturing is worn by animals belonging to widely separated groups, while conversely related forms inhabiting diverse surroundings have frequently adopted the particular cryptic design appropriate to their respective haunts and habits. Adaptive convergence is found in the coloration of various creatures associated, respectively, with the woodland leaf-carpet, with the trunks of trees, with moor and marsh, with shingle and rock, with weed and coral. For instance, striped grass-patterns form the conventional livery of many grass-breeding birds like the Meadow Pipit, Corncrake, Quail, and Eider Duck ; of grass-frogs such as *Rana mascareniensis* in East Africa and *Hyla nasuta* in Queensland ; of various longitudinally-striped ground lizards like the East African *Mabuia quinquetæniata* ; and of innumerable caterpillars and grasshoppers. Of great interest in this connexion are Lepidopterous larvæ which feed upon, and live among, the needles of pine trees, and which, in harmony with their striped surroundings, are themselves dressed in a disruptive uniform of stripes—an arrangement independently adopted in a number of unrelated forms, for example, the Pine Hawk (*Hyloicus pinastri*—Sphingidæ), Pine Beauty (*Panolis griseo-variegata*—Noctuidæ) and Grey Pine Carpet (*Thera variata*—Geometridæ).

Yet more remarkable is the agreement between coloration and background configuration seen in the Oriental Sphingid larva *Leucophlebia lineata.* Quite unlike the vast majority of its congeners, which are marked with diagonal disruptive patterns, this larva exhibits bold whitish longitudinal stripes and no diagonal markings, and its habits are as exceptional as its appearance, for Bell and Scott state that it feeds on grasses (Gramineæ) ' which do not form the food plant of any other Sphingid caterpillar ' (44). Such cases of background-picturing lead up to a more specialized condition in which the resemblance has been carried yet further, and in which the animal seems to simulate some definite object in the environment—a grass-stem, a leaf, a flake of bark, a piece of lichen, a twig, a stone, a flower, a hydroid polyp, or the excrement of a bird.

Conversely, adaptive radiation in colour—examples of which are given under the headings of Colour Resemblance (p. 11) and of Special Protective and Aggressive Resemblance (p. 336)—is seen in the patterns developed within many groups. A single instance may be cited here. Tillyard (624) has pointed out that most dragonfly larvæ which live hidden in sand or mud, or beneath débris, are uniformly coloured, with no pattern. On the other hand, larvæ living on the river bottom, or amongst water weeds, wear cryptic patterns which are effective in making them inconspicuous both to enemies and prey. Not only do the patterns occur especially in the species which live exposed, and which therefore have the greatest need for concealment, but the precise colour-scheme suits the environment. Thus bottom-dwellers, like most Eucorduliini and Libellulinæ, are pale brown mottled with dark-brown and olive ; weed-dwellers, like many Agrionidæ and Lestidæ, are yellow, green or olive marked with dark-brown or olive-green ; larvæ living on sticks, like many Brachytronini, may be dark-brown or black, with more or less secondary loss of pattern ; others living on rocks are either black, or grey, or brown, like the colour of their surroundings.

Secondly, we may say that close resemblance to the pattern of a particular environment is typical only of animals limited to a narrow range of habitat or restricted to particular kinds of food-plant, resting-site, or breeding-place. In other words, specialized cryptic patterns are correlated with specialized habits ; and, generally speaking, they are not to be found among more versatile, wide-ranging or unspecialized species. This relation between coloration, habits, and environment is applicable to many groups of animals and is apparent in all kinds of surroundings. For instance, referring to the fishes of Samoa, Longley (346) states that ' in general it may be said that the more narrowly a fish is confined to a certain environment, or the more commonly it occurs in such, the more clearly its color tends to reproduce those dominant in its surroundings '. The general truth of this is fully borne out in the most specialized cases where background-picturing gives place to resemblance to particular objects—of which numerous examples will be given under the heading of Special Protective and Aggressive Resemblance.

Thirdly, background-picturing is often associated with special attitudes and habits, whose effect is *to bring the pattern into appropriate relation to the environment simulated.* Frequently the pattern is itself adjusted to the normal attitude of its wearer. This is the case, for instance, in the Angel Fish, whose transverse dark bars break the countershaded body into a series of vertical dark and light bands which doubtless harmonize with the background of river weeds against which it is likely to be seen. The vertical stripes of the Tiger provide a parallel example from a very different environment.

A beautiful instance of the same kind has been described from the Chaco by Professor Graham Kerr (307). He writes: 'Many of the South American butterflies have on the under side of the wings a pronounced pattern of light and dark stripes or elongated markings so arranged that they are approximately vertical when the butterfly is in the resting position. I remember one chilly morning on the Pilcomayo river being quite startled by suddenly becoming aware that the still dew-laden grass all round was peopled by thousands of these butterflies clinging to the grass stems, the light and dark striping of their wings blending with the general light and shade effect of the grass so perfectly that I had missed them entirely up to that moment.'

Many bark-haunting moths illustrate the same principle, showing a wonderful combination of adaptive coloration and adaptive attitude in reference to particular resting-sites. The hawk moth *Xanthopan m. morgani*, of East Africa, attains a wonderful degree of concealment through the pattern on its fore wings, which exactly reproduces that of Casuarina bark (Plate 30). The dark diagonal disruptive markings are well correlated with the oblique carriage of the wings, so that in the natural resting posture they form an approximately parallel series. The moth instinctively settles with its body in a vertical position, thus bringing the pattern of the wings parallel to that of the bark which it simulates. Moreover, the insect applies itself flat against the surface, almost eliminating tell-tale shadows. Thus we see the interesting fact that real shadows are concealed and false shadows suggested. In any other position (except with the head downwards) the insect would be more conspicuous than it actually appears in the one naturally adopted.

Of even greater interest, however, are those cases in which this effect is arrived at by means of special adaptive orientation. Many moths, like the Geometrid *Hybernia leucophæaria*, have the disruptive elements in the pattern so disposed that when the wings are in the resting attitude, the dark shadow-markings run across at right angles to the body. When seen against a background of bark such an insect would appear more conspicuous if it were to rest with its body vertical, than if it turned round so as to bring its body at right angles to the axis of the tree-trunk. Hamm (227) made the interesting observation, since confirmed by many other naturalists, that with the Spring Usher (*Hybernia leucophæria*), the Engrailed (*Tephrosia biundularia*) and the Brindled

Pug (*Eupithecia abbreviata*) the majority of individuals do habitually come to rest in the latter position, thus bringing their horizontal wing-markings into alignment with vertical cracks and shadows of the bark.

A striking example of the principle has recently been described from New Zealand by Cornes (106), who observed that the moth *Venusia verriculata* habitually adopts an attitude which brings the parallel brown markings on its wings into alignment with the parallel veins of the dead monocotyledonous leaves of a palm lily (*Cordyline australis*) on which it conceals itself by day. A remarkable photograph published by Nicholson (440) of the Geometrid *Syneora silicaria*, from Australia, beautifully illustrates the same device—while good British examples are furnished by *Eucosmia certata* (Plate 32), and *Boarmia gemmaria* (Plate 33).

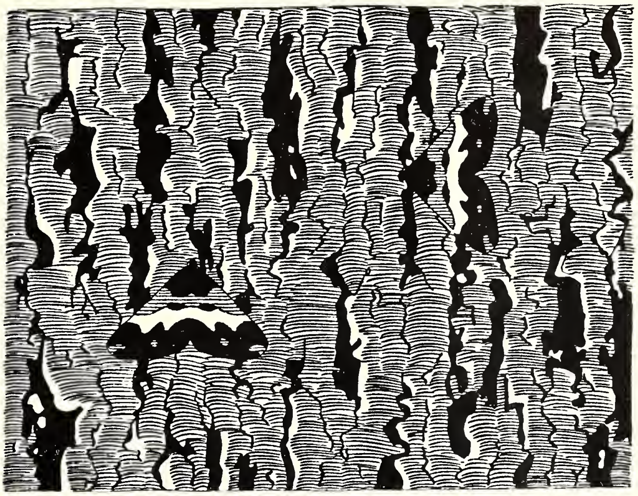

FIG. 42.—Diagram illustrating the relation between visibility and conformity of patterns to surroundings, in a moth with a transverse wing-pattern

The habit reaches its climax among birds like the Nightjars, Frogmouths, and Bitterns. For example, the reed-haunting European Bittern has the buff-coloured throat and breast feathers streaked vertically with dark patches in such a way that when the bird assumes the well-known cryptic attitude—with the breast directed towards the intruder, the back stretched and the beak pointing upwards—the dark streaks wonderfully simulate dark interstices between the reeds, while the latter are represented by the buff ground colour.

This bringing of the pattern into correlation with the surroundings is most interesting—not least so because we see in it an extension of the principle of coincident disruptive coloration.

In the latter, *the pattern is so correlated with the attitude of rest as to exhibit a design coincident across adjacent surfaces of the body*—thus distracting attention from their contours and masking the divisions between them.

In the present phenomena, *the habits are so correlated with the pattern as to present a design consistent with the adjacent environment*—thus obscuring the contour of the body and its connexion with the surroundings.

An extreme development of this principle is seen in animals which go a step farther, and prepare a background to resemble themselves (see p. 355); and in forms like the spider *Ariamnes gracillima*, which carries its cocoon in such a way that spider and cocoon together resemble a thin straight stick (p. 356).

6. CONCEALMENT OF THE SHADOW

> You will find that many objects of no essential interest in themselves . . . may yet become of singular value in consequence of the fantastic shapes of their shadows ; for it happens often, in distant effect, that the shadow is by much a more important element than the substance.
>
> RUSKIN

Hitherto I have attempted to show how colour and tone, light and shade, form and contour—by whose virtue alone any object appears to stand out from surrounding objects, so that it may be seen and recognized—have been modified, subdued, or obliterated in different animals, so as to produce a deceptive appearance, leading to concealment. It will be remembered that the extinction, or effacement, is brought about by suppressing differences of colour, by subduing differences of shade, and by superimposing more or less strongly differentiated patterns and substituting false for real relief. Nature employs the same fundamental principles upon which every artist depends for expression when painting, though since her aim is to *conceal* rather than to *reveal*, to hide her works rather than to exhibit them, the same principles are used with opposite effect.

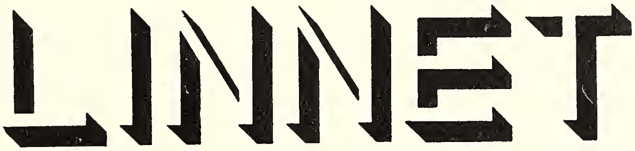

FIG. 43.—An example of shadow-lettering

Now supposing we were to ask an artist to represent in a monochrome painting some object, while denying him the use of the very devices—of tone differentiation, relief in light and shade, and expression of form in contour and perspective—upon which his technique depends, he would still be left with one last means of suggesting the thing which he could no longer figure : he could paint its *shadow*. That indeed is the technique employed in certain kinds of lettering frequently used for advertising purposes (Fig. 43). Such type represents, not letters, but the shadows cast on a flat surface by solid letters which are themselves the colour of the background and hence invisible : nevertheless they are easily legible.

In the patchwork configurations which the eye sees in nature, shadows take a prominent place, just as they form an important element in the composition of most painted landscapes, and in the details of aerial photographs. Under conditions of intense illumination, and especially in sunlight, the shadows which are cast by different objects may be both conspicuous in tone and characteristic in form. Indeed, *in the case of cryptic animals, the shadow will in general be more conspicuous than the animal which casts it.* The same, of course, applies to camouflaged buildings whose shadows will often be glaringly conspicuous when special steps have not been taken to obliterate them.

It must be realized that none of the concealing devices which we have yet considered can help in the least towards eliminating these tell-tale dark patches which accompany different animals when in motion and display them when at rest. But the need for concealment is pressing, and nature is versatile and ingenious in her methods. Even this difficulty she contrives to overcome, and we shall now consider briefly how that tenacious and unwelcome companion, the shadow, can be hidden or extinguished.

The character of a cast shadow depends, among other factors, upon the nature of the surface upon which it happens to fall. If spread upon a smooth surface (for instance, on flat sand, or bare ground, or a wall) its form will be preserved regular and typical: if thrown upon an uneven surface (as of broken ground, or bark) its continuity of outline will be more or less destroyed: if cast over numerous irregular surfaces lying at various angles and at different levels (as happens among grass, or ground vegetation, or in foliage) it will be much diffused by the scattered surfaces upon which it falls and also veiled by an intervening screen of high-lights reflected from surrounding objects.

As a result, it is animals such as various lizards and birds, moths and butterflies—which habitually rest on the freely exposed and relatively flat surfaces of rocks, walls, tree-trunks, and bare ground—whose shadows tend to be a source of danger to them. And since these shadows are normally best seen *from the air* whence a vertical or ' bird's-eye view ' may be obtained, it is especially against those keen-sighted aerial enemies, the birds, that shadow-elimination becomes a vital need in nature—a need which is met by many interesting devices, some depending upon modifications of structure and some upon modifications of posture and instinct; a need, moreover, which has its counterpart in modern warfare and which has led to the scientific development of shadow-eliminating devices as a means of deceiving that more recent, more swift, and more deadly bird of prey, whose acute eye is the camera, but whose weapon of destruction finds no counterpart in the lower orders of creation.

I. SHADOW CAMOUFLAGE IN ANIMALS OF COMPRESSED FORM

It is well known that many butterflies which habitually rest with wings closed over the back, orientate the body on alighting in relation to the sun, so that the shadow cast by the wings is reduced to a mere inconspicuous line. The significance of this heliotropic habit lies in the fact that in any other position the wings will cast on the ground a shadow which in the case of highly cryptic species must be far more apparent than is the insect itself. The habit has been observed in the case of *Melanitis ismene*, in Ceylon, and has been especially studied by Longstaff (352, 353), who describes heliotropism in the Indian *Pararge shakra*, and in different British Satyrids. In Africa the same thing has been recorded by Swynnerton (610), occasionally in *Acræa* and *Amauris*, and habitually in all the species of *Charaxes* which he observed. Swynnerton has also drawn attention to a second cryptic effect of this habit, which in addition to reducing the shadow to a minimum, at the same time causes shadows of the nervures on the wing membrane itself to break up and obscure the colour of the wing, which in any other position, in sunlight, must appear either as a brightly lit surface or as a conspicuously dark silhouette.

As a parallel example from an entirely different group of animals, it is very interesting to note that what appears to be adaptive behaviour of almost the same kind has been recorded of certain ground-nesting Nightjars. Thus Fairbairn observed a female Standard-wing Nightjar (*Macrodipteryx longipennis*) in Nigeria sitting on her nest one evening 'facing the sun setting in the West. On the following morning the same bird was again facing the sun rising in the East . . .' (18). Similar observations have been made on the European species (*Caprimulgus europæus europæus*). Before one can say how general is the habit of heliotropism in these birds, further observations are greatly needed, not only at the nest, but at other times when at rest on the ground.

But to return to the concealing devices of butterflies: in different Satyrine species a similar concealing result in relation to enemies looking down from above is effected by the remarkable habit of tilting the body over to one side in a more or less pronounced 'list'. The angle of tilt varies with different species. In the British *Epinephele ianira* it is 15°–30°; in *E. hyperanthus*, 20°; in *Pararge egeria* and *P. megæra*, 25°; in *Satyrus semele*, 40° or even 50° (352). Longstaff observed the same habit, in increasing degree, in the Indian *Mycalesis indistans*, slight; *Hipparchia parisatis*, 20°–30°; *Aulocera swaha*, 45°–50°. One individual which he watched made three efforts, getting farther over each time.

It must not be imagined that these instinctive habits are casual reactions, without reference to sunlight or to enemies. Observations indicate that orientation and inclination are directly related to the need for concealment. The 'list' may be either to the left or right in the same individual (352). From observations on English Satyrids, Longstaff satisfied himself that the attitude was more often adopted in sunshine than in shade. And there is evidence to show that heliotropism occurs, at any rate in species of *Charaxes*, especially when the butterflies are approached (610). Thus, for instance, when Swynnerton made a slash towards a *Charaxes neanthes* which was feeding on the ground, it at once heliotroped by a 'quick little movement'. In such cases, then, we have a definite cryptic attitude especially resorted to in times of danger, and thus comparable to the specially adopted cryptic postures of other animals—as seen, for instance, in the Stone-Curlew, Bittern, and Frogmouth.

Perhaps the greatest adept at wing-tilting is the British Green Hairstreak Butterfly (*Thecla rubi*), which has been observed by Poulton to let itself down so completely on one side that it appeared to lie flat on the leaf where it settled (506). The effect of this habit is for the wings (more or less) *to cover and screen the shadow which they cast.* In fact, we have in these extreme cases a class of behaviour leading on to the second class of cases, which we shall now consider, and which refer to animals whose form is naturally, rather than by habit, depressed —that is, flattened in a horizontal plane.

II. SHADOW CAMOUFLAGE IN ANIMALS OF DEPRESSED FORM

Different dorso-ventrally flattened animals get over the difficulty by instinctively crouching low, with the body or wings closely adpressed to the surface on which they rest, so that their shadow is entirely covered over by the cryptic body-surfaces. A beautiful example of this is seen in the Hawk-moth *Xanthopan m. morgani* photographed by the writer in its natural resting attitude on a Casuarina trunk, Beira. Many unrelated moths adopt this habit. In the case of ground-alighting species it has been observed by Longstaff (352), who found that *Hamanumida dædalus* rests on the banks of the Zambesi with the wings outspread and closely applied to the mud. With somewhat different significance the same thing is effected by excrement-like moths, such as species of *Stenoma* in Guiana, which Hingston records as resting with the wings widely expanded and pressed down close against the surface of leaves (265).

In certain Racing Crabs, such as *Ocypoda ceratophthalma*, whose habits I have observed in Portuguese East Africa (109), the same end is attained in a different way. Being expert burrowers and mainly nocturnal in their habits, these remarkable inhabitants of tropical shores usually seek safety from an enemy by retreating into their burrows, or, when hard pressed, by dashing to the breakers for shelter. But if a specimen be surprised far away both from the surf and from its dug-out refuge, so that retreat is impossible, it avoids capture by the skilful way in which it uses its speed in dodging and redoubling on its tracks, just as a hunted hare will do. Having outrun or outwitted its pursuer, it suddenly stops dead in its flight, and proceeds at once with the utmost haste to bury itself in the sand. Many times at Beira I released a captive crab on the beach, where there was no cover, in order to watch the clever way in which it would rush off at top speed for a short distance, and then suddenly begin with vigorous oscillating movements to scoop out a hollow, where it would appear to melt into the sand. Sometimes, indeed, a crab would disappear entirely from view, the eyes only remaining above the surface. But frequently the creature does not even trouble to cover itself with sand, but merely squats down in a footprint or some other hollow. Crouching thus, its cryptic coloration renders it almost impossible to detect at a few yards' distance, and the crabs instinctively rely upon escaping detection in this way. Alcock (2) mentions this habit as practised by the same species at Cardamum, in the Laccadive group, where he observed that the crab ' simply crouches in a rudely-scooped hollow, and there lies perfectly still, looking like a stone partly embedded in the sand '.

Now when these crabs are abroad, they carry themselves high off the ground on their long legs. Seen thus, whether in sunlight or, more especially, by the light of the moon, one realizes that they have been aptly named ' Ghost Crabs ' —for while the creatures themselves are scarcely visible on account of their close resemblance in colour to that of the sand, their shadows, scurrying swiftly and silently hither and thither across the beach before the intruder's path, are conspicuous enough and seem to be cast by no material object. It will be clear to any one who has observed the Racers in nature that their trick of instinctively seeking out a hollow in which to hide, or of rushing away from their enemy to excavate a squatting-hole, is an effective means of concealment—but concealment not so much of the crab, as of its conspicuous shadow.

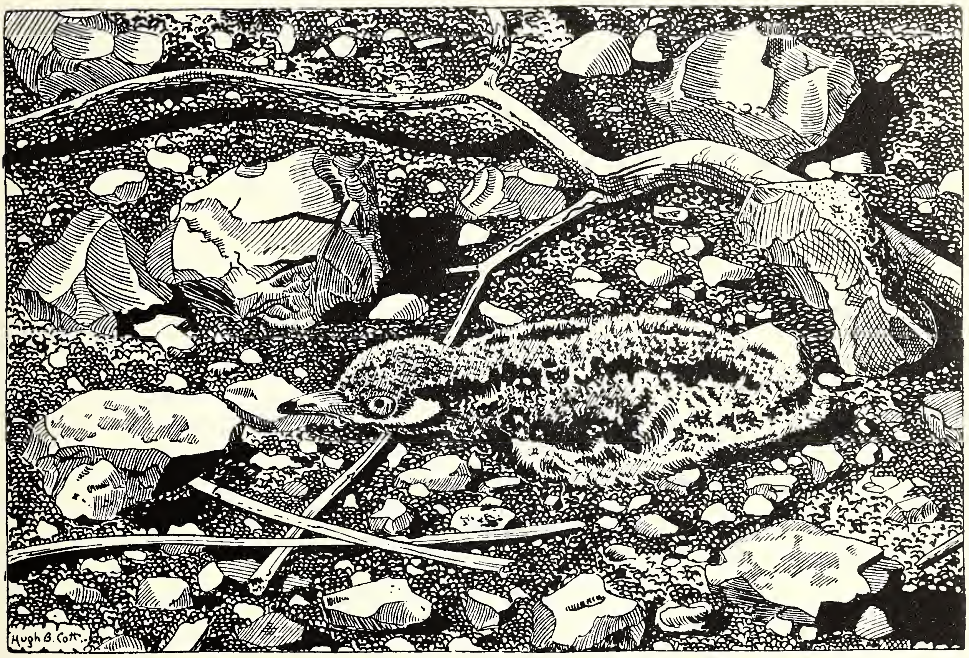

FIG. 44.—Squatting attitude of young Stone-Curlew

The above habits, which constitute the Racing Crab's second line of defence, are closely comparable to the well-known crouching attitude assumed by the young of many birds such as the Oyster-Catcher and Ringed Plover. The habit reaches its highest development in the Stone-Curlew (*Burhinus œdicnemus œdicnemus*) : when alarmed, the young, and even the adult birds, squat flat and motionless on their barren flint-strewn territory, with the neck outstretched along the ground and the chin and throat pressed downwards. In this attitude only the cryptic upper surface is visible, while the shadow is rendered relatively insignificant.

Even among mammals, similar tactics are sometimes adopted. Selous (562) states that the smaller African antelopes, Steinbucks, Duikers, Oribis, and Reedbucks, will, while keeping their eyes fixed on the unfamiliar object, crouch slowly down, and then, with their necks stretched along the ground, lie waiting. And Vaughan Kirby writes : ' A particularly fine bushbuck had evidently been walking along the bank, or perhaps drinking at the river, as I came along, and had seen me, and at once lain down close to the bank, amongst the stones, with his head stretched out along the ground, and his horns consequently pressed flat back upon his neck. Crouching thus amongst the dark stones, the tops of which were rounded, and just about the height of his back as he lay down, his colour—

FIG. 45.—*Uroplates fimbriatus*. Above : Lateral view of the head, showing the mandibular frill. Below : The tail, from above, showing lateral expansions

darkened by the rain which was falling heavily—so exactly assimilated with that of the grey rocks around that he was practically secure from detection (311).

A similar effect is produced by different lizards of depressed form, like members of the genera *Phrynosoma*, *Proctotretus*, and *Zonurus*, which crouch flat on the ground and expand the body sideways, as though attempting to spread themselves out over the surroundings which they more or less closely resemble in appearance. Still more remarkable is the case of certain specialized tree-dwelling Geckos, where the squatting habit is greatly enhanced by structural modifications of the body (Fig. 45). *Ptychozoon kuhli*, the so-called 'flying gecko' of Malaya, whose coloration gives the animal a remarkable resemblance to lichen-covered bark, possesses a wide projecting flap of skin on each side of the body, and lateral lappet-like outgrowths on the tail. These processes have sometimes been regarded as planes adapted for parachuting; but observations in the field led Annandale to conclude that their main function is undoubtedly cryptic (8). Annandale also found that *Hemidactylus platyurus* is certainly less conspicuous on a stone wall when its lateral folds were spread out, as was usual, on each side. Various other geckos possess caudal flaps, narrow in the West Indian *Aristelliger* and very wide in the Australian *Phyllurus*. Each of these forms wears a disruptive pattern well harmonizing with bark, and the dermal expansions, besides camouflaging the animals' general appearance, act as screens obliterating the shadow cast by the tail (see Fig. 46). The wonderful cryptic effect is well seen in the photograph (Plate 42) of *Uroplates fimbriatus*, taken from a specimen exhibited in the Reptile Gallery of the British Museum (Natural History).

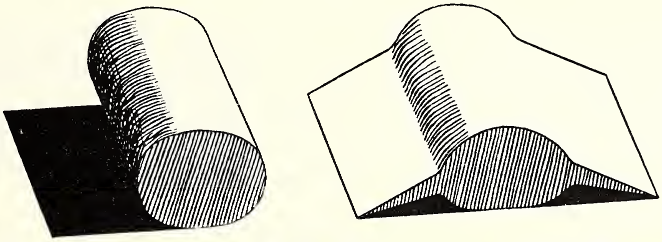

FIG. 46.—Diagrams illustrating the use of the tail-flange for shadow elimination

Besides bringing about a reduction or elimination of shadow, the close application of the body to the substratum—enhanced, as we have seen, in some forms by lateral outgrowths of the body—tends to fill up and obliterate the space between the animal and the surface which it resembles, so that it seems *to form part of, and be continuous with, its surroundings.* This is an important principle which undoubtedly accounts for the remarkable perfection in the resemblance of different cryptic moths and lizards.

It is most instructive to observe that this is precisely the arrangement applied in the German method of camouflaging roads with overhead screens, made to imitate from above the real road surface which they cover—shadows being prevented by the use of gently sloping side-screens simulating parts of the adjacent fields and other local incidents.

Besides reducing cast shadow, the low, flattened attitudes which we have described help to obliterate tell-tale variations of light and shade as seen from above. In other words, these devices tend to flatten out modelling and relief. All this is in accordance with the science of applied camouflage. ' Keep everything low ' was one of the camouflage instructions found on a German prisoner during the War (581). This is important advice, for lower structures cast shorter shadows, and more gradual slopes tend to neutralize variations of tone due to surface relief.

Many years ago Poulton pointed out that certain twig-like Geometrid larvæ, such as those of the Early Thorn Moth (*Selenia bilunaria*) and Brimstone Moth (*Rumia cratægata*), *appear to grow out of the branch in a natural manner*: this effect is due to a number of fleshy tubercles which partially fill up the furrow where the hind part of the caterpillar makes contact with the cylindrical twig, and which, being light in colour, also tend to neutralize the shadow which might otherwise betray the junction (496). The principle involved is illustrated diagrammatically in Fig. 47.

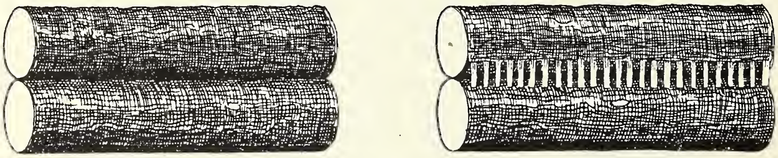

FIG. 47.—Diagram illustrating the use of an interrupted fringe for shadow elimination

Now in contrast to such Geometrid larvæ, certain bark-like Catocalid and Thyatirid larvæ habitually lie flat with the whole length of the body closely applied against twigs: such caterpillars also have the tell-tale furrow partially filled and the shadow neutralized—by a row of fleshy flaps, as in the Red Underwing (*Catocala nupta*); or by rows of hairs, as in the December Moth (*Pœcilocampa populi*): and Poulton has drawn attention to the significant fact that the structures are in each case distributed along the furrow that might otherwise lead to detection—that is to say, along the whole length of larvæ which apply their whole length to the twig, but confined to the short posterior line of contact in those which stand out at an angle from the twig.

On a larger scale a similar effect has been achieved by a number of arboreal and deserticolous lizards of depressed form. *Amphibolurus barbatus*, the Bearded Lizard of Australia, has its flanks bordered with whitish tapering scales, which project laterally and doubtless act like a curtain to neutralize shadow beneath the flanks. *Phrynosoma cornutum*, another desert-dwelling lizard from North America, has a fringe of light-coloured scales similarly placed. The arboreal gecko *Hemidactylus richardsoni*, a highly cryptic inhabitant of tree-trunks in the Ituri forest, has the tail laterally fringed. Among fishes a beautiful example is seen in the lip-fringes of species like the Electric Star-gazer, whose habits are referred to in another place.

In the previous account of disruptive patterns, we saw that a certain class of patterns which coincide or run across from one part of the body to another—for instance, from the back to the leg, as in many grasshoppers and frogs—have an important concealing function in that they optically join up elements which are morphologically separate. Now the same result is sometimes effected by the development of flanges or fringes of the type which we have here been considering, and which serve to unite different parts of the body and to obliterate the intervening spaces.

A beautiful example is afforded by the remarkable stone-like grasshopper *Eremocharis insignis*, from Algeria, which is figured on Plate 44. Very stout and short in form, this little Acridian is uniformly coloured a light sandy-buff, even to the eyes, in perfect harmony with barren stony surroundings. Dead specimens deepen to a chocolate brown, and as so often happens in the cabinet, the animal then loses much of the significant appearance which it possesses in life. Through the kindness of Mr. L. C. Bushby, of the Zoological Society of London, I have had the opportunity of keeping this species in captivity. When alarmed it remains motionless, and unlike active leaping species, makes no attempt to escape, but relies simply on its cryptic appearance. At such times, it immediately drops its antennæ, like the lowering of a signal, so that these come to rest curved flat against the face, in which position they are quite inconspicuous. Meanwhile the large hind legs are habitually tucked closely in against the body—an attitude reminding one somewhat of the resting posture of a tree-frog. In this position the femora fit accurately against the sides of the abdomen—each being furnished with a wide dorsal and ventral flange-like chitinous expansion, the upper one terminating in a fringe of hairs which serves most effectively to screen the crack between ' femur ' and body, the lower one forming a shield behind which the remaining segments of the limb are folded neatly out of sight. As a result, the leg no longer betrays itself—it becomes part and parcel of the weathered rock fragment for which the animal so well passes. Here, then, we have the same type of apparatus employed in a somewhat different manner: in the earlier cases the modified extensions of the body serve to unite the animal to its surroundings; in the present instance they appear to unite different parts of the body.

These flanges and fringes and flaps—all of which tend to deceive enemies by blending and uniting the edges of cryptic objects with the surrounding surfaces which they so closely resemble—have a parallel in modern warfare, and find their analogous application in the projecting overhead diffusion screens, whose function is to defeat aerial photography and reconnaissance by the obliteration of the shadows cast by objects whose nature and whereabouts it is important to conceal from the enemy.

III. IMITATION SHADOWS SUGGESTED BY DISRUPTIVE PATTERNS

When dealing with the appearance of projection due to light and shade, we have already seen that deceptive visual effects may be achieved by two diametrically opposite methods: the one—obliteration of real relief by counter-shading; the other—simulation of false relief by constructive shading. So, too, with shadows, as with shade, two antagonistic principles are involved. For while actual shadows may be effaced, spurious ones may be suggested. And this dual method of optical illusion is commonly seen at work in the coloration of animals. For it frequently happens that the dark elements in disruptive patterns themselves strongly resemble shadows cast by stones or foliage, or the dark interstices between masses of bark, or vegetation.

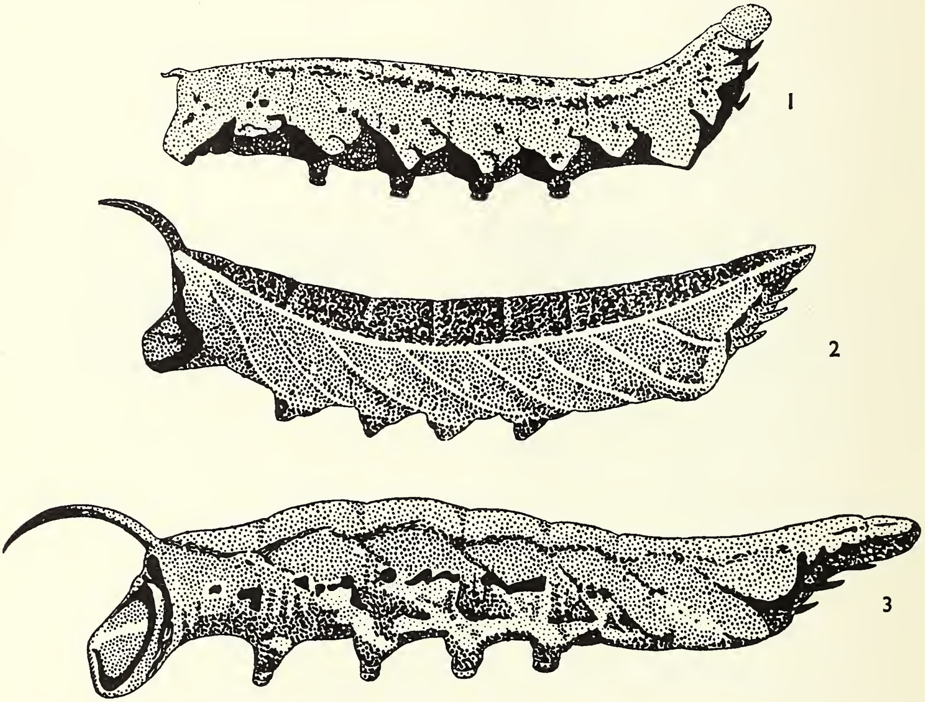

FIG. 48.—Shade- and shadow-patterns in South American Sphingid larvæ: 1 *Enyo j. japix* 5th instar; 2 *Epistor gorgon*, final instar; 3 *Epistor cavifer*, final instar. (*After A. Miles Moss*)

The shapes of such shadow-markings are of course out of all relation to the shape of the animal which displays them, though often enough typical of shadows in the animal's environment; and they tend, therefore, greatly to strengthen the deceptive appearance which the pattern creates. The principles of maximum disruptive contrast combined with pictorial relief frequently lead to imitation shadow effects, as when the light edge of a leaf is seen outlined against the deep shadow which it casts. Many birds, snakes, lizards, frogs, moths and other animals illustrated in this book bring out the point better than any written description can do. A beautiful example is seen in the Quail (*Coturnix coturnix*), where yellowish-white streaks on the back and sides are accentuated by adjacent blackish markings, which recall to the eye the appearance of dry grasses and grass-shadows.

Such dummy shadows are ordinarily quite general in form; but in certain cases they are highly specialized and represent the shadow cast by particular objects. To cite but one example: the dark diagonal lines on the sides of many Sphingid larvæ, like those of Privet and Eyed Hawk-moths, closely imitate in their form, arrangement and colour, the shadows cast by lateral leaf-veins, which are themselves represented in relief (as though illuminated from the side) by the adjacent light lines (Fig. 48).

THE FUNCTION OF CONCEALING COLORATION IN NATURE

7. CONCEALMENT IN DEFENCE, MAINLY AS ILLUSTRATED BY BIRDS

> Nay more, the very birds of the air, those that be not hawks, are both so many and so useful and pleasant to mankind, that I must not let them pass without some observations.
>
> IZAAK WALTON

IN the foregoing pages I have attempted to give a clear account of the principles upon which concealment depends, and to describe the various devices—embracing modifications of structure, colour, pattern, and habit—by which cryptic appearance has been achieved in animals belonging to widely different groups and inhabiting widely different environments. So far, then, we have been concerned with the *nature of concealing coloration*: we have dealt with facts—with appearances and optical affects—and of these it has been possible to speak with a degree of certainty. For that these devices do in actual fact make for concealment can be doubted by no one who will take the trouble to appreciate the optical principles involved, and to study the animals in the field.

But now we must pass on to consider a different aspect of the problem, namely, the *function of concealing coloration.* Here we are no longer merely dealing with appearances *per se,* but with their value to the organism in which they are exhibited. This functional or ecological aspect of concealment opens up many questions which cannot always be answered with certainty.

There is still no general agreement among biologists as regards the function and effectiveness of these contrivances. What we have to consider is this: Are cryptic colours and resemblances *adaptive*? Do they confer upon the species concerned a chance of survival which it would not otherwise possess? Or, alternatively, must we regard them as in a sense accidental, with no more vital significance to their possessors than the tints of autumn foliage to the trees which they beautify? In short, has concealing coloration been evolved as an end in the struggle for existence, or is it merely a meaningless by-product of secondary significance?

The attempt to answer these questions is met by many difficulties. Sometimes the evidence is inaccessible: often it is inadequate: sometimes it appears conflicting; or the same evidence may be used to support diametrically opposite views. Much further accurate information is yet required on the relations between predatory animals and their prey. Of the former, we need to know in each case the times at which a species feeds; its method of finding and capturing prey; the part played by vision in hunting—including a knowledge of the animal's visual acuity, colour sense, nocturnal vision and other aspects of visual perception; the amount and nature of the food eaten, compared with that which is available; its food-preferences and the relative edibility of prey; its power of discrimination, and memory. Conversely, of the prey we desire information as to the times of feeding and resting; the attitudes and habits when at rest, and when alarmed; its relative conspicuousness throughout the normal range of habitat; its potential enemies and its actual enemies. There are very few species, whether of hunter or hunted, for which adequate information on these points is available. For example, so far as I am aware, for no single wild species of predator have we a statistical comparison of the food *eaten* with that *available* in a state of nature. Is it then any wonder that the storms of controversy rage so furiously round the concealment problem? What we want at present are not more theories, but new facts and fresh evidence.

Of all living creatures, birds are the most restless, the most active, and the most mobile. Their high degree of specialization for flight, and their vigorous metabolism, give them a degree of freedom enjoyed by no other animals; their food requirements and their breeding habits lead them before many a background and through many an environment. Considered as a class, no other group can compare with them in the daily range of their movements; no other group can compete with them in the seasonal range of their migrations. For this reason, if for no other, few birds—whatever their coloration—can be expected to harmonize cryptically with surroundings which vary constantly and widely, from moment to moment and from month to month. The most that can be achieved under such circumstances is a compromising or average uniform, an unspecialized colour-scheme of general utility, which in the changing scenes of life may be now better, and now worse, but rarely perfect as a concealing dress. In this respect birds differ from other groups, such, for instance, as fishes, many of which live the great part of their days in a tolerably uniform and restricted environment, and are presented to enemies or to prey against a constant background—whether of clear surface waters, of gravelly bottom, of tropical reef organisms, or of sea weeds or river weeds; and as a result, for such forms more perfect colour-harmony, more effective colour-adjustment and more specialized cryptic resemblances are both possible in theory and found in nature.

Indeed, in general it is true to say that the most perfect examples of concealing coloration can only, and do only, occur where an animal is confined, at any rate for a particular stage in its life-history, to a special and restricted type of surroundings—as also happens, for instance, with different toads, tree snakes, tree geckos, and chamæleons, and many desert-dwelling vertebrates, which more or less exactly simulate their natural environment of fallen leaves, trailing lianas, lichen-covered bark, fresh foliage, or sandy wastes. And what is true of such vertebrates is more especially applicable to innumerable procryptic invertebrates —crustaceans, spiders, and insects, which in group after group, and stage by stage in their life-histories, resemble more or less accurately some part of their food-plant or normal resting-place, as happens, for example, with different grasshoppers, bugs, weevils, caterpillars, moths, and mantids.

Even among birds there are some—desert forms like different Larks, Nightjars, and Bustards, shore-dwellers like the Turnstone and Purple Sandpiper, and reed- or bough-haunting species like Bitterns and Wrynecks, whose habits restrict them more or less closely to a definite environment, and whose appearance in the field presents a highly effective cryptic colour-scheme.

I. CONCEALMENT CONSIDERED IN REFERENCE TO OTHER MEANS OF PROTECTION

But apart from the above considerations, it is very obvious that both sexes of many, and the males of most species of birds, are not coloured so as to be inconspicuous at all, in any normal surroundings, while few classes of animals appear to comprise such a large proportion of species which are positively conspicuous—as are many Gulls and Gannets, Razorbills and Hornbills, Tanagers, Titmice, Spotted Woodpeckers, Ravens, Magpies, Crows, Starlings, and a host of others. How then are we to reconcile that large numbers of birds are conspicuous with the view which would stress the vital importance of inconspicuousness in nature ?

(1) **Cryptic Coloration needed more especially by Certain Species**—Now a little investigation of the habits and inter-relations of birds clearly shows that many species are—for various reasons—relatively free from the danger of attack by predatory species : they are protected in other ways, so that concealment becomes unnecessary. Moreover, it is evident, as will be seen presently, that it is in such species concealing coloration tends to be absent, while it is most highly developed in those which are otherwise unprotected and hence relatively liable to attack.

In order to make this point clear, I must first mention briefly the compensating factors which, whether operating singly or in combination, tend to discourage predators and to eliminate attack. The subject has been discussed by Beebe (35) in relation to the birds of British Guiana, and from a somewhat different aspect by Mottram (425) in a stimulating paper on secondary sexual dimorphism in birds generally. In the first place, large birds of prey, like Eagles, Falcons, Harriers, Kites, and Buzzards, as well as certain oceanic wanderers, like the Albatross, have no natural predaceous enemies. With others, such as Swans, Pelicans, and Gannets, large size and fighting strength normally confer a like degree of immunity from attack. Powerfully armed birds such as Macaws, Cockatoos, Ostriches, and Ravens are protected by their terribly effective beaks and legs ; Terns and Skuas by sheer pugnacity of disposition ; Hornbills, Vultures, and Drongos by evil odour and inedibility. With others, such as Jays, Herons, King Crows, and Orioles, fighting ability provides a relatively effective deterrent, especially since birds of prey are generally more ready to swoop down and carry off injured or sitting birds, or callow young, where no resistance is possible, than to attack where there is the risk of counter-attack. Thus Beebe observed a single female Spur-wing Jaçana successfully standing off repeated darts by a small falcon. Sometimes the colony, rather than the individual, is the potential fighting unit. This applies especially to forms such as Rooks, Terns, Cassiques, and Cormorants, which are gregarious roosters or gregarious nesters, and which for purposes of defence have evolved a system of collective security. At a strong Cormorant rookery on the Megstone rock, in the Farne Island group, I have watched numerous marauding Lesser Black-backed Gulls awaiting their opportunity to steal eggs or young, but yet unwilling to attempt a robbery in the face of opposition by brooding parents. But immediately a passing boat or landing-party disturbed the latter, the gulls would at once slip in to enjoy a feast at the unguarded clutches.

But most important, because of its most general and extensive use among birds, is the power to evade attack—either by diving, by bolting to cover, or by speed. The first method is practised by many Ducks, Grebes, Divers, Cormorants, Guillemots, Puffins, and Razorbills, and gives them a ready means of avoiding terrestrial or aerial enemies. Others, including many aquatic, woodland, and forest birds, such as Coots, Rails, Woodpeckers, Wrens, Tanagers, and Humming-birds, escape by running and by flight into or through cover: this method is especially applicable to forest birds, when the environment naturally favours escape and hinders pursuit. Finally, different species are effectively defended by aerial habits, combined with speed and agility. There is no doubt that many birds—such as Kingfishers, Curlews, Cassiques, Swallows, Swifts, Oyster-Catchers, Terns, and Petrels—like many butterflies, make unsatisfactory quarry on this account: they are so active and skilful in flight that they are not worth the trouble of hunting. Major R. E. Cheesman observed a combined attack on a Hoopoe (*Upupa epops epops*) by a Peregrine Falcon (*Falco peregrinus*) and a Pallid Harrier (*Circus macrurus*): ‘ By skilful turns in the air the Hoopoe evaded the strokes of the Peregrine from above, and the Harrier striking upwards from below. The battle continued for two or three minutes until the two Hawks were exhausted and left the Hoopoe in peace. I do not intend to imply that Hoopoes never fall victims to Hawks, but it was a case where no protective colouring was needed ’ (94).

Conversely it is to species lacking these methods of avoiding enemies—forms, that is, of terrestrial or arboreal habits, of timid disposition, non-gregarious, non-carnivorous, unarmed, of small or moderate size, with palatable flesh, and with feeble powers of flight, and especially such as habitually nest on the ground and in the open—it is to birds such as these that concealment is vitally important, at any rate for the sex responsible for incubation, for it is species belonging to this class—which are well illustrated by the game birds and smaller waders, as well as by the eggs and young of species making open ground-nests—which are most subject to attack.

(2) **Cryptic Coloration needed more especially at Certain Times**—With birds generally, protection by escape, due to the use of cover or of speed,

is highly important, for it is effective, in at least some degree, in most species: the fact is, that so long as a bird otherwise unprotected is healthy, alert, active, and within reach of shelter, it has not much to fear from predation, and concealment ceases to be of primary importance *except during periods of stillness.* Conversely, it is, of course, true, as we have repeatedly asserted, that no degree of cryptic coloration can of itself avail when its possessor is in motion. Inconspicuousness is, and can only be, effective when combined with immobility; and this fact has sometimes been used as an argument against its general usefulness in active animals such as birds. But that is to put the cart before the horse—for the point at issue is *not merely that stillness is needed for effective concealment, but rather that concealment is needed for periods of enforced stillness.* Now in the life of a bird such critical periods are of two kinds, namely, the *daily periods of rest* and the *seasonal period of incubation.*

II. CONCEALMENT IN RELATION TO NOCTURNAL HABITS

In regard to the first, with the large majority of species the resting or roosting phase is passed under cover of darkness. But a few, notably the Owls, Frogmouths, Owl-Parrots, Nightjars, and Woodcock, whose crepuscular or nocturnal feeding-habits, or whose need of safety led them, like burglars and night-watchmen, to turn night into day, are obliged to spend the hours of daylight in a passive or resting state, when they will be peculiarly liable to attack. If concealment is really a vital biological necessity, then of all birds it is in such forms that we should expect to find it most highly developed. Now that is what we do typically find in the relatively few nocturnal birds, belonging to several different orders.

Taken as a whole, the Nightjars (*Caprimulgi*) present some of the most perfect examples of protective resemblance to be found anywhere in the animal kingdom for forms of their size, while for harmony of hue and delicacy of marking they must surely be numbered among the most beautiful of the feathered creation. And their quiet unobtrusive behaviour is in keeping with their cryptic appearance. These lovely creatures are variously dressed in subdued cryptic tones of russet, fawn, cinnamon or golden brown, and ashy greys, or neutral sandy tints, broken with darker bars, or finely freckled or pencilled with sad browns and black vermiculations, or spotted with bold touches of cream. Nightjars are among the closest sitters of all birds. Crouching low, and well-nigh invisible, on the ground, they will permit themselves almost to be trampled upon before suddenly rising up, to slip silently away on their easy, erratic flight. This I have repeatedly seen, both in the Minas Geraes highlands of Southern Brazil, and in low-lying sandy districts of the Zambesi valley. Whether one is riding or on foot the birds will hardly trouble to take themselves to safety, instinct rightly telling them they are safer in trusting to the marbled tones of their soft plumage; and in the field one rarely recognizes them until they rise up right in one's path, and for each bird thus accidentally forced to disclose its presence many must be passed by within sight, but never seen.

The effectiveness of their cryptic dress is, of course, known to every one acquainted with these birds in their native haunts, and it is perhaps especially marked in species inhabiting the stony or sandy wastes of desert places—that is, in an environment where the almost complete absence of natural cover has led to the most perfect adaptive coloration. For example, speaking of the extreme difficulty of detecting motionless desert animals of all kinds that exhibit the typical desert coloration, Buxton writes: 'The most remarkable example that ever came to my notice was in Baghdad, Mesopotamia, in September. There was a small patch of ground of perhaps an acre, walled off but not at that season cultivated. In it one could always be certain of finding at least a score of Egyptian Nightjars (*Caprimulgus ægyptius*), but though the ground was absolutely bare, and though I visited the place repeatedly, I never succeeded in detecting a Nightjar before it flew, and this in spite of the comparatively large size of the bird' (76).

With the related Frogmouths (Podargidæ), of the Oriental and Australian regions, the case is similar. Like the Nightjars, these strange birds are nocturnal or crepuscular in their feeding arrangements; but unlike them, they are more decidedly arboreal in their habits, haunting well-wooded districts, where they spend the day at rest on tree-stumps, logs or boughs, with which the mingled lichen-grey and browns combined with the upright carriage of their dusky freckled forms closely assimilate. Seated motionless in such surroundings, and in such an attitude as they adopt, the several species must be wonderfully hidden from the prying eyes of would-be disturbers of their peace. Saville-Kent has given us an interesting account of the habits of *Podargus* in Australia (555), from which I quote the following passage: 'This notable correspondence of the bird's plumage with its environment is habitually utilized by *Podargus* in a remarkable manner for the purpose of concealing itself from the observation of recognized enemies or possible assailants. Should for instance a hawk appear in sight or any other object of an apparently unfriendly aspect, this bird will at once straighten up stiffly and, with its mottled feathers closely pressed to its body, assume so perfect a resemblance to a portion of the branch upon which it is seated that, even at a short distance, it is almost impossible to recognize it. Under these conditions, in fact, it so readily escapes detection that several instances have been related to the writer in which people have actually placed their hand on the bird, when seated on a rail or log fence, before being conscious of its presence. Trusting in its wonderful mimicry of nature, it will thus remain stiff and motionless, and not attempt to fly away until forcibly removed.' It is noteworthy, and characteristic of such adaptations, that the cryptic attitude is instinctively adopted in times of danger; for instance, one bird was seen to assume its concealing pose at 'the well-nigh invisible presence' of a Wedge-tailed Eagle. The same writer found that the stick-like posture was always preceded by the utterance of a very characteristic alarm note, which is evidently the signal warning other birds in the vicinity to become invisible—for even by imitating this sound Saville-Kent was able at will to command the birds to 'stand to attention'. At such times the eyes were closed to the merest slits.

The same general relation between appearance and habits is seen in other and entirely unrelated nocturnal birds. Woodcock, whose diet of worms leads them to prefer darkness for feeding, are among the most perfectly cryptic of all woodland species. The Painted Snipe (*Rostratula benghalensis benghalensis*), a crepuscular feeder, is another wonderful example of cryptic coloration, of which the most striking element is the broad, dark-edged, buff scapular streak on each side of the back, which cannot fail to have a strong disruptive effect among the tangle of grass in the marshy surroundings chosen for a nesting-site.

Similarly the Owls, which constitute an important and cosmopolitan group of predators—mainly nocturnal—are in general well concealed by their coloration, which varies widely with different species in relation to districts of the most varied description—being white in Arctic snowlands, yellowish buff in deserts, deeper shades of brown and grey in forest areas. Sometimes, too, they adopt cryptic attitudes. Thus in the Arabian desert Cheesman (94) found that the Eagle-Owl (*Bubo bubo desertorum*) would squat flat to avoid danger. In the forest-dwelling Screech Owl (*Otus asio*) of North America, the defensive attitude is erect rather than prone: when startled, he makes himself tall and thin, 'raising the ear-tufts straight upward, closing the eyes to narrow diagonal slits, and drawing the feathers so close to the body that the usual fluffy bird is reduced to about one third its ordinary thickness' (619). Here, then, in two related birds, we have different reactions adapted to different environments, the one appropriate to a bird resting on the ground, the other to one perched in a tree.

A very interesting case is presented by the Owl-Parrot (*Stringops habroptilus*). Now confined to the North Island of New Zealand, these handsome ground parrots frequent open green mossy glades of the beech forests, where they crouch during the day among rocks or tree roots, in surroundings where their plumage of sap green, variegated with yellow and dark brown markings, cannot fail to render them most inconspicuous. Being flightless, their nocturnal habits are directly related to the need for concealment, for they are vegetable feeders, and like many cryptic Geometrid caterpillars, they wait for the friendly shades of darkness to hide their movements.

The Kiwi is a defenceless, flightless form, which, like the Owl-Parrot, seeks safety in a night life, and, like the Woodcock, is an eater of worms. However, unlike both, it lacks a cryptic costume—a fact doubtless related to its secretive habits, for it spends the day hiding in holes and burrows where it cannot be seen.

It thus appears that the birds whose nocturnal habits necessitate periods of inactivity in exposed situations during the daytime tend to be especially protected by their cryptic dress, which in certain groups reaches a high degree of specialization and perfection, and which is rendered particularly effectual by adaptive behaviour. We may mention here, in passing, that similar effects are found in other groups. With lizards, for instance, the most specialized night-feeders are the geckos, and among the whole class it is with members of the Gekkonidæ that we find the most remarkable cases of concealing coloration, as exemplified by bark-like, bark-haunting species such as *Aristelliger* in the West Indies, and *Ptychozoon* in the East Indies. And what is true of these nocturnal birds and lizards is true also of innumerable night-feeding insects, such as nocturnal caterpillars and moths, whose resemblance to twigs or bark, combined with instinctive immobility, protects them during the long periods of rest by day.

III. CONCEALMENT IN RELATION TO NESTING HABITS

The foregoing remarks refer to the daily times of rest. We have now to consider that other type of enforced quiescence, the seasonal period of incubation —that difficult, prolonged, critical time when a bird's life is at once most valuable and most vulnerable.

(1) **Colour of the Sexes in Relation to Nidification**—Taking a broad view of the birds of the world, if we consider the mode of nesting and the coloration of the sexes in those species which for various reasons are relatively most liable to attack by enemies, certain highly significant facts emerge. The main issues have been fully discussed by Darwin (136) and by Wallace (646), and I need here only refer briefly to the essential relevant points, which may be best summarized in Wallace's own words: 'When both sexes are brilliant or conspicuous, the nest is such as to conceal the sitting bird; but when the male is brightly coloured and the female sits exposed on the nest, she is always less brilliant and generally of quite sober and protective hues.'

We have here two important generalizations of great biological significance. (It must be understood that I am referring now only to the use of colour as a life-saving device, and not to its use in rivalry between males, or in courtship between the sexes.) In support of the first part of Wallace's statement, we find that *among otherwise unprotected species* belonging to several different orders and to many families, where the females (like the males) are gaily coloured and perform the nursery duties of incubation and care of young, these birds nest almost invariably where they will receive effective adventitious concealment. They have acquired the habit of making covered or domed nests, or of concealing them in holes in trees or in the ground. That is the case with Starlings, Titmice, Barbets, Trogons, Kingfishers, Cassiques, Puff-birds, Motmots, Toucans, Woodpeckers, Petrels, and others.

To take an example from a single kind of environment, the principle is well illustrated by the birds breeding in deserts, where, as pointed out by Cheesman (94), cryptic coloration is more fully developed in the females of ground-surface breeders, like Larks and Bustards, than in any others. In marked contrast to these, conspicuous forms, like the Bee-eaters (*Merops apiaster* and *M. persicus*), Rollers (*Coracias garrula* and *C. benghalensis*), and Kingfishers (*Alcedo ispida* and *Halcyon smyrnensis*), are all hole-breeders; the Wheatears (*Œnanthe deserti*) are well concealed, when nesting, in rock crannies, and at other times 'depend on their eyes and wings'; and the Raven (*Corvus corax ruficollis*) has no need of protective coloration and 'never desires concealment'.

The same general thesis is supported by special cases in which a species differs from its congeners both in regard to its appearance and habits, as, for instance, happens with the Sheld-duck, where the female resembles the male in being highly conspicuous and breeds deep in a rabbit burrow, in both of which respects she differs from most duck, which are cryptic in colour and nest in exposed places. An apparent exception is presented by the Oyster-Catcher—a species in which both sexes are highly conspicuous and which breeds quite in the open. But in this case the parent bird is a strong flyer and thus tolerably safe from attack (so that it hardly falls into the present category) : but what makes the case so interesting is that this handsome bird is very shy and alert at the nest, quickly slipping away when danger threatens, while in the whole range of British species there are very few in which both eggs and young are more perfectly concealed by their procryptic coloration. Thus it is that the exceptions which seem to break the rule are as significant as the examples which prove it.

Whether the colour has determined the mode of nesting—the conspicuous females being gradually forced to seek protection by building domed or concealed nests, as Darwin believed ; or whether, according to Wallace's view, the building of such nests in the first place has influenced, through the cessation of selection, the development of conspicuous plumage in the females, need not concern us here. Indeed, it is hardly necessary to regard these explanations as mutually exclusive, for both factors may well operate together, a gradual change in appearance both leading to, and resulting from, a gradual and correlated modification of nesting habits—just as the structure and colour of different flowers have evolved side by side with the form and habits of the insects adapted to pollinate them. In any case, the general fact remains that species which are otherwise unprotected and in which the females are conspicuous, nest where the sitting bird is concealed, and this correlation between appearance and habits is both inexplicable and meaningless except in terms of the need for protection from predatory enemies during the period of incubation.

Passing to Wallace's second generalization—we have here the complementary aspect of the subject, namely, a class of cases in which the nest is exposed, and incubation is by the female alone. Whether or not the males of such species are conspicuous, the females are typically inconspicuous or highly cryptic, as seen in the Reeve, Pheasants, Partridges, Ptarmigan, Grouse, Capercaillie, Quails, and most species of Duck. It is noteworthy that among British members of the last group, the only species in which the male habitually assists the female with her duties of incubation is the Sheld-duck, whose exceptional hole-breeding habits enable him to do so without endangering his own safety or that of the brood by attracting the attention of enemies by his conspicuous livery. The case is somewhat similar with many Terns and Gulls, and with certain Plovers such as the Lapwing, which habitually slip off the nest when danger threatens so that the whereabouts of the cryptic eggs or downy young may not be betrayed.

It is, moreover, a very remarkable fact that the very species which are best protected by their procryptic coloration are the very species which sit closest on the nest—as is the case, for instance, with Woodcock, Bustards, Nightjars, Short-eared Owls, and Skylarks. But this is a point which will be discussed in a later section referring to the general activity of birds and other animals when in danger.

In another class of cases, incubation on an open nest is shared by both sexes. When this happens, as with the Ringed, Kentish, Golden and Grey Plovers, Turnstone, Knot, Dunlin, Curlew, Sandpiper, Wood Sandpiper, Bar-tailed Godwit, and Nightjar, the upper parts of the male—that is, the parts exposed to view when he is on duty with the eggs—are either similar to, or not more conspicuous than, those of his mate. This, at any rate, is invariably the case with British species, and appears to be so in general with birds belonging to this category. I do not know of any relatively unprotected ground-nesting species in which the male, when notably more conspicuous than the female, habitually assists with incubation.

I must conclude this inadequate, broad treatment of the main facts by referring to the interesting, but comparatively rare, cases in which the females of certain species which nest in the open are more conspicuous than the males, a condition found, for instance, in the Dotterel (*Charadrius morinellus*), Painted Snipe (*Rostratula benghalensis benghalensis*), Grey Phalarope (*Phalaropus fulicarius*), Red-necked Phalarope (*P. lobatus*), Australian Tree-Creeper (*Climacteris erythropus*) and Cassowary (*Casuarius galeatus*), and Bustard-Quails (*Pedionomus torquatus*, *Turnix sylvatica*, etc.). Now in every one of these exceptional cases it is the male and not the female who alone performs the ' maternal ' duties of incubation and care of young.

All these facts are in perfect accord with the view that the correlation between appearance and nesting-habits in the incubating parent is adaptive, that is to say, an expression of the need for concealment during the time when its life is most vulnerable to its enemies and most vital to its own species—concealment which is effected, as we have seen, on the one hand adventitiously, by means of an invisible nesting-site, or on the other hand cryptically, by means of inconspicuous plumage.

(2) **Colour of the Eggs in Relation to Nidification**—Both on account of their edibility and defencelessness, the eggs of birds are especially desirable and liable to attack by numerous vertebrates that have acquired egg-eating propensities, such as Monitor lizards, various snakes (*Pituophis*, *Elaphe*, *Dasypeltis*), many birds, including Jays, Magpies, Hooded Crows, Rooks, Harriers, Greater and Lesser Black-backed Gulls, and mammals belonging to several orders, including Opossums, Foxes, Badgers, Stoats, Skunks, Mongooses, Hedgehogs, Rats and Squirrels.

Of course in many cases the eggs are not readily available to predators, either because the nest itself is inaccessible or concealed, or because the eggs are actively defended by the parent or by the colony. In such cases concealing coloration can be of little consequence. On the other hand, many eggs are not so protected. This applies especially to a large class of relatively defenceless species, such as Larks, Pipits, Snipe, Sandpipers, Dunlin, Dotterel, Redshank, Plovers, Quail, Sand-Grouse, Stone-Curlew, and many others which nest on the ground and in the open.

It is well known that the eggs of such species are coloured so that they harmonize, more or less closely, with the general colour of their surroundings, whether pasture or fallow, moor or marshland, sand or shingle; and that in the field they are often extraordinarily difficult to detect. Owing to the wide range of site selected by certain species, no very close correspondence is always to be expected. Nor do I for a moment suggest that there are not exceptions, especially among cliff-breeding species such as the Common Guillemot and Razorbill. But I refer here essentially to ground breeders, and particularly to such timid or wary species as are inclined, like the Lapwing, Curlew, Redshank, Oyster-Catcher, Stone Curlew, and certain Terns and Gulls, to quit the clutch early and slip quietly away on the approach of danger, as opposed to forms like the Woodcock, Nightjar, Partridge, Ptarmigan, Pheasant, and Eider Duck, which sit close, relying instinctively on the concealing effect of their own plumage.

Such eggs are typically coloured some shade of buff, greenish-olive, or yellowish-brown, variously broken with darker tones. But what I wish to emphasize here is the optical principle—and its practical application in the field—that while any shade of green or brown will tend to harmonize more or less in nature, what will never do so is any uniformly coloured regular symmetrical *form*, whatever its colour. The environmental background is always composed of irregular patches of colour—confused, variable, and inconstant in appearance. A symmetrical body like an egg, with its regular smooth curving outline, must inevitably stand out more or less conspicuously and attract attention *when seen against the intricate, strongly contrasted broken patchwork of light and dark tones* such as is presented by broken earth-texture and ground-vegetation. Hence the essential step leading to visual deception must be to break up that smooth surface, to destroy that rounded symmetrical form, to obliterate that regular contour—all of which clearly differentiate the egg from its surrounding background. Now, as a matter of fact this is precisely the effect produced by the heavy black or sepia or chocolate markings typically found on the eggs we are considering; and it is precisely these markings, and the *false appearance of broken light and shade, of separate reflecting surfaces and deep interstices* which they produce, which is of far greater consequence as a concealing factor than any optical effect of mere colour-harmony alone.

Sometimes, however, a deceptive, disruptive effect is nicely combined with close colour-resemblance to the environment. For instance, various species nesting normally among greenish ground vegetation have eggs with a decidedly greenish ground-tint—as is the case with the Curlew (*Numenius a. arquata*), Whimbrel (*N. p. phæopus*), Snipe (*Capella g. gallinago*), Ruff (*Philomachus pugnax*), and Dunlin (*Calidris alpina schinzii*). Perhaps the most perfect examples are to be found among birds which in their nesting haunts tend to restrict themselves to a particular environment. For instance, among British-breeding species are some—notably the Ringed Plover (*Charadrius h. hiaticula*), Little Tern (*Sterna a. albifrons*) and Oyster-Catcher (*Hæmatopus o. ostralegus*)—which generally breed on sandy shores or shingle beaches close to high-water mark. The eggs of the first are pale stone-buff, finely speckled with dark-brown; those of the second are similar in ground-colour, with deep-brown blotches and ashy shell-marks; those of the third are yellowish-grey or clay-coloured, spotted and streaked with blackish-brown and ash-grey. As a matter of fact, though they differ considerably in size and shape, the eggs of these three species bear a considerable resemblance in *coloration* both to one another and to their environment, while they differ from those of related species like the Golden Plover (*Charadrius a. apricarius*), Arctic Tern (*Sterna macrura*), and Turnstone (*Arenaria interpres interpres*), which usually lay darker-coloured, more heavily marked eggs in darker surroundings. Moreover, a fourth species, the Stone-Curlew (*Burhinus o. œdicnemus*), though quite unrelated to the first three, and normally nesting in a totally different environment away from the sea, likewise lays a buff-coloured egg in close harmony with the pale sandy surroundings which it chooses for a nesting-site. And in this respect the bird agrees closely with unrelated Asiatic desert breeders such as Pallas's Sand Grouse (*Syrrhaptes paradoxus*) and the Cream-coloured Courser (*Cursorius c. cursor*), both of which lay eggs matching the prevailing environmental colour-scheme.

Here then we have a number of unrelated birds laying similarly coloured eggs in two totally different but similarly coloured surroundings—a state of affairs which finds its parallel on a wider scale in the coloration on the one hand of other shore-dwelling animals such as the Racing Crab (*Ocypoda ceratophthalma*), and on the other hand of desert animals such as Jerboas and Jackals, Horned Vipers (Pl. 2), and Horned Toads. Furthermore, as we have already seen, the same principle is known to operate on a still broader basis, which includes different unrelated forms—such as the Swimming Crab (*Matuta*), the Skate (*Raja*), numerous flat-fishes (*Pleuronectes*, *Solea*, *Rhombus*), the Pogge (*Agonus*) (Pl. 2), and others—from estuaries and inshore waters. Thus we find various groups of animals, differing widely both in affinity and physiology, that dwell respectively in water over sandy shores, and in the arid conditions of desert wastes, where the only obvious factor common to both environments and to their respective inhabitants is a sandy coloration. In short, we have here an interesting example of convergent adaptation, relating to and affecting, without regard to affinity or anatomy, creatures so widely dissimilar, *in everything except coloration*, as crabs, scorpions, flat-fishes, skates, sand eels, vipers, bustards, baboons, and birds' eggs; and in which, furthermore, the coloration itself is carried and exhibited on such diverse substances and structures as chitin, scales, feathers, hair, and lime. The consequence of this is, practically, that however the effect is attained, such animals are, in actual fact, concealed and relatively difficult to detect in nature; and the phenomena, taken together, can hardly be accounted for except on the view that this type of coloration has arisen in direct relation to the need for concealment from enemies.

To return to the coloration of birds' eggs, this view is indirectly supported by a second large class of cases, namely, the relatively defenceless species whose eggs are laid where they cannot be seen, either in concealed places, or in covered or domed nests in the open, or such as are hidden or actively defended by adaptive behaviour on the part of the parents. It is significant that in such cases—where cryptic coloration could be of no avail—it is rarely found. On the contrary, such eggs are normally most conspicuous, being either white, or palely tinted, and usually devoid of any except light markings. Looking at the matter in another way, and considering the extreme case of *white* eggs, these seldom occur under conditions where their inherent conspicuousness is likely to prejudice their safety.

So long ago as 1838 Hewitson drew attention to the common occurrence of uniform white in the eggs of species that lay in holes. The facts, which have been discussed and enlarged upon by Wallace (646), are the more remarkable in that they apply to a considerable number of species embracing many families and several orders, including species with the most diverse nesting habits, and inhabiting widely different surroundings and countries—that is, quite independently of affinity, ecology, and distribution.

Among the various birds with white eggs: some, like the Wrynecks and Woodpeckers (Picidæ), Owlet Frogmouth (Podargidæ), Rollers (Coraciidæ), certain Owls (Strigidæ), Hornbills (Bucerotidæ), Barbets (Capitonidæ), Trogons (Trogonidæ), Parrots (Psittacidæ), and Toucans (Rhamphastidæ), nest in holes in trees; some, like certain Petrels (Procellariidæ) and the Owl-Parrot (Stringopidæ), nest on the ground in crevices beneath stones; some, like the Black Redstart (Turdidæ) and Swift (Cypselidæ), in crevices among rocks, or beneath the eaves of buildings or in holes in thatch; some, like the Sand Martin (Hirundinidæ), Kingfishers (Alcedinidæ), Todies (Todidæ), Jacamars (Galbulidæ), Bee-eaters (Meropidæ), Sheld-duck (Anatidæ), and Manx Shearwater (Procellariidæ), in holes or burrows in the ground; some, like the Oil Bird (Steatornithidæ) and Edible Swift (Micropodidæ), in caves; some, like the House Martin (Hirundinidæ), Dipper (Troglodytidæ), Senegal Coucal (Cuculidæ), Ovenbird (Dendrocolaptidæ), and Hammerkop (Scopidæ), in domed or covered nests. That of the last-named species is an enormous structure of sticks and twigs, cemented with mud and resembling a huge dome, with a side entrance 'most difficult of access to enemies' (18).

Still more striking is the type of case in which this correlation between egg-colour and nesting habits is found in a particular species that differs markedly from its congeners in respect of both. For instance, Major R. E. Cheesman has shown that the Crab Plover (*Dromas ardeola*), in marked contrast to all other waders found by him in Iraq, is the only species which nests in a burrow, and it is significant that this bird is also the only one whose eggs are white, and whose young are not protectively coloured (94).

Among ducks we find a closely parallel state of affairs. The great majority have eggs ranging from creamy-buff to yellowish-green or greenish-grey. Of all British breeding-species, only one, the Sheld-duck (*Tadorna tadorna*), lays a white egg, and this bird nests deep in rabbit burrows. Two others, the Ruddy Sheld-duck (*Casarca ferruginea*) and the Goosander (*Mergus m. merganser*), have creamy-white eggs, the former breeding in holes or among ruins, the latter in holes of trees or among rocks. The only other British (non-breeding) species whose eggs are white is the American Hooded Merganser (*Mergus cucullatus*), which habitually nests in holes of trees (674).

In the present connexion may be mentioned another large class of small and relatively defenceless species, of which House-Sparrows, Chats, Warblers, Wrens, Finches, Starlings, Titmice, and Swallows are examples, whose eggs, though not white, are nevertheless pale-hued, or lightly marked, and moderately conspicuous. Now these birds build nests which are either well-concealed among ground-herbage, or domed, or placed in hedgerows, bushes, or buildings—that is, in situations where the egg-coloration could in any case have little concealing significance. When, as must often happen, such nests are hidden from, or inaccessible to, enemies, then cryptic coloration could give them little additional protection: when, on the other hand, such nests can be found and visited by egg-eating predators, no cryptic coloration could save them.

The argument is further strengthened by another class of cases in which concealment of white eggs is due to adaptive behaviour of the parent birds, rather than to the nesting-site, and which are particularly interesting as affording further indirect evidence of the need for concealment in open nests. When freshly laid, the eggs of Grebes are chalky white in colour, and would appear highly conspicuous on their floating raft of decaying vegetation were it not for the fact that the bird on duty is careful to cover them over with weed before quitting the nest. The same habit is practised by various ducks, and by Pheasants, whose unspotted eggs, though not white, are so light as to attract attention if left exposed.

The Cayenne Crake (*Creciscus viridis*) might at first sight appear as an exception, since it is a ground-nesting species whose conspicuous eggs are an unspotted glossy white. But here, again, adaptive behaviour on the part of the parent prevents betrayal of the clutch, though in this case it is the parent who remains on duty in the face of danger, and conceals the eggs with her body. One of these birds allowed Beebe to approach within a few feet, its body filling the opening of the nest and so perfectly blending with the surrounding vegetation that 'no entrance could be seen and the whole affair looked like an ordinary ball of dried material that had chanced to lodge among the reed stems' (35).

A parallel case is found among certain Australian Ground Pigeons, which are themselves protectively coloured and habitually sit close, thus effectively concealing their white eggs (646). Similar among British species is the case of the Short-eared Owl (*Asio f. flammeus*), which is likewise cryptically coloured and very loth to leave the nest (208). Again, though the eggs of the Woodcock (*Scolopax r. rusticola*) are not white, they are often much too pale to be anything but relatively conspicuous when left uncovered. So also are those of the Nightjar (*Caprimulgus e. europæus*) and Ptarmigan (*Lagopus mutus millaisi*). But with these species also it is only as a last resort that the sitting bird will rise and reveal her treasures. And much the same may be said of the Partridge (*Perdix p. perdix*) and Pheasant (*Phasianus colchicus*), in both of which the females sit very close on open nests, on eggs that are not particularly well concealed by their coloration. Finally, among arboreal nesters parallel conditions obtain in the nesting arrangements of the Tawny Frogmouth (*Podargus strigoides*), which incubates its two white eggs in a horizontal attitude on a horizontal bough, from which it seems to be merely a dry projecting stump (see p. 352).

In all these cases we have a close correlation between a concealed site and a conspicuous egg. Whether the latter is the result or the cause of the former —that is to say, whether the relation is due to a change in the egg caused by the cessation of selection, or due to a change in nesting habits caused by the need for concealment—we are not here concerned. The point which I wish to stress at present is that the facts themselves are inexplicable except on the view that we have to do with adaptive characters in some way related to the biological necessity of protecting conspicuous, helpless, and palatable prey from potential enemies.

There are, of course, a number of exceptions which cannot be accounted for in this way, but with many of these compensating factors obviate the necessity for concealment. Thus, to this general thesis the white eggs of Swans, certain Geese, Fulmar Petrels, Gannets, Shags, and Cormorants—all of which are exposed—prove no exception, for they are either defended by the parents or laid on inaccessible cliff-ledges, and are thus relatively secure from attack.

Most Pigeons and Doves deposit their white eggs on open, loosely constructed platforms of sticks. Doubtless in certain cases they are well hidden by a screen of foliage from above ; and it may be noted that these nests are not placed at the tops of trees in exposed positions. Frequently, with species like the Wood Pigeon (*Columba p. palumbus*), they occur among dense coniferous growth where visibility in any direction is very limited ; while with the Stock Dove an old Magpie's nest or rabbit-hole may provide some protection. Moreover, the plumage of some species is highly cryptic and provided the bird sits close, the nest may easily escape detection among the confused lights and shades of woodland surroundings. For instance, speaking of the Red Mountain Dove (*Geotrygon montana*), a common jungle resident of Guiana, Beebe states that it was seldom seen, ' for it merged so completely with its surroundings that one passed it by, time after time, without ever knowing that such a bird existed. If it were discovered, careful watch had to be kept or it would seemingly disappear where it sat ' (35).

Nevertheless with the Turtle Dove (*Streptopelia t. turtur*) and many related species the eggs are fully exposed to view, and the question arises : How are these exceptions to be accounted for ? To what compensating principle do such birds owe the survival of eggs, which are conspicuous in appearance, exposed in position, and undefended by the parents ? Wallace's suggestion, so frequently repeated by other writers, that such eggs are protected from enemies beneath, because they look like the sky when seen through interstices in the loosely built platform, is not at all convincing, and is quite unsupported by evidence. Jays, Crows, and Squirrels hunting for eggs would be just as likely to come upon the nest from above, whence its contents are, of course, extremely conspicuous.

A more probable explanation has been put forward in a suggestive paper by Swynnerton (608), who has shown experimentally that different birds' eggs (like different insects and other forms of prey) differ in their relative palatability to particular enemies, which were found to exhibit preferences of a marked kind. When tested with eggs of a number of species, those of Doves (*Turtur capicola* and *Chalcopelia afra*) were rated as relatively unacceptable by a rat. It is significant that this applied also to those of *Colius striatus*, a Mouse-bird that lays ' in an open nest in isolated, often semi-leafless, small trees and shrubs in grassy-country '. Experiments with a mongoose yielded similar results both for the eggs of *Turtur* and *Colius*. There is therefore reason to believe, as Swynnerton suggests, that relative nauseousness or unpalatability may be a partial explanation of the survival of white, and otherwise unprotected eggs.

Doubtless other apparent exceptions remain to be accounted for : for instance, the nesting arrangements of Touracos (Musophagidæ) which are somewhat similar to those of doves ; and the apparently exposed site selected by certain Oriental Tree-Swifts (*Macropteryx*), whose tiny cup-shaped nests are cemented to the side of a branch. But these cases are so rare as to tell but lightly against the weight of evidence under consideration.

In short, the main facts are such as strongly to support the theory of concealing coloration. The position may be summarized by saying that, in general, there is a close correlation between the coloration of birds' eggs and the conditions under which they are incubated ; and that with eggs, as with the birds which lay them, cryptic coloration reaches its highest development with those species whose nesting habits most demand it, and under circumstances when it can best be employed.

(3) **Coloration of the Young in Relation to Nidification**—What we have said above of the parent birds and their eggs applies also in general to the newly hatched young. During their babyhood, birds fall into two more or less distinct classes, known respectively as nidicolous and nidifugous. The first, which includes the perching birds (Passeres), Swifts, Kingfishers, Woodpeckers, Cuckoos, Owls, Birds of Prey (Accipitres), Herons, Bitterns, Pigeons, Parrots, Petrels, Cormorants, and others, are at birth typically immature, relatively small, naked, sluggish, and helplessly confined to the cradle. The second, comprising the game birds, Bustard-Quails, Grebes, Divers, Geese, Ducks, Plovers and Waders, Gulls and Terns, are typically precocious, relatively large, clothed in down, and active—often almost from birth.

Correlated with these differences in the condition of the young at birth, it may be stated in general terms that nidicolous young are born in nests that are covered or concealed among herbage, or in holes, or in bushes or trees, or on cliff ledges, or in other cases are defended by the parents. In such nests, relatively protected by invisibility or inaccessibility, they remain until fully fledged and able to fly. With the nidifugous type, on the other hand, the case is very different, the birds being born in relatively open and exposed situations on the ground, or near water, under conditions where neither natural cover nor difficulty of access could furnish protection to a youngster that was neither precociously developed and able to escape by running or diving, or by remaining unseen; and where, therefore, they are liable to the attacks of innumerable foes from which the defenceless nidicolous type are relatively immune. If concealing coloration is ever a vital factor for life-saving, then, in theory, it is surely such nidifugous youngsters which need it most desperately. Now in actual fact it is precisely with such young that we find that most wonderful combination of cryptic coloration and instinctive immobility which renders forms such as young Woodcock, Golden Plovers, and Oyster-Catchers among the most perfect examples of natural camouflage to be found in the whole realm of nature.

So effective is the downy disguise that one may search in vain for young Oyster-Catchers or Ringed Plovers in the vicinity of the nest in which they were hatched but a few hours previously.

To human eyes, optical deception of this kind is often almost unbelievably successful, as the following will show. I was walking one July afternoon with Mr. Richard Elmhirst through a strip of woodland near Millport, Cumbrae, intent on finding nesting Woodcock—which I was anxious to photograph. Suddenly, as we neared the edge of the spinney, a Woodcock flew up a yard or two in front of my companion. We both went forward to the place, and stooping down, Mr. Elmhirst pointed out to me a small drop of fresh excrement which, left by the rising bird, revealed the exact spot she had just quitted. I mention this trivial circumstance because it was only a moment later that we realized that there, right under our very eyes, were crouching four recently hatched chicks. A spot of watery fluid on a leaf had been easier to recognize than the young birds, so effectively were their fluffy forms broken up by the disruptive pattern of their coats of down. These youngsters, photographed in situ, are the ones figured on Plate 19. Unless, or until they happen to move, it is literally as easy to find such birds by touch as it is to find them by sight.

IV. THE GENERAL RELATION BETWEEN CRYPTIC APPEARANCE AND CRYPTIC BEHAVIOUR

Another very important class of facts relates to the everyday behaviour of cryptic animals. I refer here especially to the general relation (found in otherwise unprotected species) between coloration and activity—that is, between conspicuous as opposed to concealing coloration on the one hand, and the tendency for such species to rely respectively upon escape by flight, or escape by ‘ freezing ’.

(1) **Concealing Coloration and Instinctive Immobility in Birds**—There is among birds a striking general coincidence between highly specialized cryptic resemblance and highly developed crouching instincts, both on the nest and at other times, the birds which allow the closest approach of an intruder being usually those which are best concealed by their coloration. This relation between appearance and activity reaches its zenith in many widely unrelated kinds of birds (and indeed in many groups of animals besides birds), in every type of environ-

ment, and in each of the five continents—whether the resemblance is to stone or to sand, to the patterns of tangled grasses or of fallen foliage, to the trunks of trees or the stems of reeds; whether it occurs in the barren tundras of Siberia or the fertile forests of Guiana; whether it relates to members of the orders Passeres, Ciconiiformes, Galliformes, Anseriformes, Gruiformes, Charadriiformes, Psittaciformes, Strigiformes, or Caprimulgiformes. It was one which was sufficiently general to lead Beebe to base his estimate of the colour-status of forest species in British Guiana on the actions of the birds themselves at the approach of danger. He says: 'A bird which flew at once, either to a point of vantage where it could see clearly about it, or flying on out of sight was plain evidence of lack of protective coloring, at least in its own estimation. If it squatted or "froze" either for a moment or until we had crept up to within a few feet, I felt that it unconsciously, but surely, counted upon being overlooked, or confused with its surroundings' (35).

The same relation between protective colour and protective instinct is referred to by Hingston in his account of the life in these forests, whose cryptic ground and tree avifauna includes Tinamous, Trumpeters, Curassows, Partridges, Guans, Sun-bitterns, Jungle-Pigeons, Rails, Wrens, Tree-creepers, Wood-Hewers, Thrushes, Bitterns, Owls, Nightjars, Parakeets, Parrots, Vireos, and many other forms.

This general truth is well illustrated by British birds when nesting, and is known to every countryman, to every student of bird life, and to every photographer of wild birds. Standing in the open and moving cautiously, but freely, I have photographed a nesting Woodcock, which was so confident that she suffered me to place one leg of the tripod within a few inches of her body, and to remove with my hand unsightly grasses from her very nest. Nightjars likewise may be photographed without any use of the bird-photographer's paraphernalia and patience which must be expended on the more conspicuous and shy species, and they will even permit a hand to touch them. My friend, Mr. P. W. T. Boughton-Leigh, tells me that the Wood-Lark is likewise an exceptionally close sitter, and will allow the hand to be placed within six or eight inches of the nest before quitting. Similar are the close-sitting habits of Partridges, Ptarmigan, Short-eared Owls, and many Duck and other species which are highly inconspicuous at the nest—and this in marked contrast to those relatively conspicuous species like the Lapwing, Oyster-Catcher, Coot, Moorhen, and different Gulls and Terns, which avoid the danger of betraying the nest, not by 'freezing', but by flight.

There are a few exceptions to the rule, certain species combining cryptic coloration with alert, secretive habits. For instance, the Stone-Curlew will slip silently out of sight at the first sign of an intruder on the breeding territory. Similarly, according to Captain C. R. S. Pitman (in Bannerman, 18), Denham's Bustard (*Neotis cafra denhami*) will leave its clutch 'at the first suspicion of alarm, running or crouching among the grass tufts and probably first seen far away from the nest'. But it is noteworthy that in such cases (like those in which the parent bird itself is conspicuous and leaves the nest early) both eggs and young are themselves generally well protected by cryptic coloration.

Nidifugous young, like their parents, instinctively crouch rigid when danger threatens. Indeed, different species—Lapwing, Golden Plover, Partridge, and others—have each evolved their own system of air-raid precautions. At the approach of hostile aircraft—in the form of Lesser Black-backed Gull or Carrion Crow or Peregrine—alarm notes of the mother provide the stimulus for an automatic squatting response in the nestlings, who 'take cover' and remain motionless until they receive the all-clear signal. A beautiful example of this arrangement for the frustration of a predator is provided by the Oyster-Catcher's shrill piping notes, at the sound of which the callow young crouch low and motionless, and remain invisible until the danger is past—clothed as they are in the armour of light.

(2) **Concealing Coloration and Instinctive Immobility in Lizards**—Though limitation of space prevents me from carrying the thesis much further here, it is not to be imagined that birds are unique in this respect. The same principle is equally applicable to widely different groups of animals—including lizards, snakes, turtles, toads, frogs, fishes, and innumerable insects belonging to many different families, as well as spiders, crabs, and other arthropods. For instance, every naturalist who has collected lizards in the tropics knows that while these creatures, like birds, have many means of avoiding enemies—some relying on speed, others on the use of cover, others on active self-defence, or on burrowing—different members of the most diverse families, Agamidæ, Iguanidæ, Scincidæ, Lacertidæ, Gekkonidæ and Chamæleontidæ, have become specialists in camouflage, and these, especially such as have cryptic coloration highly developed, are easily approached and captured by hand once they have been detected. Like the birds, such forms rely instinctively upon *escaping detection.* In the lower Amazon this applies to many members of the Iguanidæ, forms like *Polychrus marmoratus* which is fairly plentiful around Pará, and *Anolis ortonii* which I have taken at Itacoatiara, near Manaos, being no trouble to *catch*, but a good deal of trouble to *find.* Hingston noticed the same thing in British Guiana. 'Some of the forest lizards,' he says, 'even more than the birds, instinctively rely on their colour protection. If one can detect an *Ophryoessa* [Iguanidæ] on a dead branch it is perfectly easy to capture it by hand, its instinct being to freeze and make no effort to escape' (265). In Africa, where these cryptic forms have their counterparts in other families, one finds the same thing. For instance, in the forest of Amatongas, near Beira, a fine arboreal bark-like Agamid, *Agama atricollis*, is as simple to seize as it is difficult to discover. But in this continent the Chameleons are the extreme example of the principle. No one who has not searched for species like *Chamæleon dilepis*—which is common enough in the lower Zambesi valley, and, incidentally, conspicuous enough when seen in a museum jar—can realize how marvellously these creatures harmonize with, and melt into, the medley of foliage where they have their home, and where they are relatively secure from every eye.

In the following section I propose to deal with the further question of cryptic attitudes, as opposed merely to cryptic habits in general: and it will be pertinent here to point out that with lizards and many other groups of animals besides birds, this special posing and assumption of absolute stillness in times of danger forms part and parcel of the cryptic make-up. An excellent example of the kind has been given by Schmidt, who refers to a Chameleon named *Rhampholeon boulengeri* from the Belgian Congo as follows: 'In forest regions, where leaves of all sizes and shapes attract little attention, the strongly curved, irregular outline of the back, the dull shrivelled skin with the two peculiar dark markings suggesting the venation of a leaf, make the simulation perfect in every color phase. At the slightest noise they usually stop in any position, even with one front and one hind leg lifted, and may remain motionless for hours' (558).

The same thing applies again and again in group after group of animals. With frogs and toads it is most striking, and I have referred elsewhere to an example in the little leaf-like *Bufo typhonius* of tropical South America (see p. 316). So far as my own experience goes with insects, when studying or photographing them in the field, this relation between cryptic colour and cryptic behaviour appears most striking and significant: grass-like grasshoppers, twig-like caterpillars, leaf-like insects, bark-like moths—all combine these two classes of characteristics, the one relating to appearance, the other to activity—and in general it is true to say that in all these unrelated animals, both vertebrate and invertebrate, the more perfect the procryptic resemblance the more implicit is the instinctive reliance upon invisibility.

Now there is only one possible explanation of all these facts, and that is, that concealment is vitally important to the animals in question, and that their cryptic coloration and cryptic instincts have been evolved and perfected in response to the need for concealment from enemies. No other theory of animal coloration ever propounded will meet the case.

(3) **Adaptive Cryptic Attitudes in Birds**—It is interesting to find that in the most specialized examples of this general relation between *concealing coloration* and *cryptic habits*, its effectiveness is almost without exception perfected by special cryptic attitudes, which are *instinctively and instantly adopted in times of danger*, *and adapted to the nature of the surroundings*. Where there is no cover, for instance in desert places, or on shingle, the tendency is to assume the crouching posture already referred to in the case of certain nightjars and owls, and practised by many other unrelated species, whether as downy youngsters, or as adults. This is well seen in the chicks of different waders, which squat low the instant danger threatens. The prone position is perhaps seen at its best in the Stone-Curlew, whose young, while still tiny mites of down, instinctively place their trust in camouflage. In his careful study of the habits of this remarkable bird, Mr. William Farren states that 'at the expiration of a week not only is the body more depressed, but the neck is fully extended and pressed to the ground, and long before the end of the second week of its existence the young bird assumes the extremely flattened attitude. When fully fledged

the young show but slightly diminished confidence in the device'. So compelling is the instinctive habit, and so implicitly do the little birds appear to trust their invisibility, that they can hardly be persuaded they have been discovered. 'I have lifted one from the ground', he says, 'and laid it across two outstretched fingers, yet the rigidity of the attitude has not been relaxed in the slightest, nor has the bird given a sign of life' (169). So strong is this squatting instinct in many young plovers, game birds and terns that, as pointed out by Russell (548), they will squat on an artificial carpet indoors—where they are not in the least hidden, just as readily as on the natural 'carpet' out-of-doors—where they are wonderfully hidden; and Tomlinson (cited by Russell) has shown that young Lapwing and Little Tern will remain stationary even when turned on their backs, though, of course, in this attitude their white bellies render them extremely conspicuous. The same writer describes how on one occasion he came across a young Little Tern squatting close to the water's edge, when the tide was on the flow. 'As I watched the bird it remained, as I expected, so motionless that it might have been thought dead. Near and nearer came the wavelets lapping on the beach, and great was my astonishment to find that the bird allowed the water to pass over it rather than move and thereby betray its presence!' (548).

These and similar cases illustrate in the clearest terms how adaptive quiescence, when combined with a cryptic costume, forms an instinctive and essential part in the drama performed by these attractive little actors. And the play is by no means one for the young alone: the same part is rehearsed by adults of many kinds—reptilian, amphibian, and arthropod as well as avian. Stone-Curlews practise it, so do numerous other waders, and many of the terrestrial birds, such as the Short-eared Owl, Nightjars, and Owl-Parrot. Palmer has described the behaviour of a Spotted Sandpiper on noticing the approach of a Vulture (*Catharistes aura septentrionalis*). Instantly the creature crouched down, with its head and bill pointing obliquely towards the water, and stood thus 'as if turned to stone while the shadow passed within a few feet' (453).

When photographing Golden Plover I have witnessed similar adaptive behaviour. So long as the sitting bird feels that she is unobserved, she carries her head high and is tolerably conspicuous: but at the first alarm, she seeks to avoid detection by lowering the head so as to hide the plumage of the throat and breast. When *that* happens, she seems to form part of the moorland, and can scarcely be made out at six or eight yards' distance. In fact, seen under these circumstances, the Golden Plover presents one of the most perfect examples of general protective resemblance to be found in any British bird. I became fully convinced of this a few years ago, by the following experience. I had been shown a nest at which I was anxious to obtain photographs of this species. Being somewhat pressed for time, I decided to dispense with a hide, and instead set up the tripod a few yards from the site, concealing the camera and stand with heather shoots. A line attached to the shutter release was led twenty-five yards back into dead ground which I could reach by crawling, without being seen from the nest. Allowing the bird time to return to her clutch, two exposures were made, and on each occasion as I afterwards approached the camera to change the plate and reset the shutter, she slipped off the nest and flew away. At the third attempt, I returned to the camera as before, but was disappointed to find (as I thought) that I had scored a blank, for no bird flew up. Evidently I had been too hasty and she had not returned to duty. But where *was* the nest? Though it was no more than fifteen feet from where I stood, and though I knew the eggs were tolerably visible from that point, I quite failed for the moment to locate the site. Much puzzled, I checked the exact spot by the direction in which the camera was pointing, and there, to my delighted astonishment, was the bird, crouching low and looking for all the world like any other patch of its heathery surroundings. Now this difficulty of detection was due mainly to the cryptic attitude, as I found the same evening—for on developing the plate, this revealed the bird sitting up with head erect in an alert but unconcerned manner, the light plumage on her neck and breast showing up quite conspicuously.

Moreover, it is remarkable that even large birds can thus entirely escape observation, and this at close range in open country utterly devoid of cover. Yet such is undoubtedly the case with various Bustards. Speaking of the Houbara (*Chlamydotis undulata macqueeni*), a bird about the size of a small turkey, Major Cheesman states that when it lies ' prostrate on the ground its beautiful pale buff shades, interrupted by fine brown vermiculations and barring, defy the eye of Hawk and man to detect it at ten yards' distance in spite of its size, so long as it remains motionless. If it were coloured black or black-and-white it would attract attention at 600 yards. Its power of disappearance in its proper environment is almost incredible. We once drove up to a ruin near Baghdad in the barest desert in order to shoot Blue Rock Pigeons. Four men got out of the car and, after half an hour's battue, to our amazement an Houbara rose from the bare ground, near one of the car-wheels, as one of the party nearly trod on it ' (94). The same author brings forward evidence (see p. 186) to show that the Houbara is effectively concealed, when incubating on the nest, from the keen eyes of trained Falcons.

I have been dealing above with cases where no natural cover is available, and where consequently the most appropriate cryptic attitude—and that which is actually adopted in the field—is a crouching one. In marked contrast we find many tree-dwelling and reed-haunting species adopt an erect posture, which is best adapted to the general configuration of the background. A most striking example presented by the ' Poor-me-one ' (*Nyctibius griseus*), whose habits are referred to on a later page. Like Mr. Charlie Chaplin in his famous film *Shoulder Arms*, when threatened by danger these curious nightjars straighten up stiff and motionless, assuming the attenuated attitude in which the bird forms, or seems to form, a mere continuation of its perch. According to Belcher and Smooker (41), the appearance is altogether different when the bird is off its guard: at such times ' the large, beautiful eyes are fully open, so that the Owl-like gold iris is plain ; the tail, and sometimes a wing, may be outstretched, and the air is one of ease. Once an intruder is seen the first-described pose is developed, not by any hurried movement, but by a slow lengthening and attenuation of the figure'.

The same upright posture is practised in an entirely different environment by Bitterns, whose reed-assimilating attitudes and cryptic habits are shared by several species, such as the British *Botaurus s. stellaris*, and the North American *Ixobrychus exilis*. Palmer relates how he once marked the place in a marsh where one of these birds had alighted : on reaching the spot he had the 'greatest difficulty in finding it clinging motionless, with bill almost erect, to a stem of wild oats (*Zizania aquatica*)' (453). Similar habits in the British bird have been described by several writers. But more remarkable is the case of the Little Bittern or Variegated Heron (*Ardetta involucris*), a small South American species about the size of a Snipe, of silent and solitary habits, which frequents marshy places and breeds among rushes.

Its wonderful powers of self-effacement when in danger have been described by W. H. Hudson (276), whose account is so illuminating, so pertinent to our subject, and so full of interest, that I quote his words in full. 'One day in November when out shooting,' he says, 'I noticed a Variegated Heron stealing off quickly through a bed of bulrushes, thirty or forty yards from me ; he was a foot or so above the ground, and went so rapidly that he appeared to glide through the rushes without touching them. I fired, but afterwards ascertained that in my hurry I had missed my aim. The bird, however, disappeared at the report ; and thinking I had killed him, I went to the spot. It was a small, isolated bed of rushes I had seen him in ; the mud below and for some distance round was quite bare and hard, so that it would have been impossible for the bird to escape without being perceived ; and yet, dead or alive, he was not to be found. After vainly searching and re-searching through the rushes for a quarter of an hour I gave over the quest in great disgust and bewilderment, and after reloading, was just turning to go when, behold ! there stood my Heron on a rush, no more than eight inches from, and on a level with, my knees. He was perched, the body erect, and the point of the tail touching the rush grasped by its feet ; the long slender tapering neck was held stiff, straight and vertically ; and the head and beak, instead of being carried obliquely, were also pointing up. There was not, from his feet to the tip of his beak, a perceptible curve or inequality, but the whole was the figure (the exact counterpart) of a straight tapering rush : the loose plumage arranged to fill the inequalities, and the wings pressed into the hollow sides, made it impossible to see where the body ended and the neck began, or to distinguish head from neck or beak from head. This was, of course, a front view ; and the entire under surface of the bird was thus displayed, all of a uniform dull yellow, like that of a faded rush. I regarded the bird wonderingly for some time ; but not the least motion did it make. I thought it was wounded or paralysed with fear, and, placing my hand on the point of its beak, forced the head down till it touched the back ; when I withdrew my hand up flew the head, like a steel spring, to its first position. I repeated the experiment many times with the same result, the very eyes of the bird appearing all the time rigid and unwinking, like those of a creature in a fit. What wonder that it is so difficult, almost impossible, to discover the bird in such an attitude! But how happened it that while repeatedly walking round the bird through the rushes I had not caught sight of the striped back and the broad dark-coloured sides? I asked myself this question, and stepped round to get a side view, when, *mirabile dictu*, I could see nothing but the rush-like front of the bird! His motions on the perch, as he turned slowly or quickly round, still keeping the edge of the blade-like body before me, corresponded so exactly with my own that I almost doubted that I had moved at all. No sooner had I seen the finishing part of this marvellous instinct of self-preservation (this last act making the whole complete) than such a degree of delight and admiration possessed me as I have never before experienced during my researches, much as I have conversed with wild animals in the wilderness, and many and perfect as are the instances of adaptation I have witnessed. I could not finish admiring, and thought that never had anything so beautiful fallen in my way before: . . . and for some time I continued experimenting, pressing down the bird's head and trying to bend him by main force into some other position; but the strange rigidity remained unrelaxed, the fixed attitude unchanged. I also found, as I walked round him, that as soon as I got to the opposite side and he could no longer twist himself on his perch, he whirled his body with great rapidity the other way, instantly presenting the same front as before. Finally I plucked him from the rush and perched him on my hand, upon which he flew away; but he flew only fifty or sixty yards off, and dropped into the dry grass. Here he again put in practice the same instinct so ably that I groped about for ten or twelve minutes before refinding him, and was astonished that a creature to all appearance so weak and frail should have strength and endurance sufficient to keep its body rigid and in one attitude for so long a time.'

Full as is this account of significant details, perhaps the most remarkable point is the bird's instinctive habit of presenting its *narrowest* aspect to its intruder. In another place (p. 210) we shall see that similar instinctive orientation, but with a precisely opposite result, is found in certain birds, reptiles, amphibians, and insects, which present to an enemy the *greatest* rather than the least surface of their bodies. But in such cases the function of the attitude is also of an opposite nature, its method being self-enlargement rather than self-effacement; its purpose being to reveal rather than to conceal; its result to intimidate enemies rather than to simulate surroundings. (And, of course, the same principle applies to the submission—or display—attitudes of different birds and mammals to rival males of their own species, or to members of the opposite sex.) I mention these facts here because they prove that such instinctive orientations as we have considered are not isolated or freakish phenomena. Rather do they fall in line as a fundamental part of those admirable mechanisms—whose elements comprise modification of form, adaptation of colour, instinctive behaviour, and symbolical attitudes; whose occurrence is so widespread in different groups of animals and different types of surroundings; whose effect is so nicely adjusted to the environment and manner of life; whose significance can only be explained in terms of concealment and advertisement, of defence and offence; and whose success or failure, often in terms of life or death.

8. CONCEALMENT IN OFFENCE

National life is chiefly controlled by the desire to capture markets. Animal life is chiefly concerned with the occupation of feeding grounds.

ARTHUR WILLEY

In an earlier section, dealing with the methods by which concealment is attained, we have referred to the cryptic coloration of different predatory animals. We have now to consider certain ecological aspects of aggressive concealment. While the value of anticryptic coloration and habits in predatory mammals, snakes, fishes, insects, and other animals is supported indirectly by a variety of facts and lines of evidence, the question is one which has yet to be thoroughly investigated in the light of observation and experiment, and which will provide a fruitful field for research. We shall here refer to collateral evidence bearing upon the problem of concealment for aggressive purposes.

Cryptic appearance and habits are not, of course, a *sine qua non* of the successful hunter. For instance, aquatic plankton-feeders like herring, and aerial ' plankton ' feeders like swallows, have no use for aggressive concealment, for their own speed or agility is immeasurably superior to that of the animals on which they live. In lesser degree the same applies to swift forms like wolves and dolphins which combine in packs or schools to hunt down prey by sheer power of pursuit.

But with others, which surprise, or ambush, or allure their prey, the case is very different. Most fishes are themselves fish-eaters, and often enough the hunted animal is actually swifter than the hunter. With these, successful attack depends absolutely upon an unseen approach, or upon unrecognized or mistaken identity—*the element of surprise at close range is everything.* Only by *remaining unrecognized* are they enabled to approach, to ambush, or to allure the unsuspecting victim until within range for the sudden assault. The methods of ambush and allurement depend more upon deception than upon concealment, and are a subject which will be taken up later. It is with the tactics of the unseen approach that we are here concerned.

I. SURPRISE AS A FACTOR IN THE ATTACK

Animals may become aware of events happening at a distance through three channels—those of sight, sound, and scent. And it is significant that the coloration and behaviour of animals which depend upon an element of surprise for the capture of prey are modified in these three directions—namely, for the disguise of visible appearance and of visible movement, for the reduction of noise, and for the obliteration of scent.

In regard to the first point—disguise of appearance—little need be added here. It is, however, well to remember that the optical principles involved, and the visual properties of the dress worn, are essentially the same for hunter and hunted. And in each case the same essential devices have been evolved—general and variable colour-resemblance, obliterative shading, disruptive coloration, coincident patterns, camouflage of the eye, blurring of the contour, special deceptive resemblances, adventitious coloration and so forth. The evidence given in a later section dealing with the theory of concealing coloration (p. 147) applies in general as much to the aggressive as to the protective function.

At its best, the effectiveness of the disguise is not less perfect in offence than in defence—as may be seen, for instance, by referring to the wonderful mantids figured on Plate 40. Even in large predators such as the big cats and constrictors, visibility in the field is greatly reduced by coloration alone. Major Walford, an experienced tiger-hunter, writes in a letter cited by Wallace (646): 'I once, while following up a wounded tiger, failed for at least a minute to see him under a tree in grass at a distance of about twenty yards—jungle open—but the natives saw him, and I eventually made him out well enough to shoot him, but even then I could not see at what part of him I was aiming. There can be no doubt whatever that the colour of both the tiger and the panther renders them almost invisible, especially in a strong blaze of light, when among grass, and one does not seem to notice stripes or spots till they are dead.' This writer also informed Wallace that the haunts of the tiger are invariably full of long grass, dry and pale yellow for at least nine months of the year.

II. THE REDUCTION OF VISIBLE MOVEMENT

I have referred elsewhere to the importance of stillness for concealment. Moving objects, however well camouflaged, tend at once to catch the eye. Stevenson-Hamilton, in his *Animal Life in Africa*, remarks that game are attracted by *moving* objects at great distances, but pay little attention to a man standing still at very close range. Selous and other writers have stressed the same point, which is familiar to all naturalists.

When photographing birds from a hide, it is movement, rather than noise, which mainly causes alarm. Many birds, such as Puffins, can be closely approached in the open, provided the photographer moves in a direct line, and *extremely slowly, so that his actions are not noticed.* This is also the case in marked degree with active insects like butterflies, which allow themselves to be touched by the net before attempting to escape, if approached with sufficient caution.

The same applies, of course, to many animals. At Beira I found that Racing Crabs belonging to the genus *Ocypoda*, which are excessively alert, shy, and difficult to approach, and go scuttling for their holes at the least sign of danger, would remain at the surface—scavenging along the tide wrack or excavating their burrows—quite unaware of an observer's presence provided he kept absolutely still. But at the slightest movement they would bolt for shelter. And, as every country-bred boy knows, the same is true of rabbits.

It therefore follows that the problem of concealment in attack differs from that of concealment in defence in an important particular. In their mutual relationships, the hunted animal plays a passive, the hunter an active, part. The former, as we have seen, may remain motionless by day, or when danger threatens, and so escape observation. The latter, on the contrary, must take the initiative. Active hunters therefore work at a disadvantage. Unlike their prey, they cannot combine cryptic coloration with immobility. To the one, stillness may mean safety: to the other, it must mean starvation. Hence it is hardly surprising to find that with wild predators, *elaborate precautions are taken to reduce visible movement* in the advance upon their quarry—namely, (1) by a slow, stealthy approach; and (2) by the skilful use of cover.

(1) **The Stealthy Approach**—Stealth is to the anticryptic animal what stillness is to the procryptic. The vital importance of surprise in attack is reflected in the skill needed, and shown, by predatory species when working up within striking distance of active prey.

Many fishes are perfect masters of the stealthy advance. When hunting, the John Dory (*Zeus faber*) stalks the small fishes upon which its livelihood depends, moving very gradually, with caution and precision, ‘ like a man working up to game in open country where there is no cover ’ (26). During these manœuvres, its deep, excessively thin body undoubtedly assists in rendering the fish most inconspicuous to its prey. Norman describes the attitude as one of suppressed excitement, the eyes being kept fixed intently on the prospective victim (446). When within a few inches, the immense, mournful mouth opens, the protrusible jaws shoot forward, and the small fish is engulfed.

The Long-nosed Garpike (*Lepidosteus osseus*), another devourer of small fishes, drifts slowly towards its prey, looking more like a lifeless log of wood than a dangerous enemy, until the jaws are in position for the ‘ sudden, convulsive, sideways jerk of the head ’ which is their undoing. ‘ It seems to be possessed of infinite patience, for many are the preliminary manœuvres and tentative snaps before the body of the little fish is finally transfixed by the teeth ’ (446). There can be little doubt that the approach is facilitated by the very perfect obliteration of the eye, to which we have already referred in the related *Lepidosteus platystomus*.

This stealthy, unobserved method of attack reaches its extreme development in the South American Leaf Fish (*Monocirrhus polyacanthus*), which, as described on a later page, drifts up to its prey—a wolf in sheep's clothing—without exciting any alarm, until so close that flight from the final assault is scarcely possible. Pipe-fishes practise similar methods when approaching the shrimps on which they feed, the tubular mouth being pushed gradually right up to the unsuspecting crustacean.

It is interesting to note that in each of the above cases the appearance of fish is more or less deceptive; in each the approach is slow and stealthy; and in each the actual locomotion is effected not by tell-tale body-movements but by inconspicuous undulations of transparent membranous fins.

Many other animals, of totally dissimilar habits, belonging to widely separated groups, and from entirely different environments, adopt similar tactics. When hunting, spiders of the family Salticidæ may be seen to halt on sighting a fly. They then proceed to work in very gradually, moving with ' a stealthy cat-like creep ', followed by ' a lightning leap over the intervening space ' (479).

Now this comparison to the movements of a cat is very appropriate. Not only do members of the Felidæ move up for the assault with wonderful skill, they also show considerable judgment according to circumstances. For example, my cat ' Queenie ', who is fond of insects, hunts for them with untiring zeal when in the mood for sport: but he uses a different technique for different types of prey. If the immediate attraction is a ' crane-fly ' (Tipulidæ), he knows by experience that he can easily overtake it by speed alone: the insect is pursued, struck down with a paw, and swallowed. But when a ' blue-bottle ' (Muscidæ) has to be captured, the difference in his mode of attack is nicely adjusted to the activity of his victim: employing all the stealth at his command, he will work up actively behind cover, then approach deliberately, slowly, until within a foot or so; then there follows the sudden rush, and the lightning stroke of a paw, and the disabled insect is transferred to the mouth.

Closely similar antics are familiar to those who have watched geckos on the prowl after insect-prey. At Pará I have repeatedly seen the ubiquitous House Gecko (*Hemidactylus mabouia*) stalking prey attracted indoors by the light. The preliminary approach is often rapid: this is followed by a slow, stealthy advance, one leg being moved at a time; then, when within about five inches of its victim, there is a sudden lightning dash, and the insect is seized before escape is possible.

Now it is surely a singular fact that animals so dissimilar in appearance, in affinity, and intelligence as geckos, cats, and spiders should employ almost identical methods when approaching active prey—methods which seem obviously those best suited to achieve the desired result, and which involve *the minimum of visible movement*. In their actions all these animals behave as though to remain unrecognized were essential to success. On any other view their habits are unaccountable.

(2) **The Use of Cover**—The writings of big-game hunters contain many references to the remarkable way in which the larger Carnivora exploit available cover when working up to game. For instance, Vaughan Kirby states: ' The leopard's mode of attack is similar to that of all the larger Felidæ. Ever on the alert, he soon hears the distant bleating of calves or goats, and ascertaining by the direction of the sound that the luckless animals are a little distance away from the sheltering kraals, he advances quickly but stealthily upon them from below wind. No snake in the grass moves more noiselessly; the long lithe body accommodates itself to all the intricacies of the thorny tangled bush, and the most watchful would never know of its dreaded approach. . . . They charge with lightning speed, and from the smallest bit of cover that one would think barely sufficient to cover a hare ' (311).

III. ADAPTIVE SILENCE

Cryptic silence is to the ear what cryptic appearance is to the eye. The silence of which I speak is not a passive condition—a mere absence of sound. It is an active quality, a significant attribute of hunting-animals, rendered possible by structural modifications or achieved by adaptive behaviour. In the brooding nightjar, soundlessness is simply a negation of noise : but in the cat stealing towards its prey, silence is more than this—it is achieved, not by the absence of movement ; but in spite of movement ; it is due, not to stillness, but to the suppression of sound.

Silence as a habit reaches its highest development in the higher vertebrates, where it is correlated with the greater ranges of activity in a warm-blooded predator. No one who has studied animals in the field can fail to marvel at the noiseless approach of predatory birds and mammals who depend for the capture of food upon an element of surprise.

One of the most singular of adaptive features is the equipment of owls for silent flight. When hunting, most owls depend absolutely on surprise tactics. The flight of a Barn Owl or other typical member of the group is wavering and slow, and as it cruises over the fields it depends upon the combination of darkness and silence to allow a near approach for the fatal pounce. Such methods of hunting would not be practicable by day, when the predator would be seen ; nor without ' silenced ' wings would they be successful by night against such small mammals as mice and voles whose hearing is presumably acute.

In these respects the habits of owls differ markedly from those of diurnal birds of prey, where neither silence nor concealment, but rather speed, is the important factor in the chase. Such birds adopt many methods of attack. They may, like the Kestrel, practise dive-bombing tactics, hovering above their victim and dropping suddenly out of the blue ; or after the fashion of a fighter 'plane they may, like the Hobby, fly down other birds such as Martins, Swallows, and even Swifts by sheer powers of pursuit.

The flight of such birds, especially when travelling at high speeds, is noisy. Coward states that ' the rush of a swooping Peregrine when heard at close quarters is like the sound of a rocket '. However, the circumstances of the attack are such that flight noises can scarcely affect the issue.

Owls have solved the problem of the silent air-raid. From time immemorial they have adopted a method of approaching their objective without being detected by the ' listening posts ' of their prey—a method which has recently been rediscovered and put into practice by German and Italian airmen who developed the technique of approaching Barcelona from a great height, and, with the engines shut off while still some miles out to sea, of gliding noiselessly down towards their victims.

The soundless spectral flight of the Tawny Owl, who flaps leisurely past, quartering the ground on noiseless wings, like a shadow in the twilight, is one of the marvels of nature. Now this phantom-like quality in the flight of owls is due to structural modifications of the feathers, whose peculiarities have been described in a most illuminating paper by Lieut.-Commander R. R. Graham (213).

For details of the silencing mechanism, the reader is referred to Graham's work. It will be sufficient to indicate here that the modifications serving this end are of three kinds, namely, the leading edge comb ; the trailing edge fringe ; and the downy upper surface. (1) The first of these devices is a modification of the front margin of wing feathers which function as a true leading edge in flight. It consists of a stiff comb-like fringe whose teeth jut forward with a slight lateral and upward inclination. In the Barn Owl this extends along the leading edge of the first primary. In the Short-eared Owl, there is an additional length of comb on the distal leading edge of the second primary, e.g. where it acts as a leading edge owing to emargination of the feather in front. In other species these combs may occur on as many as four flight feathers—always where they are cut away so as to form wing-tip slots. Graham points out that the noise produced by an aerofoil is said to come from the region in rear of the leading edge of the suction surface where there is a sudden fall in the air-pressure. Such noises would be diminished by the comb, which reduces the speed of the air-stream over the leading edge, and at the same time deflects the flow after the fashion of a Handley Page slot, thus damping the noise by raising the pressure immediately in rear of the leading edge. (2) Noises produced by the leading edge are in the normal wing apparently augmented ' by sounds emanating from the region in rear of the trailing edge where the lower air-stream at high pressure mixes with the upper stream, which is not only rarified, but is travelling at a higher speed '. In owls the rear margins of all primary feathers bear a fringe, somewhat like the fringe of a shawl. These trailing edges are evidently designed to deal with air-flow, allowing the upper and lower streams to pass through it before joining. The process of mixing is thus delayed and the combined stream is smoothed out so as to prevent noise-producing vortices. (3) Part of the upper surface of the feathers is downy in texture, and their softness serves to muffle the noises that otherwise would be produced by adjacent feathers sliding over one another during flight.

All this is remarkable enough. But what is especially significant is the total absence of these devices in the Asiatic Fishing Owl (*Ketupa flavipes*), whose special prey, being under water, is unable to hear the noise of its wings. In this species, then, which in striking contrast to its congeners has no need of a silencing device, such a device has either never arisen, or has been secondarily lost.

Similarly, the domestic cat, like its larger congeners of forest, savannah, and desert, is, when stalking prey, a marvel of soundless movement. The same is true of other—especially of nocturnal—prowling predators. For instance, this is what Phillips says of the Slender Loris in Ceylon : ' The word " slow " as used in connexion with this loris is hardly an apt term. Certainly in the glare of the sun and bewildered by unusual surroundings and noise, he is hesitating and cautious in the extreme ;—he is nervous, defenceless and rather pathetic, knowing not which way to turn to escape. But see him at dusk, in familiar surroundings, and he is a very different animal. Wonderfully agile and absolutely noiseless, he arrives like a fleeting shadow and departs again in ghost-like silence—a true spectre of the gloom to the lesser folk of the woodlands, on whom he preys ' (469).

Primitive man himself has retained this capacity in high degree. Dependent upon simple weapons and relying upon a close, unobserved approach to prey, Indian and Bushman are able, like Agag, to walk delicately. The native of South America makes his way through the forest trails noiselessly, while his white companion, untrained and unused to the ways of the forest and of forest creatures, blunders along, with the rustling of leaves and the cracking of twigs to herald his every step.

IV. MASKING THE SCENT: THE APPROACH UP-WIND

Of all the devices leading to surprise in the attack, none is more remarkable than the instinct possessed by the larger cats to approach their quarry into the wind—thereby greatly delaying the moment of recognition. Antelopes and other game have the olfactory sense keenly developed, and this habit must therefore be an important factor in the chase. Further use of this principle is shown in the strategy by which prey are driven towards their enemy, as described by a number of writers. Selous gives the following account of the method adopted by Lions: ' They understand as well as the most experienced human hunter the art of approaching game below the wind, when hunting singly; but when there are several lions hunting together, I believe that some of them will sometimes creep close up to a herd of game below the wind, whilst one or more of their number go round to the other side. The buffaloes, zebras, or antelopes at once get the scent of these latter, and run off right on to the lions lying waiting below the wind. . . . As lions have played this game with my cattle upon several occasions, I presume that they often act in the same way with wild animals ' (562).

9. OBJECTIONS AND EVIDENCE BEARING ON THE THEORY OF CONCEALING COLORATION

> The truth of nature is a part of the truth of God; to him who does not search it out, darkness, as it is to him who does, infinity.
>
> RUSKIN

The phenomena of adaptive coloration have always provided a fertile field for speculation and controversy, and in the present section I have attempted to review, and to answer, the various lines of criticism directed against an adaptive explanation of the facts—an explanation, in other words, based upon the conception that these visible characters have been evolved in relation to the fundamental needs of the individual—security and sustenance; and that they occupy a vital place in the struggle for life. While the arguments which follow have special reference to the theory of visual concealment, much that will be said under the various headings applies in principle and with equal force in the spheres of advertisement and deception.

I. THAT CRYPTIC RESEMBLANCES ARE INCIDENTAL EFFECTS RATHER THAN ADAPTIVE MODIFICATIONS

(1) **Examples of Accidental Resemblance**—Bashford Dean (138) has called attention to the uncritical attitude which would claim any resemblance between an animal and its surroundings as biologically significant, without scrutinizing the evidence. He brings forward the view that accurate cryptic or mimetic resemblances may occur which mean nothing; and that in probable or imperfectly proved cases, what seems to be adaptive coloration may turn out to be accidental and meaningless. This thesis he supports by citing several striking instances of resemblances which *can* only be accidental and meaningless, and which are even more complicated than many supposed instances of cryptic or mimetic adaptation. Such, for example, are the meaningless resemblances seen in a Japanese crab, *Dorippe*, on whose carapace an oriental face is strikingly portrayed; in a whale's 'ear-bone', which suggests in profile the face of a Scandinavian fisherman; in a Japanese fish, *Salanx*, whose head appears to bear the badge of the Tokugawa family; in the Death's Head Moth (*Acherontia atropos*), with its thoracic skull and cross-bones; and in the larva of the Crane-fly (*Tipula abdominalis*), which in end-view looks like a cuttlefish. It would not be difficult to add to Dean's list other instances, like that of the well-known Sea Cat-fish (*Arius proops*), whose skull bears a rough resemblance to a crucifix; or of the

Butterfly-fish (*Holacanthus semicirculatus*), with markings that resemble old Arabic characters, ' reading on one side of the tail " Laillaha Illalah " (There is no God but Allah) and on the other side " Shani-Allah " (A warning sent from Allah) ' (446).

When one considers the overwhelming variety of form and colour and pattern exhibited by the innumerable species of animals living in different surroundings, it would be more embarrassing to have to explain the absence of such chance likenesses, than their occurrence. Their inevitable existence does enforce the demand—so often stressed in these pages—for inquiry and proof into the particular instances of supposed adaptive significance, but their occurrence cannot be reasonably used as an argument against the theories of concealing coloration and mimicry.

(2) **Classes of Facts which cannot be Explained as Fortuitous**—If the various optical devices making for inconspicuousness are fortuitous and incidental, rather than adaptive, then how can we explain the following classes of facts ?

(1) In the case of cryptic resemblances, the very optical principles upon which, in theory, concealment must depend, are those actually employed and applied in nature. Can chance explain, for instance, the combined use in one animal of colour-harmony, obliterative shading, and disruptive coloration—to say nothing of habits which in relation to an animal's particular surroundings and mode of life add further significance to its appearance ? or the widespread occurrence of obliterative shading in all kinds of animals and in all kinds of environments ? or the relationship between pattern and anatomy exhibited in the various types of coincident disruptive coloration ?

(2) Within group after group of animals occupying, severally, widely different types of environment, a general or a special correlation is often found between the coloration of different species and that of their respective surroundings—as reflected, on a wide scale, for instance, in the anticryptic colour-schemes of cats (Felidæ), and in the procryptic colour-schemes of grasshoppers (Acridiidæ) ; or on a narrower scale, in the cryptic races of rodents, larks, lizards and other animals whose range extends over differently coloured surroundings. Such diversity of appearance, correlated with diversity of surroundings, and occurring in more or less closely related animals, cannot reasonably be ascribed as accidental.

(3) With special cryptic resemblances, in case after case the deceptive appearance depends upon accurate simulation of form, frequently involving marked structural modification and divergence from type ; upon close reproduction of detail, involving resemblances of colour, design, and texture ; upon adaptations of behaviour, involving special cryptic attitudes ; and upon deceptive movements, adaptive stillness, special feeding habits, and other factors described in another place. The combined result of these factors, as seen, for instance, in *Podargus*, *Phyllium*, *Eremocharis*, or any one of many other examples mentioned in this book, would hardly support the view that the phenomena are chance effects, without biological significance.

(4) In different types of environment, such, for instance, as the Sargasso weed, or the bark of forest trees, or the sand and rock of desert wastes, or the sandy bottom of in-shore seas, many members, or even a great proportion of the whole fauna, reproduce the coloration characteristic of their surroundings. It must be remembered, moreover, that this common cryptic uniform worn by different members of a particular fauna has been evolved independently in group after group of unrelated forms and is reproduced in each group by different means and by modifications of fundamentally different types of coloration, structure, and habits. It would surely be ridiculous to suggest that such results are the work of pure accident.

(5) Among animals which wear two sets of colours, the one set making for concealment, the other for advertisement, a close correlation typically occurs between the disposition of the colours, the anatomy of the wearer, the attitude of rest, and the parts exposed during movement or in display—a correlation beautifully exhibited, for instance, in the various cases of flash coloration, and one which is so widespread in the animal kingdom, so precise in the individual animal, so varied in its method, and so consistent in its effect, as to preclude chance as a satisfactory explanation (p. 374).

In short, accidental resemblance is inadequate to account for any one of the above classes of facts; and taken together, these provide the strongest indirect proof that concealing coloration has been an important end, rather than an incidental by-product, in the age-long process of organic evolution.

II. THAT CRYPTIC COLORATION IS THE RESULT OF PHYSICAL OR CHEMICAL CAUSES

An argument upon which great stress is laid by certain critics, including Roosevelt and Selous, is that which attempts to explain concealing coloration as due to the direct effect of physical or chemical causes—as opposed, or without reference to, the need for concealment in nature.

The attempt to discredit the functional significance of coloration has been raised in various forms by different writers. It has been suggested, for instance, that the transparency of pelagic animals may be due to the direct influence of the medium in which the animals live (417); that the assumption of a white winter dress by Arctic animals is a seasonal response to cold (406); that the light coloration of desert animals is brought about by the effects of physical conditions (76); that the colour patterns worn by different animals are of structural origin, and correspond with underlying anatomical features (4, 333, 380, 633); and that the rapid colour adjustments in animals with chromatophore apparatus are to be accounted for as tropistic responses. Hence, it is argued, any protective or aggressive explanation of the phenomena is both unnecessary and unjustified.

(1) **Mechanism not to be Confused with Function**—These views are based upon a misunderstanding and are the result of confusing the mechanism of an adaptation in the individual, with its significance in the field: of confounding the means with the end which it serves. To account for the mechanism in terms of chemistry and physics is one thing: to account for its origin in evolution and

its function in nature is another. But such critics assume that having explained the first problem, the second problem does not arise, nor even exist. A photograph like any of those in this book may be ' explained ' in terms of variously sized dots of printing ink, reproduced through the mechanism of the half-tone process ; but this ' explanation ' does not disprove that the photograph has also a history, and a purpose.

It was Poulton, the greatest exponent of the adaptive explanation of concealment phenomena, who drew attention to the direct derivation by certain caterpillars of green pigments from their food-plant ; but he did not make the mistake of assuming that the coloration has therefore no biological use (499). Colour-change in the Dog-fish *Mustelus canis* is induced, in the dark phase, by secretions carried from the pituitary gland to the dermal melanophores by the blood (371), and in the light phase, by independent nervous action (457) : nevertheless, the result tends to be homochromatic with the fishes' surroundings, and therefore adaptive.

(2) **The Argument Illustrated in Reference to Countershading**—Again, Cunningham's experimental production of pigment on the lower side of Flounders (128, 129) has been used as an argument against Thayer's hypothesis of obliterative shading. Whether in certain cases countershading is the direct result of insolation is not known. (As Longley has pointed out (340), Cunningham's experiments demonstrate in the case of flat-fishes the power of light to recall pigment once present in the racial history, but not to induce it anew in tissues where it had never previously appeared.) What is known and beyond dispute is that its *effect* is to conceal—whatever the mechanism immediately responsible for this widespread type of pigment-distribution. But to contrast as incompatible a result produced by the direct action of sunlight, and one brought about independently by the action of natural selection, is to confuse the mechanism within the individual with the mechanism within the species. Hjort puts the matter in these words : ' I fail to see any necessity for controversy over the two theories, one claiming the colours as due to adaptation serving the purpose of protection, the other explaining them as being due to peculiar processes of assimilation. Perhaps the latter theory alone may in many cases be sufficient, but may it not possibly signify the very mechanism by the aid of which the organisms adapt themselves in order to obtain protection ? ' (431).

No explanation of countershading, from whatever cause, can be satisfactory or complete which fails to account for the *appearance produced*—an appearance whose effect in nature is to render recognition more uncertain and more difficult. If, as has been suggested, the presence of dark pigment on the backs of pelagic fishes is caused by the stimulus of light, and its absence from their bellies is due to their lower surfaces being shielded from its rays—how can we account, on the one hand, for the fact that many young fishes and other animals which live in the intense illumination at the surface of tropical seas are quite transparent and colourless ; while deep-sea fishes, which live altogether beyond the limit of effective sunlight, are as a class more deeply pigmented than any others, being uniformly coloured with the black or blackish-violet hues typical of abyssal forms? And how, on the above view, can we explain the bright coloration of nocturnal species which habitually rest by day beneath clumps of coral, or the *patterns* worn by innumerable fishes living in patterned surroundings? It appears therefore that critics who attack the theory of countershading on the above grounds impute opposite effects to the same cause. Such important exceptions are quite inconsistent with the view that sunlight is a sufficient explanation of the phenomena; but at once become intelligible in terms of adaptation. Delicate pelagic forms lack obliterative shading, but are concealed by the alternative device of transparency. Most reef-dwellers and other in-shore forms are both countershaded and decorated with disruptive patterns, in an environment where patterns are most necessary for concealment. The inhabitants of the abyss and nocturnal reef fishes, which lack both countershading and patterns, need no such protection in a world where they are already concealed by eternal darkness.

(3) **Coloration of Desert and Arctic Animals**—I have already alluded (p. 126) to the buff or isabelline or sandy hues typically found in inhabitants of the desert places of the earth, and of estuarine or coastal waters over sandy bottoms. If, in the view of J. A. Allen (5), the pale coloration in deserts is due to climatic conditions such as insolation, high temperature, and aridity, then how can we account for the similar style of coloration in marine forms, living over a similarly coloured background, but in an environment where the physical and physiological conditions of life, as well as the anatomy and affinity of the animals themselves, are so widely diverse?

Regarding the local races of desert mammals, which have been so extensively studied in south-western North America, we have already referred to the difficulties of attributing the phenomena of colour-resemblance on different soils to atmospheric causes. Not all desert races are pallid. It frequently happens that differently coloured races of the same species occur on adjacent mountains which differ in no important detail either as regards climate or vegetation. Many rock-dwelling mammals from dark-coloured lava-beds are themselves exceptionally dark in colour. Conversely, pale races occur in regions of high humidity on soils which for one reason or another are unusually pale. While Skunks provide a significant exception to the general tendency towards colour-resemblance so widely present in other mammals of the region.

Again, as already mentioned, the white of Arctic mammals and birds has been ascribed to the effects of cold. Yet several forms, like the Sable, Glutton, and Raven, which come under the influence of this very factor which is supposed to have produced whiteness, remain brown or black throughout the year—an inconsistency which is at once explained in terms of appearance and habits, for they are forms in which for one reason or another white coloration is unnecessary. Thus the Raven, an omnivorous scavenger, with no potential enemies to fear, retains his black coat in winter; while the Snowy Owl, a predator to whom cryptic dress must undoubtedly be advantageous when hunting by daylight during the long Arctic summer, is clad in white both summer and winter. The Polar Bear, Arctic Fox, and Ermine likewise wear a white hunting habit, the first throughout the year, the others during winter; but the Sable, who is partly frugivorous and lives and hunts prey among fir trees, with whose bark its rich brown coat harmonizes; and the Glutton, who is exclusively nocturnal and partly a carrion feeder—both retain a brown dress throughout the year.

Similarly with different herbivorous animals: in North America the Moose and Reindeer and the Musk Ox are protected by large size and gregarious habits, and lack the white cryptic coloration assumed in winter by the Prairie Hare and Willow Grouse, to whom inconspicuousness is the main means of protection. In the north of Scotland, the Pine Marten and Rabbit both retain the dark pelage at altitudes in which the Stoat, Weasel, and Mountain Hare assume white. But the former, unlike the terrestrial weasels, is chiefly arboreal; and the latter has a ready means of retreat in its warren.

(4) **Disruptive Patterns Independent of Underlying Structure**—In regard to the patterns and markings of animals, attempts have been made by Tylor (633), McCook (380), and others to refer these to a basis of underlying structures, such as ribs, nerves, blood-vessels and so on. Doubtless in some cases this may provide a partial explanation of the mechanism by which different elements in the pattern develop in the individual. But, as we have seen from a study of the distribution and form of disruptive markings on the body, any explanation in terms of structure alone is quite inadequate. The plain fact is that such patterns are, on the contrary, completely independent of anatomical units, both in their form and disposition. Frequently they cross all barriers of structure, traversing different organs, meeting across independent parts of the body, or even spanning spaces between them—*in complete disregard of structure, except where structure can be enlisted to enhance the appearance produced, an appearance whose effect is to make for concealment and to render recognition by the eye more difficult.*

(5) **The Adaptive Nature of Concealing Coloration**—The argument may be illuminated if we refer for a moment to another type of protective or aggressive adaptation, such, for instance, as speed. In these days of rapid locomotion, and of speed-adapted ships, submarines, motor-cars, aircraft, and railway locomotives, every one has a rough idea of what is meant by the term ' streamlined '. There is a certain definite type of body-contour conforming to mechanical principles, which tends to eliminate resistance to movement through a relatively dense medium and which therefore makes speed possible (just as there are definite types of coloration which conform to the optical principles which tend to obliterate visibility, and which therefore make concealment possible). Such a contour is seen in the streamlined form of certain Squids, Sharks, Tunnies, Ichthyosaurs, and Dolphins, where it has evolved independently in different classes of animals living in a similar habitat (just as common cryptic dresses have been assumed by unrelated animals from particular environments, like the dust-coats of desert animals, or the green mantle of innumerable tropical tree lizards, tree snakes, tree frogs, and tree-dwelling Coleoptera, Hemiptera, and Orthoptera). Now there is a

sense in which the streamlined form of these animals has been moulded and determined by the surroundings in which they live (272). But that it is also correlated with *the kind of life which they lead in those surroundings*, namely, that it has been developed in relation to the need for speed, is evident from the fact that numerous other ocean-dwellers have bodies shaped far otherwise, adapted for floating, for sailing, for leisurely swimming movements, for rocketing, or for lying in ambush ; and I would stress the point here that whatever part the environment may have played in producing the streamlined form, this spindle-shaped contour so beautifully seen in the Squid (*Todarodes sagittatus*), Blue Shark (*Carcharinus lamia*), Ocean Bonito (*Gymnosarda pelamis*), Mackerel (*Scomber scombrus*), Killer Whale (*Orca gladiator*) and Dolphin (*Delphinus delphis*) has no meaning *except in relation to the need for speed.* Critics of the concealment theory on the present grounds would be obliged to admit by analogous reasoning that speed is not the function of a streamlined contour (just as they argue that concealment is not the function of cryptic coloration) : whereas those who support the concealment theory hold that concealment, like speed, is functionally significant, and indeed vitally important to different animals, which depend upon it as a means of securing prey or of avoiding capture.

In making the above remarks I must not be understood to doubt the evidence that in different cases environmental factors such as light, temperature, food and so on, lead to the production in individual animals of different types of cryptic colours. What I do stress is the point that any ' explanation ' of cryptic phenomena is incomplete and unsatisfactory which does not take into account the *appearance produced*—an appearance in which we see expressed the end, or objective, of concealment from the eyes of enemies or prey. In short, these are complementary aspects, rather than contradictory explanations, of the same phenomena. The immediate chemical and physical mechanisms are different in different circumstances : the underlying optical principles are the same in all ; and these can never be fully understood except by studying the habits and interrelations of animals in the field—a procedure which provides a ready antidote for the confused thinking which fails to distinguish between principles and objectives, and the ways and means of attaining them. The fact is, the close and learned scrutiny in the laboratory of the materials and mechanisms involved in the production of coloration phenomena has tended to distract attention from the use made of these materials and mechanisms in a state of nature—as though in the chemical and mechanical analysis of a bird's nest its function as a nursery for the young were forgotten.

III. THAT ANIMALS WHICH LACK CONCEALING COLORATION APPEAR TO FARE AS WELL IN NATURE AS THOSE WHICH POSSESS IT

Certain other criticisms of the concealment theory are based upon such obvious fallacies that they hardly deserve serious consideration. One such is the view which would discredit the value of concealing coloration on the grounds that animals which are not concealed seem to thrive in nature just as well as those which are: or, to put the objection in another way: if concealment is of vital importance to its possessors, then why are not all animals cryptic in appearance?

Such appears to be the type of objection implied by Robson and Richards (543) when they refer to the 'capricious incidence of protective resemblance' as shown, for instance, by its high perfection in the Phasmidæ and in its comparative absence in land Mollusca; and when they refer to the obvious fact that 'there are numerous instances of animals which are not thus protected'.

This type of statement might, of course, be applied to any characteristic of animal life, such as the death-feigning instinct, or the possession of poison. If employed as an argument against the value of cryptic coloration, it would be as logical to suppose that wings are of no value to birds, nor pectoral fins to flying-fishes, as a means of escaping enemies or of capturing prey, because ostriches, and fishes in general, survive and flourish in the struggle for existence though flightless. One might as well ask: why are not all animals armoured, or swift, or venomous? Or why not all parasitic, or fossorial, or inhabitants of the deep sea? Adaptive coloration is but one of innumerable devices advantageous to animals in their complex relations to one another and to their physical conditions of life.

Because some musicians obtain a livelihood by playing the trombone, we do not inquire why all musicians are not trombone players. There is a place in every orchestra for other instruments; and in every animal community for other means of aggression and protection besides concealment. Just as every musician has his particular part to play in the orchestra, so each species has a particular role to act in nature—where the cast is so rich and varied in every theatre that no one familiar with the performance would expect to find all the actors dressed only for cryptic parts.

It is an objection of this sort which Buxton implies when he suggests that the coloration of desert animals cannot be protective because certain desert forms like the Raven, and various beetles, are conspicuously dressed in black. Such a dress, he believes, must be regarded as unsuitable, 'unless we discard the theory of protective coloration' (76). Yet, in certain cases at any rate, his exceptions support rather than discredit the theory, for they refer to animals whose habits preclude the necessity for cryptic resemblance. Wheatears, for instance, are active, restless birds, extremely wary and alert in their habits; moreover, they do not rely upon concealing coloration during the critical breeding period, for the nest is well hidden in holes beneath stones, or in rock-clefts—hence they do not need desert coloration. The same applies to the Raven, who depends upon concealment neither for food nor for safety, and who wears his conspicuous black plumage from the Arctic snows to desert wastes. On the other hand, as we have already seen, the species whose habits place a premium upon concealment are typically dressed in the cryptic garb of the desert.

Similarly, in regard to the theory of warning coloration, Cuénot (124) raises the objection that different noxious animals, such as the Torpedo and many toads and poisonous snakes, are cryptically coloured. But there is nothing irreconcilable in the fact that some well-defended forms rely upon concealment as a first line of defence or as a means of approaching their prey unnoticed, while others gain an advantage by being recognized through their conspicuousness as easily as possible.

The answer, then, to the present objection is that each case must be considered on its own merits. Each animal has its special mode of life, each occupies its own niche in the environment, each has its own relation to the community of which it forms a part.

IV. THAT ANIMALS DO NOT RESTRICT THEMSELVES TO THE BACKGROUNDS WHICH THEY RESEMBLE

Most animals are active creatures, whose habits bring them into contact with a variety of surroundings. Cryptic coloration can therefore rarely approach perfection; but the theory that concealment is useful as a means of protection or aggression does not demand perfection. However, in this connexion, the following classes of facts are relevant: (1) Many animals in many types of environment do bear a very remarkable resemblance to their normal surroundings. (2) The resemblance reaches its highest development in animals which tend to be restricted to definite surroundings—as with most inhabitants of sea-weeds and deserts; or which are associated with a particular habitat during critical periods in the life-history—as many caterpillars are with their food-plant, and many birds with their breeding-ground; or which instinctively retreat for protection to the shelter of the environment which they resemble—as in certain coral fishes. (3) Where there is no such correlation between colour and surroundings, an explanation is usually to be found in the conditions of life—as, for instance, in the extreme case of deep-sea or cave animals, where adaptive coloration could be of no use because it could not be seen, and where, in actual fact, it is not worn. It is significant that such animals typically lack the *patterns* which constitute so essential an element in the disguise worn by most cryptic forms.

It must also be remembered that the observation of, say, a number of different species of birds, or of fishes, in the same place and at the same time, does not imply, as some writers like Dewar and Finn (140) seem to suppose, that they occupy the same habitat. Some may be feeding beyond their usual haunts while others are resting within them; some may be on the limit of their geographical range while others are in its centre; some may be restricted to one habitat while others are wide-ranging. In any attempt to assess the biological status of any species as regards coloration, account must be taken of many factors—of its geographical distribution and its ecological habitat; of its diurnal activities and seasonal movements; its food and methods of feeding; its attitude and place of rest; its instincts, its enemies, and its means of defence.

V. THAT SUPPOSED CRYPTIC RESEMBLANCES ARE DEVELOPED BEYOND THE POINT OF USEFULNESS

Another argument is that which criticizes the adaptive interpretation of cryptic coloration on the grounds that it is often unnecessarily detailed and perfect. This difficulty with respect to 'the last touches of perfection' is referred to by Lull, who asserts that '*Kallima* goes too far, as a much less perfect imitation would be ample for all practical purposes and we cannot conceive of selection taking an adaptation past the point of efficiency' (370).

(1) **The Competition and Search for Food**—Any one who takes the trouble to study the food and feeding habits of birds in a state of nature will find that, as a group, they are extraordinarily thorough, versatile, and ingenious in their methods of securing food. Whether their habits of life are due to tradition, to imitation, or to experiment, they exploit every available food-supply, they explore every environment, they employ every imaginable device for finding and capturing prey. To take as an illustration insectivorous species: in whatever habitat insects are found, there, too, are found birds which prey upon them—on the seashore and the desert's sandy face, in the smallest copse and the mightiest rain forest, in temperate meadowlands and subtropical savannahs, on coastal plains and mountain-tops. Or, if we consider the methods of obtaining food, once again we see endless versatility in the aggregate and adaptability in species and individuals. In the quest for insect food, Titmice and Goldcrests explore twigs and foliage; Woodpeckers chisel into bark; Nuthatches and Tree-creepers explore its surface; Sunbirds and Humming-birds probe into blossoms; Flycatchers and Bee-eaters sally forth from a perch and capture prey in the air; Nightjars, Swallows, Martins, Swifts, and Hobbies hawk on the wing; Flickers and Wagtails and a host of others hunt on the ground; Starlings and Tick-birds hunt on the backs and bellies of other animals.

Or again, if we consider another type of prey, it is the same story. For instance, the hosts of fish-eaters—Darters, Skimmers, Herons, Kingfishers, Ospreys, Pelicans, Cormorants, Gannets, Kittiwakes, Guillemots, Skuas, and Penguins: each has its special hunting-grounds—river, loch, estuary, inshore waters or open sea: each has its special hunting methods—flying or hovering over the water; perched above it, or standing in it; seizing with talons or spearing with the beak; plunging from on high, or somersaulting from the surface; fishing in companies, or in solitude; by sudden ambush, or by determined pursuit.

Moreover, when we study the special feeding behaviour of individual birds, we have further evidence of how skilful, how successful, are their methods of detecting different kinds of prey in nature. This is well illustrated in the case of the Poplar Kitten Moth (*Cerura bifida*). The pupa of this moth, which is found on the bark of Lombardy poplars and aspens, is enclosed in a cocoon composed of gnawed bark fragments, which effectively conceals it from human eyes. Yet various bark-feeding birds readily detect these cocoons, pick holes in them, and extract the pupæ. The Rev. Miles Moss tells me that at Cambridge and Norwich he has frequently found plundered cocoons from which the pupæ had been ruthlessly extracted by birds—their position being revealed by the dark holes in their sides, on trees where he had previously overlooked them in spite of the most careful and diligent search. But the birds, whose habit of tapping plays an important part in penetrating the disguise (503), and whose sharp eyes are far better attuned to their environment, and go far more intimately into its details than the most observant and experienced naturalist, discover them readily enough. Similarly certain foliage-foraging species have learned to attack cocoons like those of the Lackey Moth (*Malacosoma neustria*), by pecking a hole through the leaf against which the cocoon is spun, thus breaking in at its thinnest point (503). Different tree-feeding and ground-feeding species, like Titmice and Starlings respectively, utilize the principle that a moving insect is more easily found than a stationary one, and systematically hunt in companies, individuals benefiting when insects are disturbed by other members of the flock. This habit reaches its most specialized phase in the association of certain ground-feeding insectivorous birds with herbivorous mammals, for the purpose of capturing prey disturbed by the feet of their large allies. It is particularly interesting to find, that as with other feeding methods, this trick has been learned independently by several unrelated species and is practised in many different parts of the world. Thus in England, Pied Wagtails may frequently be seen closely attending sheep and cattle; in Paraguay cattle perform the same office for Ani Blackbirds (547); in Kenya, Buff-backed Egrets associate with Elephant and Buffalo (466); and in the Sudan Elephants are followed for the same purpose by Kites and Grey Herons (92).

What we have said here applies in general to other classes of active predators, to fishes, frogs, lizards, and mammals. Now in the face of all this activity —born of hunger—which has led all kinds of predatory animals into every type of environment, and every type of habit, for the search and capture of prey by every possible means, can any reasonable person doubt that any modification of form, or of colour, or of habit which renders such prey more difficult to discover, more difficult to capture, or more difficult to digest, is of value to its possessor in the ceaseless struggle for life?

(2) **The Struggle for Safety**—Naturalists have always been impressed by the stress of existence, and the struggle for food and for safety, in tropical forests. By day and by night the search for prey goes on. This is what the Rev. A. Miles Moss, after years of close study in the forests of South America, says in regard to the early stages of Hawk-moths, the name of whose predatory enemies is legion, including innumerable birds, mammals, lizards, snakes, tree frogs, toads, and insects: 'Assiduous and prolonged searching results in the discovery of many ova and young larvæ of these species on the out-branching tendrils and freshly expanding leaves, but not for long will you find them there. A number of empty egg-shells and recently nibbled leaves too often betoken only that the devourer has been devoured. A fortnight later you will be fortunate if you discover a

single caterpillar that had somehow escaped detection, and become too tough and fat or too snake-like to be eaten ; for in such positions the waste must be enormous, and it is clear that only the merest fraction of this potential life can ever reach maturity. Considering the perpetual depredations of lizards alone or in conjunction with other foes, the marvel is not that the majority of butterflies and moths are scarce hereabouts, but that many species which are rare survive at all' (420).

In regard to predatory insect foes he states : 'The attack of a common black predatory wasp has recently been very clearly demonstrated to me, still further explaining why the healthy young caterpillar of yesterday is no longer to be found on his perch to-day. In an attempt, which should otherwise have succeeded, to introduce a hardy species of *Citheronia*, found commonly at Pernambuco but unknown here, I reared some 300 young larvæ from the egg. These were kept in the protection of my bathroom until they had reached the second or third instar, and were an inch or more in length. Then, considering them tough enough to withstand the elements, and sufficiently heavily spined to ward off predatory foes, I placed them out in a large net open at one end upon a guava tree with profuse leaves in my churchyard. Three days later my 300 were reduced to 3 by this miserable black thief, several specimens of which were seen still exploring the boughs, while one was actually inside the net munching at mangled remains. As no further trace of the rest could be found, I presume that the majority had been carried off to the nest.'

(3) **Methods of Defence Correlated with Powers of Attack : Nature's Armament Race**—Seen in this light the argument that a particular cryptic device is too perfect to have been produced for purposes of protection seems singularly unconvincing. I see no more reason for doubting that the appearance of an insect like *Tanusia* (perfected by the leaf-like form of its tegmina, whose variegated coloration simulates the onset of decay, whose emarginate edge suggests a gnawed leaf, whose hyaline spots resemble irregular holes, and dusky markings greyish fungoid stains) is correlated with the need for concealment; than that the form of a fish like *Scomber* (perfected by the streamlined form of its body, to whose smooth and graceful curves even eye and operculum conform, so that no irregularity of contour may hinder its progress) is correlated with the need for speed. Before asserting that the deceptive appearance of a grasshopper or butterfly is unnecessarily detailed, we must first ascertain what are the powers of perception and discrimination of the insects' natural enemies. Not to do so is like asserting that the armour of a battle-cruiser is too heavy, or the range of her guns too great, without inquiring into the nature and effectiveness of the enemy's armament. The fact is that in the primeval struggle of the jungle, as in the refinements of civilized warfare, we see in progress a great evolutionary armament race—whose results, for defence, are manifested in such devices as speed, alertness, armour, spinescence, burrowing habits, nocturnal habits, poisonous secretions, nauseous taste, and procryptic, aposematic, and mimetic coloration ; and for offence, in such counter-attributes as speed, surprise, ambush,

allurement, visual acuity, claws, teeth, stings, poison fangs, and anticryptic and alluring coloration. Just as greater speed in the pursued has developed in relation to increased speed in the pursuer ; or defensive armour in relation to aggressive weapons ; so the perfection of concealing devices has evolved in response to increased powers of perception, which in many predatory animals, and especially in birds, are of such an order that there is no reason to believe that even the most elaborate cryptic uniforms of tropical insects like *Tanusia* and *Kallima* have been developed beyond the degree of usefulness.

VI. THAT BIRDS AND OTHER KEEN-SIGHTED ENEMIES ARE NOT DECEIVED EVEN BY THE MOST PERFECT CRYPTIC DEVICES

Another objection—the very opposite of the last—has been raised by different writers, namely, that the deceptive resemblances of procryptic animals are not sufficiently perfect to deceive birds and other keen-sighted enemies, against whom the most elaborate disguise is foredoomed to failure.

Selous (562) expressed it as his belief that to a Bushman, with his highly trained powers of visual perception, there is no such thing as protective coloration. He suggests that similarly the sight of predaceous animals ' would have become so perfected that no colour or combination of colours could have concealed any of the animals on which they habitually preyed '. That the South African Bushman, or the South American Indian, or different animals, are vastly superior to the European in their ability—born of life-long experience—to detect their quarry in the field is beyond question. But if—as cannot reasonably be doubted—the optical effect of cryptic coloration is *to increase the difficulty of recognition*, this increased difficulty will be experienced by the owner of any eye capable of forming a clear optical image, however practised the brain behind it may be.

(1) **Effective Protection is purely Relative, and does not Imply Immunity from Attack**—It is argued that birds penetrate the deception with a facility far superior to that of man, and destroy insects wholesale, in spite of their so-called ' protective ' coloration. Now of certain insectivorous species this is probably true ; but as an argument against the theory of concealment it cannot be seriously entertained. No one supposes that cryptic animals are immune to attack. Nor does the view that such animals depend for safety upon concealment demand that they should be.

Much of the active life of such birds as Goldcrests, Titmice, Wrens, Nuthatches, Tree-creepers, and Woodpeckers is spent in searching bark for insects and spiders. Judd (297) has shown that many species habitually feed on protectively coloured weevils, grasshoppers, and geometrid larvæ. But because the deception often fails, surely we are not justified in arguing that it is therefore useless in the struggle for life : to do so would be about as logical as to regard casualties due to night-raids on a darkened city by hostile aircraft as proof that precautions for ensuring darkness are of no avail as a means of defence against aerial attack. This view is obviously ridiculous : yet it is frequently brought forward as an argument to show that concealing coloration cannot be intended as a means of defence from enemies.

Doubtless one cause of this misunderstanding is the nature of the evidence usually available. When on examining a bird's stomach we find entombed within it the corpses of procryptic insects, we have what looks like a positive record of failure on the part of concealment. But this method of inquiry provides no complementary record of the numbers of similar insects which escaped detetection by the very adaptation which was unsuccessful in their fellows. We see the failures, but not the successes.

(2) **The Value of Protective Adaptations Illustrated in Reference to Autotomy**—This point can be made quite clear if we examine—by way of analogy—a protective adaptation which differs from concealing coloration in the essential feature that *positive proof of its effectiveness as a means of defence in nature can be readily obtained.* Now such an adaptive feature is afforded by the tails of certain lizards. Different species, belonging to families including Gekkonidæ, Teiidæ, Gerrhosauridæ, Lacertidæ and Scincidæ, have, as is well known, the power of self-mutilation or 'autotomy'. Owing to their speed and agility, or to their skulking habits, and to the nature of their surroundings which afford numerous hiding-places, they are difficult to capture and enemies often succeed only in seizing them by the tail. When this happens, the tail is rejected and left executing the most violent wrigglings and contortions in the grasp of its pursuer, whose attention is thus diverted while the lizard is running off into a safe retreat. Subsequently the lizard grows a new tail, which, however, differs from the original organ in its aberrant scaling and absence of vertebræ. This habit of autotomy—which involves special structural modifications in the tail and special reflex activities on the part of its owner—is clearly adaptive. By trapping a large number of lizards (as may easily be done with the aid of an empty kerosene tin and piece of tomato) and estimating the percentage of individuals with growing or regenerated tails, quantitative data can be obtained showing the selective value of autotomy. Every one who has collected lizards in the tropics knows how abundant such individuals are; and the evidence is confirmed by the finding of amputated tails in the stomachs of birds and snakes. Thus Mason and Lefroy (397) record two lizards' tails from a stomach of the Common Coucal (*Centropus sinensis*); and in East Africa Loveridge recovered a Skink's tail (*Riopa s. sundevallii*) from the stomach of a snake (*Rhamphiophis rostratus*), and two and four tails respectively of the Skink (*Ablepharus wahlbergii*) from stomachs of the Wolf Snake (*Lycophidion capense*) and Bush Snake (*Philothamnus s. semivariegatus*) (366). Nevertheless the fact remains that, in spite of autotomy, lizards are habitually eaten by various enemies, among which birds and snakes are undoubtedly the most formidable. Many birds include them in their normal diet, and in some cases they form an important item in the bill of fare, as may be seen by reference to the works of Bannerman (18), Loveridge (364, 365), Peters and Loveridge (468), Stark and Sclater (585) and other writers of African ornithology. In this region, for instance, lizard-eating species include Herons

(*Ardea*), Bitterns (*Tigrornis*, *Ixobrychus*), Storks (*Ciconia*), Eagles (*Aquila*, *Lophaëtus*), Buzzards (*Buteo*), Lizard-Buzzards (*Kaupifalco*), Harriers (*Circus*), Harrier-Hawks (*Polyboroides*), Harrier-Eagles (*Circaëtus*), Goshawks (*Astur*), Kestrels (*Tinnunculus*), Kites (*Milvus*, *Elanus*), Owls (*Glaucidium*), Secretary Birds (*Serpentarius*), Crows (*Corvus*), Ground-Hornbills (*Bucorvus*), and Kingfishers (*Halcyon*). Thus the stomach of one Buzzard (*Buteo rufofuscus augur*) was found to contain five skinks and four chamæleons (468), and a Secretary Bird shot on the Cape flats near Capetown had eaten no fewer than eight chamæleons and twelve lizards belonging to two species, in addition to one tortoise, three frogs, one adder, two locusts, two quails, and the remains of other animals (585)! In the same region lizards are preyed upon by numerous snakes, such as Bush Snakes (*Philothamnus*, *Coronella*), Leaf Snakes (*Chlorophis*), Wolf Snakes (*Lycophidion*), Tiger Snakes (*Tarbophis*), Sand Snakes (*Psammophis*), Kirtland's Tree Snakes (*Thelotornis*), Boomslangs (*Dispholidus*) and many others, as well as by Monitor Lizards and Mongooses (20, 360, 361, 363, 366). Yet because of this destruction, no one would argue that therefore autotomy is a fortuitous feature with no biological significance. And I regard concealing coloration in this light. No one imagines that concealing coloration protects at all times or against all enemies, any more than they imagine that speed, or burrowing, or nocturnal habits, or armour, or poisonous secretions, or autotomy are always effective. The value of each is a relative value.

It must also be remembered that the analysis of stomach-contents provides no record of the ill-fated animals' activities immediately prior to capture. Evidence to be considered later points to the significance of stillness, and to the kind of background against which the prey is exposed. The most specialized procryptic coloration can be of little avail to individuals which show movement in the enemy's presence, or which happen to rest in surroundings where they appear conspicuous, and these are the individuals against which selective elimination will tend to operate.

Moreover, the assumption of Entz (166) that birds are able to discern the prey at long distances, and regardless of cryptic coloration, is quite unsupported by evidence, while it is discredited by evidence considered below.

VII. THAT CONCEALMENT DEPENDS UPON STILLNESS RATHER THAN UPON COLORATION

Another type of criticism is that which would belittle the value of concealing coloration on the grounds that it is *stillness* rather than *colour and pattern* which prevent recognition. This view contrasts two sets of factors which tend in nature to be closely correlated.

The importance of stillness as an aid to concealment can hardly be overestimated. Once movement occurs, the best cryptic devices tend to become ineffectual. The greater facility with which a moving object may be recognized is nicely illustrated by the habit, referred to above, of certain insectivorous birds, such as Wagtails and Starlings, which have learned to attend sheep and cattle in order to feast upon the insects disturbed by the feet of the animals when grazing.

The biological value of immobility (whether for protection or aggression) is becoming increasingly apparent in the light of researches in the psychology of vision. Many animals are known to react almost exclusively to moving visual stimuli—in contrast to objects at rest, which they have great difficulty in recognizing. This is the case, for instance, with various well-known mammals such as dogs, deer, horses, and hares (300); with amphibians such as frogs, toads, and salamanders (402); with various lizards and fishes; with insects (168, 626), and spiders (236); and with Cephalopod molluscs such as the Octopus (52). Such animals may pay little attention to enemies or prey at rest, but react immediately movement takes place. Hence the importance of general adaptive stillness and nocturnal habits so commonly found among cryptic animals, and of the special 'freezing' and 'death-feigning' habits practised by young birds, beetles, and many other forms in moments of danger.

But it must not be thought—as has frequently been suggested—that cryptic coloration is valueless even during movement. This extreme and illogical notion has been expressed or implied by a number of writers. For instance, Beddard stated categorically: 'Absence of movement is absolutely essential to protectively coloured animals' (33): similar opinions are found in the writings of Palmer (453), Selous (562), Werner (660), and others.

Concealment depends upon a number of factors, of which cryptic coloration and immobility are two. The above writers justly stress the vital part played by stillness—a part so well acted in the field by innumerable cryptic creatures; but *whether at rest or in motion*, a cryptic colour-scheme will be relatively harder to recognize and to follow with the eye than one which is less in harmony with its surroundings.

This principle finds an application in the colour of the balls used for tennis, cricket, golf, and other games, where red or white is invariably chosen as affording the greatest contrast and the easiest recognition against a background of grass. No one who had attempted to play hockey with a grass-green ball would make the mistake of doubting the relative value of cryptic coloration in a moving object.

The same principle is true in the more serious game played by wild animals. In a tropical forest cryptic lepidoptera are not easily followed by the eye when in flight. Mottram recognized the same point when he wrote 'a covey of grouse flying over heather can only be followed with the eye for a short distance; should there be a partially white bird among the covey, it can be followed over the moors for a mile or so. Entomologists find some inconspicuous butterflies very hard to capture on the wing, not because of rapid flight, but because they are being constantly lost in the background' (427). This conclusion also finds support in the changing colour-phases of reef fishes like *Iridio bivittatus*, and many others which reproduce on their own bodies the dominant hues of successive environments through which they pass (340).

In striking contrast to animals whose eyes are able to detect movement, rather than form, the ability to discriminate between shapes at rest is developed well in primates and to an extraordinary degree in diurnal birds—as may be realized by any one who carefully observes a bird feeding—seeking and selecting edible motionless objects, whether seeds or insects, from their similarly coloured but inedible surroundings in a way only possible to an eye able to appreciate instantly minute differences in size and colour, form and texture. Precise evidence for such powers of discrimination is presented by experimental psychology. For instance, Katz (300) showed that fowls were able to perceive and distinguish between different shapes. ' From green pea-pods or some other edible material it is easy to cut out figures of approximately equal area. If groups of two each of these figures are now placed before the hens so that one kind lies under a glass plate and the other on it, the birds learn very quickly to take only the kind lying on top. Later they do not touch the other kind, even if it is lying above the glass plate. Such training would not be possible unless the hens could distinguish the various shapes.'

In the light of these and similar observations, the need for, and significance of, cryptic, aposematic, or mimetic coloration in insects and other animals as a means of protection from avian enemies is apparent. Such facts have an important bearing upon the illusory shapes produced by disruptive patterns exhibited upon the bodies of cryptic animals; and indeed, when coupled with the knowledge that birds and primates and various other predators can also discriminate between different colours, throw an interesting side-light upon the interpretation of adaptive coloration in terms of protection from these classes of enemies.

VIII. THAT CONCEALING COLORATION CANNOT BE ADAPTIVE, SINCE MANY ANIMALS LACK COLOUR-VISION

The visual perception of animals, and especially the faculty for colour-discrimination—an important factor which must obviously be taken into account in any consideration of adaptive appearance—is a subject about which there is now an extensive literature, and it will only be possible here to mention certain relevant points, which we shall illustrate chiefly in reference to fishes, though, of course, they apply in principle to many other groups of animals—as potential enemies, or prey. Research on colour-vision in fishes has been carried out by Bauer (27), Behre (40), Bull (68), von Frisch (186, 187, 189), Hess (250), Hineline (259), Mast (398), Reighard (538), Washburn and Bentley (650), White (665), and many others. For a comparative survey of our knowledge in this field the reader is referred to the valuable summary by L. H. Warner (649), and to Russell and Bull (549) for a bibliography of experiments.

(1) **Colour-vision in Fishes**—Data bearing upon the much-debated and difficult problem of colour-vision may be derived from several sources, namely, (1) preference experiments, depending upon the fact that fishes respond positively or negatively to light; (2) learning experiments, depending upon the formation of an association between particular colours, and food or an electric stimulus; (3) colour-adjustment experiments, depending upon the ability of fishes to assume different colours in relation to their immediate surroundings; (4) evidence

afforded by the histology and physiology of the eye ; and (5) ecological considerations, with special reference to the interrelations of animals in nature.

One of the major difficulties on the experimental side is that of establishing evidence of *colour* discrimination as opposed to *brightness* discrimination. *Intensity* must not be confused with *wave-length.* The same colour may have widely different brightness values ; and conversely, different colours may have the same brightness value : moreover, the relative brightness values of different colours are not necessarily the same for man and different animals. Such experiments therefore call for an elaborate and careful control of the intensity factor, to insure that what is really only a response to differences of brightness may not be interpreted as a response to differences in wave-length.

One method of doing this is by demonstrating that when a food- or shock-association has been formed for light of a particular wave-length, the discrimination between this and other colours persists even when the brightness of the given colour is varied within wide limits. For example, Washburn and Bentley (650) trained a Creek Chub (*Semotilus atromaculatus*) to take food from red but not from green forceps, both forceps being presented simultaneously. When the association has been established, the red pair of forceps, which to the human eye appeared the darker of the two colours, was substituted for a red pair which appeared lighter, without interfering with the association. But Hess (250) rejects this work, and that of Reighard (538) and others on the grounds of inadequate intensity control. Later von Frisch (187) found that when *Phoxinus lævis* was trained to take yellow-coloured meat, it would snap at yellow-coloured decoys, even when shown against a long series of greys. In further experiments, *Phoxirus* trained to take food from a glass tube lined with coloured paper, would go directly to the coloured tube (even when it contained no food and irrespective of position) while avoiding a whole series of similar tubes ranging in tone from white through greys to black, and in no case confusing any shade of grey with the colour to which it had been trained.

More recently striking evidence of colour-discrimination has been presented by Bull (68) in a series of carefully controlled experiments with the Shanny (*Blennius pholis*). Conditioned motor responses were built up in these fishes by the presentation of a visual stimulus of known wave-length and intensity, followed by a mild electric shock. Once the association between light of a particular wave-length and shock had been established, the motor response was elicited by the light signal unaccompanied by shock. Discrimination was then tested by the fishes' reactions to lights of different colours. Bull eliminated the intensity factor by demonstrating that once established, the association persisted through widely varying intensities of the source of light. The behaviour of different individuals, conditioned severally to lights of various wave-length, suggest that *Blennius pholis* ' has a definite and wide range of colour vision as we speak of it '.

(2) **Colour-vision in other Groups**—As with fishes, so with birds, mammals, and insects, most of our knowledge on colour-vision is based upon training experiments. Research carried out by Porter (485), Hess (249), Yerkes and

Eisenberg (680), Hahn (225), Hamilton and Coleman (226), and others, has established the view that diurnal birds have the capacity for distinguishing between lights of different wave-lengths. In the Pigeon, for instance, Hamilton and Coleman found that the eye is but slightly less sensitive to wave-length differences than that of man.

Apart, however, from the direct evidence of experiments, it is well to remember that diurnal birds, like men, are so intimately concerned in everyday life with brightly coloured objects—in themselves, their food, and their surroundings—as to provide strong additional grounds for believing that theirs is a world, not of monochrome light, but of colour. This conclusion is certainly supported by the brightly hued advertisements, often so elaborate and striking, exhibited by the partners which they woo, the fruits which they eat, the flowers they visit, and the aposematic insects they avoid.

Recent researches on insect vision all tend to support the conclusion, as Imms observes in his summary of the subject (281), that colour-perception exists in insects. However, insects do not as a rule respond to the same range of colours as human beings. Moreover, the spectral range is not the same for different orders of insects, nor even necessarily for different members of the same order. Thus Dr. Ilse has recently shown that the well-developed colour-sense of the Peacock butterfly corresponds to that of the hive-bee, which fails to distinguish between scarlet and black ; but differs from that of the Cabbage White butterfly, which is able to distinguish red pigments from any shade of grey between black and white.

(3) **The Importance of Tone Perception, as Opposed to Colour Perception, in Relation to Cryptic Coloration**—From the above considerations it is clear that the adaptive interpretation of cryptic, aposematic, and mimetic colour cannot be discredited on the grounds that animals are colour-blind. But there is another answer to the present objection. It is true that while different members of such important groups as mammals, birds, fishes, and insects possess colour-vision, some animals are known to lack this faculty, and many others are not positively known to possess it. There is here, indeed, a vast field for inquiry, both physiological and psychological. But as an argument against the theory of cryptic coloration, the colour-blindness of some animals can carry little weight. For it will be perfectly clear to all who have studied the methods by which concealment is brought about in nature—methods which in the foregoing pages I have attempted to explain and illustrate—that the particular effects produced on the eye depend not only, and indeed not mainly, upon *conformity of colour*, but upon *modifications of tone*, as seen, for instance, in the obliteration of relief by countershading, in the general resemblance in shade between an animal and its natural background, and in the superimposition of false light and shade in the form of graded designs, or of strongly contrasted disruptive tones, or of coincident patterns. *Now the optical effects of these and many similar devices* which have evolved widely in group after group of animals, and in all sorts of surroundings, *do not depend upon colour-perception at all, but upon tone-perception*

—as may be shown by any good photograph in monochrome of a cryptic animal in its natural surroundings. Adaptive colour-schemes of this type therefore provide concealment as well from the colour-blind as from the colour-sensitive eye.

Then there are other objections which can hardly be taken seriously. A curious variation of the above argument is that suggested by Dewar and Finn (140) in connexion with the principle of countershading. According to these writers, Thayer's hypothesis rests upon the assumption that animals see with the artist's eye. Thayer rightly stressed the point that artistic sensibility is necessary for the appreciation of the *principles* upon which concealment depends, but one does not need to see like an artist to be deceived by their application. It might just as well be argued that to digest one's dinner it is necessary to be a physiologist. Countershading, like colour-harmony, disruptive patterns, and the innumerable combinations of colour, tone, pattern, and habit which make an animal inconspicuous, depends for its *effect* not upon the understanding of optical principles but upon the particular configuration of coloured and shaded masses presented to and focused upon the retina of the eye.

IX. THAT CRYPTIC COLORATION CANNOT BE EFFECTIVE AGAINST ANIMALS WHICH HUNT BY SCENT, OR AGAINST NOCTURNAL PREDATORS

One of the arguments used by Selous (562) against the protective function of concealing coloration is that various predators such as many of the Carnivora hunt by scent, and at night, when their herbivorous prey are feeding or going to drink. This latter point has also been stressed by Buxton (76). I fail to see that either objection presents any serious difficulty. The fact that some predators depend, more or less, upon scent, does not disprove the value of sight as a factor in the chase. What chance would a sightless Lion or Leopard or Fennec stand in the search for prey?

(1) **Nocturnal Habits and Visibility**—Among desert dwellers a large group of animals, including birds, mammals, and reptiles, are nocturnal in their habits. This applies to predaceous forms like Cats, Jackals, Foxes, and Owls, and to Jerboas, Gerbils, and other rodents which form their staple diet. Such rodents are fossorial, and are therefore only exposed to attack when they venture abroad after darkness has set in. Hence it has been argued that the pale coloration of these creatures is of doubtful value, because, as Buxton puts it, ' even by moonlight colour hardly exists, and the differences between shades of colour are not appreciated ' (76). I cannot agree with this view. The question of *colour* being visible by moonlight hardly arises, as it is essentially *tone* which must afford concealment under such conditions. His statement regarding the appreciation of shades is quite unacceptable. Referring to localized races of Deer-mice (*Peromyscus*), Sumner (595) uses the same argument against the utility of concealing coloration, which he regards as being doubtful in the case of animals almost entirely nocturnal in their habits.

Darkness in the desert is a very different thing from darkness in the forest or beneath the clouded skies of temperate regions. Every one who has visited a desert knows how clear is the starlight, which renders near objects visible even to human eyes; while on moonlit nights the scene is bright with a flood of silver light. In the Brazilian *campo*, on the Karroo, and in the Eastern Canary Islands (and doubtless in the deserts of which Buxton writes) it is possible to read small print by moonlight: in such places it is seldom really dark.

(2) **Vision of Nocturnal Predators**—Moreover, it is important to remember that the eyes of nocturnal animals are specially adapted for effective use under twilight conditions. This specialization reaches high development in the cats among mammals, and in the owls among birds. (1) In each of these groups the eyes are adapted optically for this purpose in having a lens and iris capable of working effectively at a very wide aperture—an arrangement which is closely analogous to that seen in cameras specially adapted for instantaneous night- or theatrical-photography, and which allows the maximum amount of light to reach the retina, or plate. (2) In each they are adapted anatomically, in having their axes directed forwards (as in man), rather than outwards (as in most animals)—thus, as Graham Kerr has pointed out, giving increased efficiency in dim light owing to the superimposition of the two sets of images to form a single intensified conscious impression (306). (3) And in each they are adapted physiologically, in the special development of the rod elements in the retina which are expressly concerned with twilight-, as opposed to colour-vision.

The ability of owls to discern inconspicuous objects on the darkest of nights is mentioned by Shelford (572), who writes of his Bornean Owl (*Photodilus badius*): 'At this time I had also in captivity a young Palm-Civet, and if I carried this pet in my arms towards the end of the verandah of my house, where the Owl lived, no matter how dark the night, I would hear the loud cracking noise and great flutterings of wings, betokening violent efforts to escape, long before I could see the bird myself. If I approached alone, the Owl, being extremely tame, would show no signs of terror at all. I feel sure that the Owl was actually able to see the Palm-Civet, that it was not indebted only to its sense of smell for the power of distinguishing its enemy in the darkness, because if after handling the Civet-Cat I went near the Owl the bird was quite at its ease, though my hands and clothing must still have borne distinct traces of the effluvium which these mammals emit.'

From the above considerations it would be most rash to assume that nocturnal desert animals can rely upon the mantle of night to protect them from the special visual equipment of their enemies. On the contrary, it would appear that cryptic coloration has its place as a means of defence, and of offence, by night as well as by day.

X. THAT 'PROTECTED' ANIMALS ARE SUBJECT TO ATTACK BY PREDATORY ENEMIES

Another argument frequently used against the selective value of protective resemblances is that supposedly 'protected' forms are widely preyed upon in nature. Thus Bequaert, in his studies of the predaceous enemies of ants (48, 49), has shown that these insects, which have been regarded by various writers as especially well protected and free from attack, are in fact preyed upon by a considerable range of enemies. He appears to regard this as evidence against the supposed value of ant-mimicry. Because the aggressive habits, stings, or distasteful qualities of ants fail to protect them from the regular ravages of specialized tropical predators, such as various Frogs and Toads, Woodpeckers and Ant-thrushes, Pangolins and Tamanduas, and from occasional attacks by many other animals, it does not follow that as a group they are not well protected from a wide range of potential enemies by their various undesirable qualities. No one assumes that protective adaptations afford protection against all enemies, but against some enemies. The advantage conferred is not immunity, but relative freedom from attack.

In the aggressive and defensive ' armament race ' between potential enemies and prospective prey, innumerable devices have been evolved and elaborated which tend, on the one hand, to facilitate capture, and on the other, to frustrate it. Caterpillars, for instance, have developed safety devices along many lines. Thus some are concealed by their coloration ; but they are sought out and destroyed by hosts of keen-eyed birds. Others are defended by an armour of irritating hairs or formidable spines ; but they are attacked by specialized foes such as Cuckoos. Others wear warning coloration and are highly distasteful to most enemies ; but certain predators find them less so than others. These several devices fall far short of perfection. But they are effective in the sense that by rendering the larvæ less visible, less digestible, or less edible, in each case attack tends to be limited to particular types of predators, whereas without these protective adaptations destruction would be wholesale.

The present type of criticism finds its chief exponent in McAtee, whose paper entitled ' Effectiveness in Nature of the so-called Protective Adaptations in the Animal Kingdom, chiefly as illustrated by the Food Habits of Nearctic Birds ', vigorously attacks the generally accepted view that different protective adaptations have survival value. The misleading way in which McAtee presents his data, the illogical conclusions which he draws from them, and his unfair controversial methods (376, 377), have drawn forth a good deal of protest both in England and America. With the exception of Uvarov, who appears to have been favourably impressed by McAtee's arguments (142, 638), his thesis has been universally discredited in this country, as is evident from the replies published in *Nature* by Poulton (522), Nicholson (441), Huxley (277), and Cott (110), and in discussions held before the Royal Entomological Society of London (142), in which Poulton, Hale Carpenter, Marshall, Brindley, Fisher, the present writer, and others took part. I subsequently published a further statement in reply to McAtee's review (113) of my paper on the feeding habits of East African Tree-Frogs (111) and the controversy was terminated by Sir Edward Poulton (113). McAtee's conclusions have also been strongly criticized by American workers, including Dunn (157), Sumner (601), and Morton Jones (142).

In attempting to prove that protective adaptations of animals are ineffective against predatory birds, McAtee bases his conclusions upon the principle of 'proportional predation '. ' Within size limits,' he says, ' animals of practically every kind accessible to birds are preyed upon, and as we consider the records for group after group a tendency for the *number of captures* to be in proportion to the *abundance of the animals concerned* is unmistakable ' (italics mine). The above statement is most misleading. In the first place, when speaking of the ' number of captures ', what he really means is the number of stomachs from which captures were taken. By presenting his data in these terms, McAtee withholds the essential figures which we require in considering the efficiency of protective adaptations, namely, those which show the relative numbers of prey captured, rather than the number of stomachs from which the prey is recorded ; and at the same time he adopts a method of tabulation which, by itself, may give an entirely false notion of the proportions of different kinds of prey actually eaten. According to his method of treatment, a grouse which had inadvertently swallowed an ant when filling its stomach with heather shoots, would count equally as an ant-eater and a vegetarian ; or a bird whose stomach was crammed with a mass of insects of a single kind, amounting perhaps to hundreds of specimens, would be recorded no differently from one which contained but a single example of the same insect.

In the second place, McAtee's method of estimating the ' abundance of the animals ' available as prey is open to question. It rests upon the assumption that the relative number of species in a particular group is necessarily a fair index of the absolute abundance of individuals in nature.

McAtee's next proposition is that birds feed indiscriminately. ' Availability undoubtedly is the chief factor involved in the choice of food, and predation therefore tends to be in proportion to population. Considering bird predation alone this principle leads to a high degree of indiscriminacy in attack upon the whole kingdom of animal life.' This fallacious belief depends, again, upon the misleading way in which he presents his data. McAtee's arguments, intended to show indiscrimination, show an almost complete lack of attention to the type of data which are most essential and relevant, namely, analyses of food eaten by *individuals* and by *species*. His method is to lump all the records together, so that the stomach contents of some 80,000 individuals belonging to over 500 species of birds scattered through the Nearctic region, and taken from every type of habitat, appear in his statistics as though representing the food of a single collective ' predator '. This collective treatment of the data for an entire bird-fauna shows (what is to be expected) that some species of each large group of animals are preyed upon by birds as a class, and that there is a tendency for the most abundant prey to have the most numerous enemies. But that is the familiar and inevitable result, *not of indiscrimination by species but of adaptive radiation within a group*. Almost any sufficiently large and well-differentiated group of animals would furnish comparable results, as might be seen, for instance, in the feeding habits of marsupials or placental mammals, fishes or lizards, crustaceans or insects.

The best method of testing whether or not different animals discriminate in the choice of food is to compare the feeding-habits of predatory forms living in the same environment, where the same food is available for different species. If predatory animals are indiscriminate feeders, and if ' availability ' be such a ' mighty factor ' as McAtee supposes, then we should expect to find that ' within the limits imposed by . . . bodily modifications, and the relative sizes of predator and prey ', different birds and other animals feeding in the same environment would agree closely in their diet. Now when such a comparison is made, marked divergences are observed in the food of different species, and selective discrimination—so vigorously denied by McAtee—is found to be the rule rather than the exception. The presentation of the evidence for this will be deferred until our discussion of the theory of Warning Coloration (see p. 290).

We must now turn to examine the direction from which McAtee launches his main attack upon the selectionists' stronghold. After repeatedly stressing his opinion that ' the ruling criterion in choice of food is availability ', and that birds are indiscriminate feeders, he states his third proposition : ' In other words there is utilization of animals of practically every kind for food approximately in proportion to their numbers. *This means that predation takes place much the same as if there were no such thing as protective adaptations. And this is only another way of saying that the phenomena classed by theorists as protective adaptations have little or no effectiveness* ' (italics mine). With these words McAtee apparently dismisses as relatively ineffective such characteristics in prey as stings, spines, stinking fluids, poisonous secretions, armour, burrowing habits, concealing coloration, warning coloration, mimicry, speed, and any other protective adaptations whatsoever. Now it would be just as logical to argue that because in an engagement a number of different units of infantry, artillery, tanks, and aircraft were found to suffer casualties approximately in proportion to their respective numerical strength, this means that casualties occur much the same as if there were no such thing as means of defence. And this is only another way of saying that the phenomena classed by theorists as bayonets, barbed-wire entanglements, poison gas, flame-throwers, armour-plating, entrenchment, camouflage, deception, strategy, and mobility have little or no effectiveness ! Or again, when a number of towns are subjected to a night air-raid by bombers, if the casualties in each are approximately proportional to the respective populations, this proves that air-raid precautions—including fire-fighting equipment, ambulance units, bomb-proof shelters, and the extinction of all lights visible to the hostile airmen—are ineffective as a means of defence !

Let us put the matter in another form. In any large photographic exhibition, such as the Annual Exhibition of the Royal Photographic Society of Great Britain, the number of entries submitted in each section—Pictorial Prints, Monochrome Lantern Slides, Colour Prints, Colour Transparencies, Photomicrographs, Astronomical Photography, Natural History Photography, Stereoscopic Prints, and so on—normally far exceeds the number of exhibits finally selected for exhibition by the judges. In some cases the rejections may reach a high percentage—say 90 per cent. of the total. There is thus a heavy ' mortality ' due to elimination by a ' predatory ' selection committee. Now let us suppose for the sake of argument that the rejections or ' casualties ' in each section are proportional to the number of entries. According to McAtee's reasoning, this is evidence that the selection committee are indiscriminate in their elimination of entries, and the ' protective adaptations ', which set the standard for survival—and which in our analogy are characteristics such as pictorial merit, composition, and design, qualities of colour and tone, originality, scientific value and the like—are relatively ineffective in the competitive struggle for a place on the limited wall-space.

The fallacy in McAtee's central argument is therefore sufficiently obvious. Supporters of the theories of adaptive coloration do not claim that cryptic or aposematic or mimetic species are not attacked, but rather that certain individuals among those species are, or have been in the past, less attacked than others. The point has been expressed by Huxley in the following words : ' A species is only adapted to *survive*, not to become immune from all enemies ' (277). Whether or not such animals are eaten in proportion to their abundance in nature is still an open question. But the real point at issue is to determine whether the proportion, whatever it may be, would remain the same in the absence of the so-called protective adaptations.

If, in a collective sense, proportional predation takes place, it merely goes to show that a balance is being maintained in nature as between different types of prey, and that the various types of protective adaptation are of approximately equivalent survival value to their respective owners. But this is an entirely different thing from saying that such adaptations are valueless.

XI. THAT THE THEORIES OF ADAPTIVE COLORATION ARE BASED UPON ANTHROPOMORPHIC CONCEPTIONS

Finally, there is the type of criticism raised by Verne (640), Cuénot (126), Uvarov (637), and others, which attempts to discredit the theories of adaptive coloration as ' teleological ', ' anthropomorphic ' or ' finalistic '. This objection is mainly another version of the outworn creed which accounted for the theories as nothing but the dreams of ' amiable closet theorists '. Unfortunately for this type of criticism, the phenomena of adaptive coloration are expressions of living animals existing in a state of nature, where alone the picture they present can be seen in proper perspective. Consequently those best qualified to form a reliable judgement on such matters are observers of wild life. But the above arguments are characterized by the fact that they emanate mainly from the laboratory. With few exceptions, the most dogmatic critics have been (to use the old terminology) 'closet naturalists ' or ' armchair theorists '—museum or laboratory specialists with little experience or knowledge of wild life in the field, and hence singularly ill-equipped to criticize theories explaining facts with which they are only remotely acquainted. On the other hand, it is significant that the greatest supporters of the theories of concealing coloration, warning coloration, and mimicry have almost without exception been naturalists in the true sense, with a wide and intimate experience of animal life in nature, and more especially in tropical nature. In support of such a statement it is only necessary to recall the names of the pioneer naturalists and explorers—Darwin and Wallace, Bates and Müller, and the recorded opinions of many other highly qualified observers of wild life, such as Alcock, Belt, Hale Carpenter, Graham Kerr, Hingston, W. H. Hudson, Julian Huxley, Miles Moss, Mortensen, Poulton, Shelford, Swynnerton, and others whose extensive experience of field natural history has convinced them of the adaptive significance of these phenomena. To quote a single opinion—this is what Graham Kerr says: 'Many of the attacks on Darwinism have emanated from the laboratory and the study, and for the reason indicated deserve far less attention than they have received. Certainly in my own case I found this type of criticism far more formidable in appearance at first than later on after I had had the intensity of the struggle for existence borne in upon me by actual experience in the tropics. It is, I think, a sound principle when assessing the degree of importance to be attached to criticisms which minimize the intensity of the struggle for existence to ascertain to what extent they rest upon extensive experience in the field' (307).

But there is another side to this type of criticism which has to be borne in mind. The theory of concealing coloration has been brought to some discredit through the tendency of certain writers to be carried away from the facts by their own enthusiasm, and they have brought down storms of criticism which are sometimes misdirected against the theory itself, rather than against particular misapplications of the theory or against its over-zealous supporters. Thus we find Thayer (619) straining the theory to a fantastic extreme in an endeavour to make it cover almost every type of coloration in the animal kingdom. He says: 'All patterns and colors whatsoever of all animals that ever prey or are preyed upon are under certain normal circumstances obliterative.' Unfortunately certain of Thayer's explanations and illustrations misrepresent nature and are deceptive because they depend upon observations made under abnormal circumstances. For instance, in an attempt to explain that certain colours have an obliterative function because they fade into the sky against which they are seen, he has a coloured illustration of a Peacock among woodland surroundings, his neck exactly matching and blending into a patch of blue sky seen through the foliage. Then, again in colour, the author figures a flock of red Flamingoes matching a red sunset sky. Another picture shows a Roseate Spoonbill whose pink plumage matches a pink cloud scheme. And in the same work the white plumage of a white Flamingo, the white dorsal markings of the Skunk, and the white rump of the Prong Buck are explained as blending against the sky—while an obliterative function is assigned to the colours of such diverse animals as Crows, Oyster-Catchers, Skunks, and Heliconiid butterflies.

Truly, as Roosevelt (546) has stated in his criticism of Thayer's work: 'No color can be imagined which will not become inconspicuous, whether on an animal or off an animal, if against certain backgrounds. . . . The raven's coloration is of course concealing if it is put into a coal scuttle; and if chalk is added to the contents of the coal scuttle, then a magpie's coloration might also become concealing under the same circumstances.'

Now I wish again to emphasize the point that adaptive coloration—in all its varied aspects of concealment and advertisement, deception and recognition, mimicry and adornment, and in all its varied references to potential enemies and prey, mates and rivals—must take its place among, and be regarded as one of, many classes of adaptation which operate in, and are related to, an animal's conditions of life. In this light, adaptive coloration appears to fall in line with innumerable other adaptive features of habit and structure, including powers of locomotion and of perception, and the possession of weapons, armour, poison, and many other attributes which cannot be doubted to have biological significance in the struggle for life. How unreasonable are extreme views like that adopted by Thayer will therefore be appreciated by applying similar arguments to other adaptive attributes. It is as though one were to claim that speed is universally useful in almost all types of animals, including, say, antelopes and ant-bears, tunnies and tunicates, zebras and snails. If it were true, as Thayer asserts, that Crows and Coral Snakes and Heliconiid butterflies are concealingly coloured, then surely one might as well suggest that snails are swift and earthworms heavily armoured.

Thus criticisms under the present heading—when directed against certain of Thayer's conclusions and various other far-fetched attempts to read into different colour-schemes a significance which they do not in fact possess—are, of course, justified. But because the theory has been misapplied by particular writers to particular cases, these cannot logically be brought up as evidence against the theory itself.

The theory of protective and aggressive resemblance interprets concealing coloration in terms of the vision of potential enemies and prospective prey. If it is anthropomorphic to hold that such coloration increases the difficulty of recognition, and is therefore useful in the struggle for life, then presumably it must also be anthropomorphic to believe that the possession of eyes facilitates recognition and is therefore useful for the evasion of enemies or the capture of prey.

10. THE EFFECTIVENESS OF CONCEALING COLORATION

The high hills are a refuge for the wild goats : and so are the stony rocks for the conies.
PSALM CIV, 18

The problem of concealment by form, coloration, and habits is one that has attracted a great deal of attention ; and there has grown round the subject a very extensive and voluminous literature which it well deserves, for it is one of unusual interest—embracing, as it does, some of the most remarkable phenomena in the whole field of biology. A great deal of this literature has been mainly descriptive ; and unfortunately much of it is also speculative. When we consider the great accumulation of facts and evidence which have been brought to light by the work of numerous investigators during the past sixty years, it is surprising to find that relatively few observations and experiments have been carried out expressly to test the validity of the theory of concealing coloration—in short, to decide the question : Is concealing coloration effective in practice ? Does it in actual fact assist an animal to escape detection ?

It will therefore be convenient to bring together here the evidence of observation and experiment bearing directly on this subject. In view of the heated controversies which surround the theory, it is of the utmost importance that further data and information regarding the function and effectiveness in nature of these resemblances should be obtained—especially bearing on the behaviour of wild animals in a state of freedom—and extensive studies on the following lines offer a wide and promising field for future research.

I. EVIDENCE FROM EXPERIMENTS WITH ANIMALS IN CAPTIVITY

(1) **Birds and Cryptic Prey**—Young (681) has put the theory of concealing coloration to the test in an extensive series of experiments, in which Crows, Buzzards, Owls, Martins, and other birds were offered a choice of prey exhibited against different backgrounds giving varying degrees of contrast. Several of his experiments furnished very conclusive results—as, for instance, one series in which a Long-eared Owl (*Asio wilsonianus*) chose House Mice from the background giving greater contrast eleven out of twelve times ; and another series of eleven experiments with a Grackle (*Quiscalus quiscula anæus*) and a King-bird (*Tyrannus tyrannus*) in which protective coloration was effective in 100 per cent. of the trials. Other experiments were rendered less conclusive (although in *every series* an excess of conspicuous over inconspicuous acceptance was noted) owing to the operation of a chance factor, namely, the birds' tendency to choose

that combination which happened to be nearest to their point of approach. Yet this factor showed perhaps even more clearly than the more defined results the protective value of colour-harmony in the animals used in the experiments. Out of 48 cases in which this factor was considered to operate, in 18 the birds were so far deceived as to pass by the inconspicuous combination in favour of the more conspicuous one beyond : on the other hand, in only five did the birds pass over the more conspicuous combination in favour of the inconspicuous one. From the valuable data which he has produced, Young concludes that protective resemblance in the case of motionless animals is effective as a means of protection. He also stresses the importance of stillness, which he regards as probably more important than colour in protecting animals from their enemies.

(2) **Lizards and Caterpillars**—The great importance of stillness has also been shown by Poulton (496) and Carrick (88). In 1890 Poulton proved that *so long as a well-concealed insect remains motionless* enemies are often unable to recognize it. Thus he found that the Green Lizard (*Lacerta viridis*) generally failed to detect a ' stick-caterpillar ' in its position of rest, although it was seized and greedily devoured directly it moved. The wonderful resemblance of the lichen-like, lichen-feeding larva of *Cleora lichenaria* was observed to deceive one of these lizards even after it had moved more than once. ' The instant the caterpillar became rigid the lizard appeared puzzled, and seemed unable to realize that the apparent piece of lichen was good to eat. After a few moments, however, the lizard was satisfied, and ate the caterpillar with the keenest relish.'

(3) **Adaptive Colour-change in Fishes as a Means of Protection against Predatory Enemies**—Conclusive results in this field have been obtained by Professor F. B. Sumner, whose detailed yet delightfully simple experiments (599, 600, 601) yield statistical data of considerable importance. In order to test the protective value of adaptive colour-change in fishes, he used, as prey, a small species of ' mosquito fish ', *Gambusia patruelis*. In common with many other kinds of fishes, these possess in marked degree the property of adjusting their colour to that of their surroundings : when transferred from light to dark, or from dark to light surroundings, they undergo both rapid colour-changes (due to temporary adjustment of pigment in the chromatophores) and also more fundamental colour-changes (due to gradual loss or development of pigment or of entire chromatophores).

Specimens were prepared for the experiments by a preliminary sojourn of seven or eight weeks in tanks painted inside black and white respectively. At the end of this period the fishes in the black tank had become nearly dead black on the back and sides, those in the white tank a pale buff or grey. In his subsequent experiments, equal numbers of these ' black ' and ' white ' fishes were emptied simultaneously into large experimental tanks painted black or pale-grey respectively. Here they were submitted to the attacks of various vertebrate enemies—the Galapagos Penguin (*Spheniscus mendiculus*) being the predator chosen for the first series of tests (599).

(1) During experiments in the *pale-grey tank*, 576 fishes (comprising equal

numbers of ‘ blacks ’ and ‘ whites ’) were offered as food : out of 270 which were eaten—165 (61 per cent.) were ‘ blacks ’, 103 (38 per cent.) were ‘ whites ’, and 2 (1 per cent.) were unidentified.

(2) In the *black tank*, 470 fishes (comprising equal numbers of ‘ blacks ’ and ‘ whites ’) were offered : out of 274 fishes eaten—201 (73 per cent.) were ‘ whites ’, and 73 (27 per cent.) were ‘ blacks ’.

(3) In the combined experiments, out of 542 (identified) fishes eaten—176 (32 per cent.) were colour-adapted, 366 (68 per cent.) were non-adapted.

Expressed so as to show the relative numbers of casualties and survivors among ‘ adapted ’ and ‘ non-adapted ’ fishes in the pale-grey and black tanks respectively, Sumner's figures may be tabulated as follows :

TABLE I

Discrimination / Coloration	Casualties	Survivors	Total
Adapted ‘ whites ’ in pale tank . . .	103 (36%)	183 (64%)	286
,, ‘ blacks ’ in black tank . . .	73 (31%)	162 (69%)	235
Total . . .	176 (34%)	345 (66%)	521
Non-adapted ‘ blacks ’ in pale tank . .	165 (58%)	121 (42%)	286
,, ‘ whites ’ in black tank . .	201 (86%)	34 (14%)	235
Total	366 (70%)	155 (30%)	521

In further experiments (600), the *Gambusia* were kept for a preliminary period of from twenty to twenty-seven hours in the experimental tanks before admitting the Penguins, so as greatly to diminish the difference between the two lots of fishes. Yet the evidence of selection was nearly the same as when the fishes and birds were admitted simultaneously : among 680 fishes (comprising equal numbers of ‘ blacks ’ and ‘ whites ’) available, 236 casualties (including specimens both eaten and injured) comprised 91 (39 per cent.) colour-adapted and 145 (61 per cent.) non-adapted specimens.

Sumner carried out a second series of tests (601), using a Night Heron as predator. Unlike the Penguin, which pursues its prey under water, this bird stands in shallow water, waiting for fish to come within range. It is interesting to note that in spite of this difference in the method of feeding, the results again furnish decisive evidence of selection against the more conspicuous fishes.

(1) In the *pale-grey tank*, 400 *Gambusia patruelis* (comprising equal numbers of ‘ blacks ’ and ‘ whites ’) were offered as food : out of 108 casualties (including individuals both eaten and injured)—67 (62 per cent.) were ‘ blacks ’, and 41 (38 per cent.) were ‘ whites ’.

(2) In the *black tank*, 600 fishes (comprising equal numbers of ‘ blacks ’ and ‘ whites ’) were offered : out of 255 casualties—156 (61 per cent.) were ‘ whites ’ and 99 (39 per cent.) were ‘ blacks ’.

(3) In the combined experiments, out of 363 casualties—140 (39 per cent.) were colour-adapted, 223 (61 per cent.) were non-adapted. (See Table II.)

TABLE II

Discrimination Coloration	Casualties	Survivors	Total
Adapted ' whites ' in pale tank	41 (20·5%)	159 (79·5%)	200
,, ' blacks ' in black tank	99 (33%)	201 (67%)	300
Total	140 (28%)	360 (72%)	500
Non-adapted ' blacks ' in pale tank	67 (33·5%)	133 (66·5%)	200
,, ' whites ' in black tank	156 (52%)	144 (48%)	300
Total	223 (45%)	277 (55%)	500

A third series of experiments (601) were carried out on similar lines to test the protection afforded by relative inconspicuousness against larger predatory fishes, which in a state of nature probably constitute the most serious enemies of smaller fishes. The predator selected for the tests was a blue-green Sunfish (*Apomotis cyanellus*): *Gambusia patruelis* was again used as prey.

Experiments in which the ' white ' and ' black ' specimens were transferred directly from their customary backgrounds to the experimental tanks gave the following results:

(1) In the *pale-grey tank*, 430 fishes (comprising equal numbers of ' blacks ' and ' whites ') were offered as food: out of 208 fishes eaten—137 (66 per cent.) were ' blacks ' and 71 (34 per cent.) were ' whites.'

(2) In the *black tank*, 200 fishes (comprising equal numbers of ' blacks ' and ' whites ') were offered: out of 37 fishes eaten—29 (78 per cent.) were ' whites ' and 8 (22 per cent.) were ' blacks '.

(3) In the combined experiments, out of 245 fishes eaten—79 (32 per cent.) were colour-adapted, and 166 (68 per cent.) were non-adapted. (See Table III.)

TABLE III

Discrimination Coloration	Casualties	Survivors	Total
Adapted ' whites ' in pale tank	71 (33%)	144 (67%)	215
,, ' blacks ' in black tank	8 (8%)	92 (92%)	100
Total	79 (25%)	236 (75%)	315
Non-adapted ' blacks ' in pale tank	137 (64%)	78 (36%)	215
,, ' whites ' in black tank	29 (29%)	71 (71%)	100
Total	166 (53%)	149 (47%)	315

It should be mentioned here that observations during the above experiments (besides further experiments carried out especially to test the relative *activity* of the 'blacks' and 'whites' as a factor which might influence the selection) led Sumner to conclude that in neither tank was the differential mortality due to differences in the fishes' ability to outdistance their pursuers.

Taking together the three series of tests tabulated above, we find that out of 2,672 individuals offered as prey, 1,150 casualties give a differential mortality of 395 (34 per cent.) for the less conspicuous and 755 (66 per cent.) for the more conspicuous fishes.

The results of these experiments appear all the more remarkable when it is realized that the confined quarters and the total absence of cover or means of retreat under the experimental conditions would undoubtedly tend, as Sumner points out, to make for a less discriminate capture of the prey than would occur in nature. This throws into even greater relief the intense selection of the more conspicuous fishes. It must also be remembered that as a result of this discrimination in the experimental tank, the colour-adapted fishes outnumbered their less fortunate fellows almost from the commencement of the several tests, a fact which gives the results an even higher significance.

Whether the experiments are considered severally, or together, they furnish conclusive proof of the vital importance of chromatic adjustment in *Gambusia* as a means of protection against predatory birds and fishes; and point decisively to the biological significance of concealing coloration as a means of escaping enemies which hunt by sight.

II. EVIDENCE FROM EXPERIMENTS WITH WILD PREDATORS

(1) **Birds and Lepidopterous Pupæ**—The importance of the sense of sight to enemies in discovering prey, and the danger of conspicuousness to the latter, has been clearly indicated by Poulton and Sanders (526), who in 1898 conducted experiments with the pupæ of *Vanessa urticæ*, to determine whether there is a struggle for existence in the pupal stage, and, if this takes place, whether concealment is a factor for survival. Over 600 pupæ were fixed against a variety of backgrounds which unequally concealed them, at stations in Switzerland, Oxford, and the Isle of Wight. Comparative immunity of the Swiss pupæ was attributed to the scarcity of small birds: of those exposed at Oxford, 55 were taken, and butterflies emerged from only 4 pupæ fixed among nettles: of those in the Isle of Wight the mortality on fences (90 taken, to 8 emerged) was much greater than on bark (135 to 84), on walls (14 to 12) or on nettle (20 to 15), in which situations the insects were less easily seen. The experiments proved that in localities where small birds were abundant 'there is a tremendous struggle with an immense mortality, in spite of the brevity of the pupal stage' (from ten days to three weeks), and that 'when . . . the pupa is suspended from a surface against which it stands out conspicuously, it is in far greater danger than when it is fixed to one upon which it is concealed.'

(2) **Sparrows and Lepidopterous Larvæ**—While investigating the inheri-

tance of dimorphism in the butterfly *Colias philodice*, Gerould (205) encountered a mutation which affected the blood-colour of the insect at every stage in its life-history. The normal caterpillars are grass-green in colour, and appear remarkably inconspicuous upon clover, their food-plant. The mutant caterpillars were blue-green, and consequently appeared as conspicuous as ' blueberries on a bush '. The relative value of cryptic coloration in preventing attack by birds is indicated by the following observations. A mixed stock of larvæ, including between a third and a quarter blue-green mutants, was for ten days exposed in the open to the attacks of English Sparrows. At the end of this period, the survivors were found to belong almost exclusively to the normal grass-green form, the birds having eliminated all but two very small and not yet conspicuous blue-green caterpillars, while leaving untouched plenty of the normal cryptic individuals.

(3) **Nocturnal Predators and Moths**—Further evidence of selective elimination by wild predators of the more conspicuous members of a species is afforded by Harrison's studies of the moth *Oporabia autumnata*, on Eston Moor, Yorkshire (230). Early in the nineteenth century a pine wood, containing isolated clumps of birch and alder, became divided into two parts, known as Wilton Wood and Normandy Intake Plantation, by half a mile of heather and bracken. At this time the two populations of *O. autumnata* were presumably similar, and they continued to live under identical conditions until the year 1885, when a gale caused the destruction of Intake Plantation, where the pines were subsequently replaced by birch. Wilton Wood, on the other hand, remained untouched, but here birch and alder were vanishing. From 1885, therefore, the colonies of *O. autumnata* had to live under fundamentally different conditions—one division in a birch wood where conifers were suppressed; the other in a pine wood in which alder and birch were disappearing. By 1907 the populations showed marked divergence in a number of characters—including coloration. In the pine wood about 96 per cent. of the moths belonged to a dark form, and 4 per cent. to a light one. In the birch wood about 85 per cent. were light, and 15 per cent. dark. This difference appears to be due to selective elimination in the pine wood of the more conspicuous paler moths by owls, nightjars, and bats. Although here the dark moth outnumbered the pale by more than 25 to 1, the majority of moths eaten by these predators (as indicated by discarded wings) belonged to the light variety. This disproportionate selection of prey cannot be due to mere chance; but is to be explained by the tendency of crepuscular predators to capture individuals which in the flight-time of twilight are more easily seen, namely, the light strains, and these are consequently being progressively eliminated.

(4) **Birds and Mantids**—Statistical results which appear to demonstrate in a very striking manner the effectiveness of cryptic coloration as a means of defence were obtained by di Cesnola (91), who conducted experiments with *Mantis religiosa*. In Italy, where the observations were made, this insect occurs in two forms—green and brown respectively. The author states that the green form is always found upon green grass, and the brown upon grass burnt by the sun. In his experiments, specimens of *each* form were tethered to green plants

in a place covered with green herbage, and to brown plants in a place where the herbage was burnt and brown, the distribution being as follows:

65 brown specimens—45 on green and 20 on brown plants;
45 green specimens—25 on brown and 20 on green plants.

Thus, out of 110 specimens, 70 were exposed in surroundings against which they were contrasted, and 40 in surroundings with which they harmonized. The resulting daily death-rate during the period of observation is shown in Fig. 49.

Nearly all the deaths were apparently due to predation by birds. It will be seen that *the elimination was confined entirely to individuals exposed in situations from which they differed in colour.* During the eighteen days' period of observation, 60 deaths resulted in these groups; but the 40 brown and green insects exposed respectively on brown and green plants were entirely untouched.

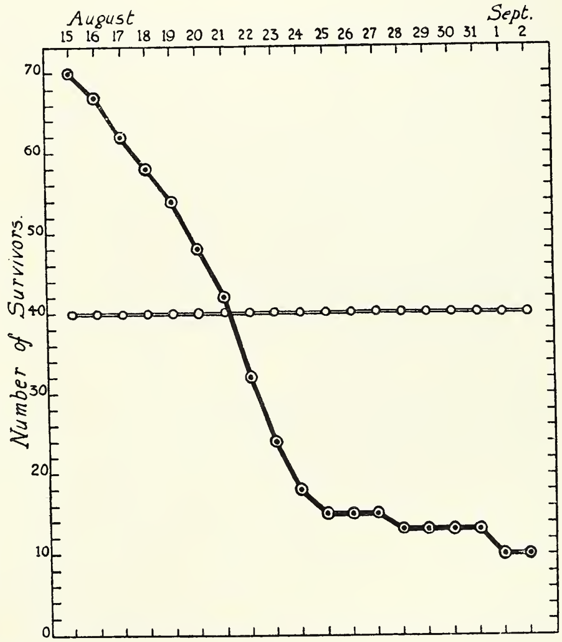

FIG. 49.—Graph showing the deaths due to predation (i) among 70 individuals of *Mantis religiosa* exposed against a revealing background—green on brown and brown on green—(black line); and (ii) among 40 individuals exposed against a harmonizing background—green on green and brown on brown—(open line). (*Constructed from the data of* DI CESNOLA, 1904)

The observed disparity can hardly be explained except as a selective death-rate based upon the ease or difficulty with which the prey can be recognized.

In 1927 experiments on the same lines were carried out by Beljajeff (42), who used green, yellow, and brown forms of *Mantis.* Out of 60 insects exposed on a brown background, 27 were eaten by birds (*Œnanthe œnanthe* and *Tinnunculus* sp.) in a fortnight, as follows:

	Green	*Yellow*	*Brown*
Number available	20	20	20
Number eaten	11	12	4
Per cent. left	45	40	80

A second experiment by Beljajeff, in which Hooded Crows (*Corvus cornix*) ate 35 Mantids in twenty-four hours, showed no selective elimination.

According to the method of assessment adopted by Robson and Richards (543) in their review of the subject, these experiments of di Cesnola and Beljajeff are relegated with those of Poulton and Sanders (526) and others to the category 'Analogy with natural process doubtful', and rejected on these grounds as unsatisfactory evidence of selective discrimination in nature. To the present writer this criticism seems irrelevant and misleading. It is most unfortunate also that Richards and Robson were unable to include in their survey of work bearing on the present problem the experiments by Sumner described above (599, 600, 601), which represent probably the most important, extensive, and conclusive series of tests yet undertaken to prove the functional value of concealing coloration. Neither do the above authors make any reference to the important and convincing experiments of Young (681) and Gerould (205). In view of these omissions, their objection to an adaptive interpretation of coloration on grounds that 'the formulæ at present proposed rely to a large extent on assumptions which have to take the place of the missing evidence' hardly conveys the meaning which these writers intended!

(5) **Crows and Poultry**—On a well-cropped pasture some three acres in extent, where about 300 chicks were running at large, Davenport (137) observed three crows chasing and killing the poultry, of which 24 were slaughtered in less than two hours. The original birds fell into three colour-groups: 40 per cent. being white, 40 per cent. black or nearly so, and 20 per cent. pencilled or striped and more or less like the female Jungle Fowl. Had there been no selective elimination, among 24 dead the chance distribution would be in the proportion of 9·6 white, 9·6 black and 4·8 pencilled birds. Actually, the numbers of killed were 10 white, 13 black, and 1 mottled grey and buff. *No pencilled bird was killed.* Davenport concludes that the evidence, so far as it goes, indicates selective elimination of the self-colours in poultry (which have arisen under domestication) by natural enemies of these birds. Commenting upon Davenport's observations, Robson and Richards (543) express the view that 'the extremely low total of 24 birds is quite inadequate as a basis of estimating the effects of selection'. This criticism appears to me an unfair assessment of the facts. Moreover, these authors omit to mention a factor tending to compensate for the low numbers of which they complain, namely, that the killed birds were largely Leghorns and Minorcas (both good fliers), while the pencilled birds which escaped were mostly dark Brahmas (poor fliers). Their further criticism that is seems 'extremely problematical whether the 'pencilled' birds are in fact less conspicuous than the black

and white ' is unjustified, and is made in disregard of the principles upon which concealment depends. The relative inconspicuousness of barred birds as compared with ' solid ' or self-coloured individuals is clearly shown in photographs by Pearl (461), and no one who has ever seen fowls in the country could be doubtful as to the extreme conspicuousness of black and of white birds, as compared with the brown or grey barred types of intermediate tone.

Pearl (461) has also studied the elimination among poultry due to the combined attacks of different enemies, including rats, skunks, foxes, and birds. From a population of 3,007 barred and 336 self-coloured chicks, 290 (9·64 per cent.) of the former and 35 (10·42 per cent.) of the latter were killed in six months. From this data he concludes that ' the relative inconspicuousness of the barred color pattern afforded its possessors no great or striking protection against elimination by natural enemies. . . .' In these observations, however, evidence of the utility of cryptic coloration appears to be masked by other factors, such as the attacks of enemies which hunt by scent rather than by sight. And we also have to bear in mind the probability that the protective effect of barring in the case of a dense population of chicks on a poultry farm would be less obvious than under wild conditions where chicks of one species would be only a single component of a varied population of possible prey.

(6) **Birds and Grasshoppers**—A remarkable series of experiments has recently been described by Isely (283), whose researches were designed to test the survival value of cryptic coloration in grasshoppers, in reference to the attacks of insectivorous birds. For this purpose an enclosure was marked off into 96 squares each measuring 16 × 16 inches. Seventy-two of the squares were arranged to represent four types of natural background: (1) black soil; (2) white soil; (3) red soil; and (4) green vegetation—growing sods of Bermuda grass (*Cynodon* or *Andropogon*). Upon these diverse backgrounds grasshoppers of different kinds were exposed to the attacks of various domesticated and wild birds.

The grasshoppers used were species normally cryptic in nature, namely, (1) White species—*Trimerotropis pistrinaria* and *Hadrotettix trifasciatus* (from white chalky subsoil of Houston clay). (2) Black species—*Encoptolophus subgracilis* and *Trachyrhachis kiowa fuscifrons* (from Houston black clay soil). (3) Reddish-brown species—*Spharagemon collare cristatum* and *Hadrotettix trifasciatus* (from red soils). (4) Green species—fourth and fifth instar green phases of *Chortophaga viridifasciata* (from stream-margins and grassy flats).

Isely exposed equal numbers of grasshoppers on backgrounds with which their coloration harmonized and contrasted. In such circumstances the insects were referred to as ' protected ' and ' non-protected ' respectively. Thus *T. pistrinaria* was classed as ' protected ' on white ground, and ' non-protected ' on other grounds. To keep the insects in place on the plots, they were either picketed with a light thread attached to a nail, or anæsthetized. When in position, the insects were charted before each experiment and checked after a period of attack by predators. The experiments fall into groups according to the predators used, namely, (i) bantams; (ii) wild birds—Mocking-birds, Cardinals, English

Sparrows, and Blue Jays; and (iii) domestic turkeys. The following is a tabulation of Isely's results with these birds:

Predator	Colour-status	Eaten	Survivors	Total
Bantams . .	Protected	81 (44%)	104 (56%)	185
	Non-protected . . .	157 (85%)	28 (15%)	185
Wild birds . .	Protected	39 (34%)	75 (66%)	114
	Non-protected . . .	96 (84%)	18 (16%)	114
Turkey . . .	Protected	37 (46%)	43 (54%)	80
	Non-protected . . .	73 (91%)	7 (9%)	80

An observation of great interest incidental to these experiments refers to what are called by Isely ‘ Long Term Survivors ’. The employment of picketed grasshoppers made it possible to check the fate of individual insects over extended periods of exposure to predatory attack. ‘ Under the constant pressure of native birds and, part of the time, of the three bantams and the turkey, 22 different individuals among the picketed specimens remained active and alive on the plot for over 20 hours. Three specimens remained picketed on the plot for over 48 hours, and one *Trimerotropis pistrinaria* for four days.

‘ It is noteworthy that *every one* of the 22 “ long term survivors ” were marked on our check-records as *protected.* On the other hand, during three weeks of continual testing, not a *single non-protected* individual appeared among the long-time survivors of the 459 *non-protected* acridians checked on our records.’

The same author carried out further experiments. In one of these it was found that the three bantams required just one minute to find and eat every one of 40 anæsthetized ‘ non-protected ’ grasshoppers on the experimental plot. Two days later the same birds could discover only 6 out of 40 anæsthetized ‘ protected ’ grasshoppers in the same time. During a further period of three minutes they had only discovered 6 more insects. Finally, the turkey was put to join the bantams on the plot, and after feeding for *one hour and twenty minutes* 2 of the grasshoppers still remained untouched.

In another type of test, open cages were set up having the floor covered with two types of soil, namely, chalk-marl subsoil and black clay. Equal numbers of ‘ protected ’ and ‘ non-protected ’ grasshoppers were introduced and allowed to adjust themselves before the advent of the turkey or bantam. The results of these experiments are tabulated below:

Predator	Colour-status	Eaten	Survivors	Total
Bantam and Turkey .	Protected . .	9 (30%)	21 (70%)	30
	Non-protected .	30 (100%)	0 (0%)	30

Isely's results thus afford striking proof of the survival value of adaptive coloration in cryptic acridians as a protection against predatory attack by a type of enemy which depends mainly upon sight for the hunting and capture of prey.

(7) **Nesting Birds and Cryptic Insects**—Results confirming the view that procryptic resemblance to surroundings is effective as a means of escape from natural enemies which hunt by sight have emerged from a valuable series of experiments conducted near Glasgow by Robert Carrick (88). In his study of the feeding-habits and food-preferences of certain small insectivorous birds, Carrick utilized the nesting habit—offering a variety of insect food, variously exposed, near nests during the period when nestlings were being fed. The following birds played the part of predator: Wren (*Troglodytes t. troglodytes*), Whitethroat (*Sylvia c. communis*), Willow-Warbler (*Phylloscopus t. trochilus*) and Sedge-Warbler (*Acrocephalus schœnobænus*).

Since observations on the actual behaviour of wild birds in relation to procryptic prey in nature have rarely been made, it is worth describing shortly the method adopted and results obtained in one of these experiments. At a Sedge-Warbler's nest situated among grass and herbage in marshy surroundings, two branches, of elm and hawthorn, were set up, and were at once adopted as perches by the parent birds in their journeyings to and from the nest. On the elm 22 Brindled Beauty Moth (*Lycia hirtaria*) larvæ were placed and 15 Hebrew Character (*Tæniocampa gothica*) larvæ on the hawthorn. The former, brown and twig-like, were very inconspicuous: the latter, green in colour, were moderately so. In addition, nettles bearing 17 Small Tortoiseshell (*Vanessa urticæ*) larvæ, which unlike the others were very conspicuous and active, were placed against the twigs. While feeding the young under observation for one and a half hours, the birds visited the elm twig nineteen times, taking 4 and leaving 18 procryptic larvæ; and the hawthorn fifteen times, taking 12 and leaving 3 less-procryptic larvæ. (Not one of the distasteful and conspicuous *V. urticæ* larvæ was accepted.) A feeding-tray experiment which immediately followed this showed that the *L. hirtaria* larvæ were quite as acceptable as the *T. gothica.*

At another nest, 7 procryptic *Selenia bilunaria* larvæ completely escaped the attentions of a pair of Whitethroats when resting in the hawthorn branch which they closely resembled, but 2 out of 4 were taken when resting in surroundings where they were more conspicuous.

These and similar observations by Carrick on other predators indicate the vital significance of concealing coloration in protecting insects from detection. In answer to the possible criticism that the prey was offered in greater concentration and was more readily accessible than is normal in a state of nature, the author points out that the crowding of procryptic individuals necessarily tends to lessen their protection, and both this factor and the probability of disturbance of the larvæ, causing movement, adds to the significance of the observed results. Birds are notoriously keen of vision. They recognize and capture their prey by sight. Yet here we have records of Wrens, Whitethroats, and Sedge Warblers actively seeking and capturing prey for their nestlings, repeatedly passing close to, and *perching among*, palatable caterpillars which they for the most part failed to notice so long as the prey remained motionless. When seen these palatable larvæ were readily eaten, and it was repeatedly noticed that it was the *moving* insect which first attracted attention. Hence the vital need for stillness—an instinct which is part and parcel of the make-up of the Geometrid larvæ under consideration.

III. DIRECT EVIDENCE FROM OBSERVATIONS ON THE BEHAVIOUR OF PREDATORS IN THE FIELD

Observations bearing upon these questions *on wild animals in nature*—as opposed to experiments which at best fail to reproduce absolutely natural conditions—have rarely been recorded. I shall therefore conclude the evidence brought together in this section by quoting a few records, which though isolated instances, are valuable as indicating the significance of vision in the hunter, and of coloration in the hunted, in the unending struggle for existence which in one way or another must be faced by all living creatures.

(1) **Ribbon Snake and Frog**—Describing an encounter between a Ribbon Snake (*Eutenia saurita*) and a frog, Ditmars (144) states : 'The writer witnessed an example feeding in a belt of swampy timber. The high rasping croak of a small frog directed his attention to the ribbon snake . . . which had grasped the frog by the hind leg. So vigorous were the frog's efforts, that it tore itself from the snake's grasp and started away in a series of rapid hops, with the reptile in pursuit. The serpent's movements were amazingly quick, and its power of vision in following the movements of the frog apparently acute. It darted after the amphibian for a distance of possibly eight feet, when the frog stopped, having secreted itself among some leaves. The snake also paused, but was all attention, with neck upraised and constantly darting tongue. It prowled about in frenzied fashion, when a movement of the frog attracted its attention, and it was instantly upon it, this time retaining its hold until the prey was swallowed.' This incident is of particular interest, illustrating as it does once again the importance of *stillness*, without which the best obliterative coloration can be of little avail.

(2) **Wasp and Spider**—Hingston has described the plan of escape in the case of a spider as follows : 'An Epeirid had its snare in the roof of a palm-leaf hut. In the web was a carpet of tangled silk intermingled with fine wood-dust. It sat on the carpet, harmonized with the background where it was almost completely invisible. A large black Pompilid came along. It was obviously hunting for a victim ; it was searching every cobwebbed cranny and making occasional swift darts into the air. It approached close to the harmonizing spider and happened with its front leg to touch a thread from the spider's carpet. At the instant of this touch the spider shot from its seat with the rapidity of a projectile. It was not a mere drop, but a violent leap after which it suspended itself on an invisible thread 8 inches below its web. It remained hanging there motionless for three minutes, then climbed slowly back to its carpet and found that the Pompilid had in the meantime disappeared' (265).

(3) **Birds and Butterflies**—Cryptic coloration, when combined with

cryptic habits, may be effective even against birds of prey whose habits and methods of feeding place a premium upon highly trained visual acuity. In a paper on the attacks of British birds on butterflies, Collenette (104) has published the following extract from a letter by Mr. F. W. Frohawk: 'On several occasions I have seen Kestrels in pursuit of the Grayling (*Eumenis semele*) and have seen them try to catch them on the wing, but usually they fail to do so. If missed in the swoop the butterfly darts to the ground and becomes invisible to the bird. This I have noticed many times. The bird hovers a moment or two, scanning the surface a few feet below, then rises again and waits until another Grayling takes wing and gives it another chance, but more often than not the butterfly escapes.'

Almost identical behaviour has been observed by Swynnerton (610) in African butterflies of the genus *Charaxes*. When attacked by a bird, he says that this butterfly 'commonly abandons flight and dashes to the nearest cover, most usually the ground It then remains motionless with closed wings until the danger is past. A large *Charaxes* that I had seen escape in this way from a Drongo remained motionless while the bird vainly searched for it. . . .'

Successful employment of the same tactics has been observed by Colonel C. T. Bingham, as shown by the following interesting note cited by Poulton (506): 'Going through some fairly open jungle close to the main road I put up *Melanitis zitenius*, which fluttered across the road and was swooped at by a king-crow (*Dicrurus*), but missed; the butterfly dodged, got to the other side of the road and dropped to the ground among the herbage and fallen leaves, as is the habit of *Melanitis*. The king-crow hovered for a minute not three feet from the ground over the exact spot where I had noticed the butterfly drop, failed to see it, flew off, but returned and again hovered over the spot, but was again unsuccessful, and flew up to a tree. I went forward very cautiously, and having carefully noted the spot where the butterfly had dropped, was enabled to make it out, but not till after fully ten minutes of patient and very cautious looking. The *Melanitis* was there among dead leaves, its wings folded, and looking for all the world a dead dry leaf itself.'

(4) **Falcons and Bustards**—Still more remarkable, owing to the great size of the prey, is the effective concealment afforded to large birds such as Bustards by their wonderful assimilation with desert surroundings. Evidence that this does deceive not merely the eye of man, but the much keener and more highly trained eyes of predaceous birds, is given by Major Cheesman, and I quote the following passage from his book *In Unknown Arabia*: 'I was anxious to photograph the nest of the Houbara, and thought that by flying trained Falcons over the ground one might induce the sitting birds to show fight and thus give away the position of the nest. We covered a lot of ground and knew we had passed many sitting hens, because the cocks were frequently seen grouped together. Yet the Hawks failed to discover a single nest, and we, quartering the ground carefully, were equally unsuccessful.'

PART II

ADVERTISEMENT

INTRODUCTORY

For, lo, the winter is past, the rain is over and gone;
The flowers appear on the earth; the time of the singing of birds is come, and the voice of the turtle is heard in our land;
The fig tree putteth forth her green figs, and the vines with the tender grape give a good smell.

SONG OF SOLOMON, II, 11–13

WE have seen in the earlier part of this work that the coloration, form, and habits of very many animals are such as to render them extremely inconspicuous and difficult to recognize in their natural surroundings; we have seen further that this end is attained in widely different classes of creatures, in widely different environments, and in almost every habitable region of the globe; that the methods by which it is attained are themselves very diverse, ingenious, and often extraordinarily successful; and we have given reasonable grounds for the belief that these cryptic devices satisfy a vital biological need in the lives of such animals—the need for concealment from enemies, or from prey.

But it is a matter of common knowledge that many animals, far from being concealingly coloured, are very conspicuous objects in nature. Such, for instance, are the familiar Red-tailed Bumble Bee (*Bombus lapidarius*), the Cinnabar Moth (*Hipocrita jacobææ*) and the Ten-spot Lady-bird (*Coccinella decempunctata*). In the light of what has been said above, it will be of interest to consider what part such bright and conspicuous colours play in the lives of the animals which exhibit them.

Every one is more or less familiar with the fact that certain colours possess in marked degree the inherent property of *conspicuousness*. This property rests on a threefold basis of physical optics, physiology, and psychology, which we cannot discuss here. The undisputed fact remains, however, that of the range of colours seen by man, or by animals whose visual perception is similar to that of man, those at the red end of the spectrum, namely, red, orange, and yellow, do tend to stand out vigorously as compared with neutral shades and with other hues such as green, blue, brown, or violet (623). This property does not depend upon a relative lightness in *tone*, nor upon purity or *saturation* (although both lightness and saturation do generally enhance the effect), for even when the red-yellow series of hues are seen among other hues of similar tone and purity, they still retain their outstanding quality, which is, as we say, to ‘catch the eye’. This remarkable attribute of such hues as vermilion, scarlet, pink, orange, chrome, and lemon yellow, and of white and black, has, of course, been familiar ground for centuries to artists, who utilize these colours *with economy, and with effect*—knowing their dominating strength.

More recently, with the development of rapid transport and travel by rail, road, sea, and air, and with the development of commercial art in advertising, the power of these colours has been employed and exploited in other fields, so that the colours which once were almost the monopoly of art and nature, and *used sparingly and significantly in both*, are to-day flaunted on every railway hoarding and road-side.

In everyday life these colours have now many applications and many functions: they are used for signalling, for warning, for directing, for alluring, for ornament, for deception, for recognition, for propaganda, for advertisement: they are used for covering jam-tins and for colouring railway signals; for painting match-boxes and pillar-boxes; they figure in the jackets of books and the uniforms of soldiers; they play their part in sport and in war, in courtship and in ceremony.

Now if we investigate the occurrence in nature of such colours among different plants and animals, we are led to the conclusion that here, too, under many and varied circumstances, these revealing hues have an important role in the economy of nature, being related to the visual perception of animals, and operating in the varied biological relationships between plants and animals, between parents and young, between rivals of the same sex, between members of opposite sexes, between predators and prey. The agent, the method, and the meaning of the exhibition in different cases all vary within wide limits. The one common factor, the one common end, is conspicuousness: conspicuousness which is concerned with those main and vital needs of all animals—food, safety, and reproduction.

THE METHODS BY WHICH CONSPICUOUSNESS IS ATTAINED

1. THE APPEARANCE AND BEHAVIOUR OF APOSEMATIC ANIMALS

Demand of lilies wherefore they are white,
Extort her crimson secret from the rose.
WILLIAM WATSON

I. THE RELATION BETWEEN VISUAL ADVERTISEMENTS AND VISUAL PERCEPTION

BEFORE turning to our main business of considering the phenomena of warning coloration in animals, we must refer here to certain facts bearing generally upon animal-advertisements as a whole. Recent studies of visual perception and of adaptive coloration tend to make increasingly clear the general conclusion that the two are closely interrelated, and that characters serving as visual stimuli have evolved parallel with the highly specialized sensory equipment of the animals towards which they are directed. This relation between appearance and vision, between transmitter and receiver, between advertisement and public, is becoming apparent in many fields, and is one yielding wide scope for future investigation.

By way of example, it is interesting to find that the efficient reception of red light by the eye of diurnal birds is linked up with the extensive use, by utterly unlike organisms and structures, of orange, vermilion, crimson, and scarlet, in typical bird-advertisements : and this, although their functions may be diametrically opposed—in the one case being attractive, in the form of flowers or fruit ; in the other repellent, in the shape of dangerous or distasteful prey. And we may remember here that for man also red stimulates the same dual and antagonistic responses, and serves equally well to colour lips, or the label of a poison bottle.

Red and scarlet predominate in the coloration of ornithophilous flowers, whether in Patagonia or Brazil, in South Africa or West Australia. Among 159 ornithophilous flowers listed by Werth (661), 84 per cent. were red. And it is very interesting to notice in passing that such flowers cater for the tastes and deficiencies of birds in other ways—being scentless ; producing nectar in great quantities ; having structures such as the styles and stigmas rigid ; and usually lacking a landing platform.

Pickens (470) points out that to Humming-birds red is a highly attractive colour. They will visit red bells of tissue-paper, red streamers of cloth, and have been seen visiting pieces of flesh from a hawk's body. Pickens found that in the Southern Appalachians the great majority of red flowers showed a tubular form, which is that preferred by Humming-birds. This was also true for most of the orange-coloured flowers in the district. Nowhere in Eastern North America was he able to find true bird-flowers outside these two colours. And of 110 species of flower to which visits by Humming-birds were observed, 45 were red, 19 were purple, and 15 orange.

It is scarcely necessary to refer here to the wide use of reds in fruits and berries attractive to birds—as displayed, for instance, by cherries and plums, currants and strawberries, by mulberries and raspberries, apples and tomatoes, by ' hips and haws ' of the hedgerow, and by the fruit of Holly and Yew, Spindle Tree, Rowan, Guelder Rose and Wayfaring Tree. Gilbert White here makes a pertinent observation. ' Birds are much influenced ', he says, ' in their choice of food by colour, for though white currants are a much sweeter fruit than red, yet they seldom touch the former till they have devoured every bunch of the latter.'

A very specialized and remarkable use of red, also adapted to attract birds, is seen in the parasitic Trematode *Distomum macrostomum*, whose appearance and life-history have been mentioned, as an example of alluring coloration, on a later page.

Again, as we shall see later, red takes a prominent place in the advertisement of dangerous or distasteful properties in insects, frogs, and many other animals. Shown to advantage in combination with black, these colours occur time and again in the make-up of aposematic Coleoptera, Hemiptera, Hymenoptera, and other groups.

This correlation which exists between visual characters on the one hand, and visual perception on the other, is illustrated in a converse way by the Mammalia. Julian Huxley has called attention to the fact that the general absence of colour-vision in mammals below the Primates is associated with the absence in them of colours other than black, white, greys, and various shades of yellowish- or rufous-brown. It is only in the colour-seeing Primates that we find developed bright hues such as blue and pink.

II. THE RELATION BETWEEN THE APPEARANCE OF ADVERTISEMENTS AND THEIR USES

We have now to notice certain special relations between the nature of advertisements and their methods of employment, which have recently been analysed by Huxley (278*a*). Visual characters vary widely according to the particular function in relation to which they have evolved—whether they are adapted to act at long range or short range; whether they are used to arrest attention or to stimulate emotion; whether their function is distinctive, or collective.

Characters adapted primarily to arrest attention, including those subserving distant recognition and distance-warning, must be as conspicuous as possible; and they consist typically in nature of simple patterns and saturated colours, often covering a wide expanse of the body. Such are the white recognition marks conspicuously displayed in flight by Bramblings, Bullfinches, Jays, Wheatears, House-Martins, and many waders and other birds.

On the other hand, visual characters adapted to stimulate emotion, including those relating to threat and eliciting fear, or those which arouse sexual emotion, are generally used at close quarters; and accordingly they tend, as compared with the last class, to be more complex in design, more elaborate in colour, and presented on a smaller scale suited to near vision. Moreover, unlike the simpler and generalized distance-recognition marks, they frequently embody special mimetic or symbolical effects suggestive of objects significant to the observer; and they are commonly accompanied by special actions and attitudes. This is seen, for instance, in the repeated use by all kinds of animals of eye-spots, whether in courtship or rivalry, in warning or bluffing; and in the sudden displays of concealed colours which transform an innocuous animal into an apparently dangerous enemy.

Then again, Huxley has indicated that patterns exclusively serving an epigamic function tend to be delicately beautiful, while those solely subserving threat or warning are bold and conspicuous rather than beautiful. In the latter category we have the crude colour-schemes of Skunks and Hornets; in the former, the wonderful displays of intricate detail, whether of structure, or pictorial relief, such as are found in the feathers of the Argus Pheasant and the plumes of Birds of Paradise and the Lyrebird.

Another illuminating method of classification is that which contrasts characters whose conspicuousness is adaptively shared by different species, and those which are specific and adaptively distinctive. The former type of character is familiar under the headings of Batesian and Müllerian mimicry. The latter, embodying Lorenz's (356) principle of distinctiveness, is less familiar, and its significance and wide application has only recently been appreciated.

Distinctiveness is a feature of most recognition marks, but any consideration of these characters lies outside the scope of the present work. We may note, however, that, as pointed out by Huxley (278*a*), there is a marked difference in type between the shared and the distinctive patterns. With shared conspicuousness, patterns of extreme simplicity may be used. But distinctive patterns, on the other hand, must have a sufficient number of different components to allow of distinctive combinations. And of course distinctive characters may be either visual or auditory: depending, for example, upon the colours which differentiate the various species of Thrushes or Doves or Toucans; or upon songs which contrast such apparently similar birds as the Chiffchaff and Willow-Warbler.

III. THE COLORATION OF APOSEMATIC ANIMALS

It is not necessary in this place to cite examples of animals which wear aposematic uniforms, or to analyse the combinations of colour employed: sufficient instances will be found in the following sections, where I have discussed in some detail the appearance, habits, and displays of aposematic animals, and the relation of these to the habits and psychology of predatory enemies.

I will only draw attention here to a fact of considerable interest, that in group after group of animals we find aposematic species wearing similar combinations of revealing hues—such as red, black, and white; yellow, black, and white; red and black; orange and black; yellow and black; white and black—that is to say, the colours which give the maximum of visibility and make for easiest recognition when seen against the normal green and brown surroundings of nature.

Any one who doubts that such colours *are* the most easily seen would quickly become convinced of his error were he to try playing a round of golf with green or brown balls instead of white ones. And it is, of course, because of this revealing property that the colours mentioned above are used for balls in games demanding precision or speed, such as cricket, croquet, polo, ping-pong, tennis, hockey, and billiards.

It is also evident that simplicity of colour-scheme—*achieved by the use of few colours and bold patterns*—must constitute an important factor in the successful advertising of inedible qualities to enemies. Because the fewer the colours and configurations used in this business of publicity, the easier recognition of unpalatable prey will become, and the fewer will be the mistakes made by predators.

Mistakes are bound to occur, both by 'learners' during the period of experimental feeding, and by adult animals—for it is highly improbable that birds and other insect-eaters could ever learn to distinguish and remember all the hundreds of species from which they must select their prey in nature. Consequently a common type of recognition badge, such as is worn by a wide variety of aposematic forms, will greatly facilitate the immediate recognition of undesirable prey.

This point is illuminated by the following observations. J. C. Mottram has drawn attention to the fact that both fishes and birds are liable to mistake inanimate objects for the insects on which they happen to be feeding (427). That such objects—especially when they roughly resemble the insect food—are closely inspected and sometimes eaten in mistake for genuine prey is proved by direct observation in the field, by the examination of stomach-contents, and most conclusively by the fact that fishes can be deluded and captured by means of the angler's crude imitations of the natural insects. That similar mistakes are also made by birds, with their manifestly keen vision, is especially significant.

Observations by Mottram show that Spotted Flycatchers, Swallows, and Martins not infrequently alter their line of flight to capture light floating bodies, such as pieces of feather, seed-plumes or chaff, which they obviously mistake for flying insects. For instance, one day in April a wagtail feeding on 'Grannom' (*Brachycentrus subnubilus*) was seen on several occasions to make for small floating objects resembling the insect: twice it picked these off the surface of the water, and then dropped them. Still more striking is the evidence that not only fish, but also birds, are deceived by the fisherman's counterfeit 'flies'. Thus, during a hatch of Blue-winged Olives (*Ephemerella ignita*) Mottram states that his artificial 'Blue-winged Olive' 'was repeatedly picked off the water and carried for a yard or two in the air, by both swallows and martins: so persistent were the birds that they interfered with the fishing'. This observer personally witnessed similar mistakes by the following birds: Meadow Pipit, Yellow Wagtail, Grey Wagtail, Sedge-Warbler, Black-headed Bunting, Swallow, Swift, Nightjar, Domestic Duck, Dabchick, a Tern in New Zealand, and an undetermined species of Bat.

Instances of birds being deceived by decoys are recorded by Young (681), who cites the case of a Duck-Hawk (*Falco anatum*) which was killed in the act of carrying away a wooden snipe decoy, and of an Osprey (*Pandion haliaëtus carolinensis*) seizing a wooden fish decoy.

Now these observations have an important bearing upon the problem of warning coloration, for they suggest the importance of effective advertising. If, as is known to be the case, predators have to learn discrimination in the school of experience; and if, in the light of such experience, they are yet liable to be deceived by crude resemblances, we can appreciate the value and the need to unpalatable prey of colours and habits which make for advertisement—which court, we might almost say compel, attention, which can be easily learned and associated with distasteful qualities, and which thus facilitate immediate recognition and avoidance by enemies.

The important principle that the colours employed for advertisement must be both *conspicuous in appearance* and *limited in number* was grasped many years ago by Poulton (496), who came to this conclusion on a comparison of the appearance of such insects as had been proved distasteful prior to the publication of his work on 'The Colours of Animals'. And this view has been abundantly confirmed by subsequent experiments and observations.

Perhaps nowhere in recent years has the principle been brought out more surely than in Morton Jones' experiments (290) on the relative acceptability of different American insects to insectivorous birds. This worker showed that the least acceptable among five thousand insects belonging to two hundred species were generally characterized by conspicuous markings of red, orange, or yellow; while of the more palatable kinds, not one exhibited these colours in the resting attitude.

The fact is that over and over again, in group after group of animals belonging to widely separate families and orders, the same hues—black, red, orange, and yellow—are employed as the outward and visible sign of dangerous or distasteful properties. Indeed, in such animals, protected as they are from enemies by a variety of disagreeable attributes, the type of colour-scheme is in general the one factor common to their appearance, which in other respects varies so widely —in form, size, structure, and texture.

Thus it is that the use of particular colour-schemes, such as the highly effective black-and-yellow combination, cuts right across the natural classification of the animals wearing them. For example, just as in its *applied use* black-and-yellow is a medium for drawing attention to a variety of unrelated objects such as railway signals; Automobile Association road warnings, direction signs, telephone-boxes, and uniforms; Belisha beacons; National Benzole petrol pumps; tins of 'Vim', of 'Zebra' Grate Polish; and many well-known posters and advertisements; so in *natural use* these colours (for instance) are the warning or false trade-mark of a wide variety of unrelated animals, such as Salamanders (*Salamandra maculosa*), tree-snakes (*Dipsadomorphus dendrophilus*), sea snakes (*Pelamydrus platurus*), sawflies (*Athalia cordata*), ichneumons (*Metopius dentatus*), wasps (*Vespa vulgaris*), bees (*Nomada alternata*), caterpillars (*Hipocrita jacobææ*, *Zygæna filipendulæ*), lepidopterous pupæ (*Abraxas grossulariata*, *Acræa horta*), moths (*Trochilium crabroniformis*), Longicorn (*Clytus arietis*) and Coccinellid beetles (*Chilomenes lunata*), weevils (*Alcides ruptus*), flies (*Syrphus ribesii*, *Volucella bombylans*), Lygæid bugs (*Oncopeltus jucundus*), and Membracid bugs (*Heteronotus armatus*).

IV. APOSEMATIC COLOURS IN RELATION TO ENVIRONMENT AND HABITS

In the preceding section we have seen that certain colours, and certain combinations of colour, which are worn by different animals, tend to make for conspicuousness. But to leave the matter here would be to give a very false impression of the methods by which aposematic animals come to appear conspicuous in nature; for we have said nothing about two essential factors which are as significant as coloration, namely, habit and environment. When dealing with concealing coloration I have stressed the importance of studying animals in relation to their habitual behaviour and their natural surroundings; and what I said applies with equal force in the case of conspicuous coloration. Vivid pigments and bold patterns do not of themselves signify advertised appearance. This will depend essentially upon how, when, and where the conspicuous dress is worn.

Many highly coloured animals are actually *cryptic* in nature: indeed, we are faced with the paradox that in certain cases the most effective self-effacement in the field will demand a costume which in the museum will present a most effective self-advertisement. A few examples will make this point clear. Black and white is in general undoubtedly one of the most conspicuous combinations of colour to be found in nature, but its advertising effect may be entirely altered by circumstances. For instance, the African monkey *Colobus occidentalis* wears a long silky fur whose coloration is essentially one of black and white stripes; but when the animal is seen 'at home' its coat has a concealing function. 'This monkey', says Gregory, 'lives in the high forests of Abyssinia, Kenya, Kilima Njaro, and Settima, where the trees have black trunks and branches, draped with long grey masses of beardmoss or lichen. As the monkeys hang from the branches they so closely resemble the lichen, that I have found it impossible to recognize them when but a short distance away' (217).

Another instance of the kind, and one which is even more pertinent, is afforded by the Madagascan weevil *Lithinus nigrocristatus*. When seen in a cabinet drawer, it is a highly conspicuous insect, boldly dressed in black and white: but amidst the black and white lichen which it habitually frequents its protective resemblance is so perfect as to render it almost undiscoverable, even when its whereabouts is carefully scrutinized inch by inch (see Plate 43).

The point is well shown among birds by the Malayan White-headed Fruit Pigeon (*Ptilopus cinctus*), which Forbes describes as resting motionless in numbers during the heat of the day, on well-exposed branches. Yet, he says, 'it was with the most extreme difficulty that I, or my sharp-eyed servant, could ever detect them, even in trees where we knew they were sitting. The peculiar coloration of the plumage of these birds in the hand or in the cabinet is so conspicuous and striking that it would scarcely be believed that they can occupy leafless branches (if there be foliage behind and above them) with the most perfect safety from detection' (180).

Various seemingly conspicuous bats nicely illustrate the same principle. A species of *Kerivoula* (allied to *K. picta*), from Formosa, is orange-brown in colour with the wings painted orange-yellow and black, and doubtless looks conspicuous enough in the museum cabinet. But a specimen taken by Swinhoe was found on the Longan tree (*Nephelium longanum*), and as he points out, the tree is evergreen, all the year through some of its foliage is undergoing decay, and leaves in that stage are partially orange and black, so that at all seasons the bat is protectively coloured when suspended from its branches (606). Similarly a species of *Mesophylla* from Guiana is pure white in colour, but as described by Hingston: 'Instead of spending the day in the hollows of trees, it hangs in the open from the leaf of a palm the under surface of which is bright and silvery, against which the white fur of the bat blends' (265).

The same is also true of many large animals, such as *Python reticulatus*. This great serpent is clad in a scaly suit of bold design, which gives it a strikingly conspicuous appearance within the unnatural confinement of a museum or menagerie. But in its native jungle haunts, whether resting coil upon coil about the roots of a forest tree, or suspended head downwards from a branch overhead, it is easily overlooked (572). In such surroundings the disruptive pattern can do its work of deception: indeed, it is the very conspicuousness of the *pattern* which renders the *snake* itself inconspicuous. It must be noted, however, that the pattern is conspicuous as a configuration of contrasted tones, and not in terms of coloration, for the colours employed are those repeated everywhere in the environment—the rich yellow, of high-lights and sun flecks; the intermediate brown hues, of bark and dead foliage; and the black, of deep shadows.

But it is in coral seas that the point is best illustrated. Coral fishes are among the most brilliantly coloured of all animals, yet in nature their bright hues and bold designs are generally cryptic: indeed, Longley's studies of reef fishes in nature have led him to reject the hypothesis of warning coloration as applied to these forms. Townsend states: 'After experiences on the coral reefs of more than forty islands in various parts of Polynesia, where the fishes are more gorgeous than in sub-tropical Atlantic waters, we are prepared to affirm that the abundance and variety of the invertebrate life alone is sufficient to give areas of the reefs such splendors in color that the most brilliant fish could soon find an environment to match without changing its own colour in the least' (629).

It is clear, then, that animal coloration must be considered everywhere in terms of the natural environment. In extreme cases, where a particular habitat is gaudily coloured, its inhabitants, too, must adopt its bright hues if they are to escape easy detection.

In these and similar cases the concealing effect is due to the special relation between the animal and its environment. In others a similar effect is due to special behaviour. Thus, we are accustomed, rightly, to regard red as a conspicuous hue which is very generally associated in animals with distasteful or dangerous qualities, and, as such, with the function of warning. But there are many red animals, like certain deep-sea fishes and crustacea, whose colour cannot have any such function in the eternal night of the abyss, and others again which observation has shown to have no such function. For instance, Longley has clearly demonstrated that among the Tortugas Reef fishes, the five truly red species—*Holocentrus siccifer*, *H. ascensionis*, *H. tortugæ*, *Amia sellicauda*, and *Priacanthus cruentatus*—belonging to three families, have in common the striking habit of lurking concealed by day in sheltered crannies of the coral-heads: from this retreat they only emerge at night. During a month of observation in places where the red fishes were known to abound, only one individual of one species was seen to venture from its shelter by day (336). In the hand these fishes would, of course, be rated as highly conspicuous. We see, then, the importance of a knowledge of animals in their natural state; and we must now consider briefly whether the habits and surroundings of aposematic animals are such as to support the view that these colours have an advertising function in nature.

V. FREE EXPOSURE OF APOSEMATIC ANIMALS

If advertisements are to be effective they must be exhibited where they can be, and will be, seen by the advertiser's public. Now it is well known that, generally speaking, aposematic animals—the animated advertisements of nature—habitually expose themselves freely in nature, in situations where they are conspicuous to their enemies.

It is significant that in numerous groups, aposematic species diverge strikingly in this respect from related cryptic species, which rest either concealed from view, or in full view but concealed by cryptic resemblance to their surroundings. For instance, the majority of marine Terebellid worms are protected from general enemies by the tubes within which they hide and live more or less securely—just as termites are protected by dwelling under cover in their 'dugouts and fortresses of concrete-carton'. But there is one species which has retained its freedom. This worm, *Polycirrus aurantiacus*, has dispensed with adventitious defence and is described by Garstang as creeping about among stones and the roots of *Laminaria*. It is bright red in colour, and it is conspicuous by night as well as by day, for when irritated its long defensive tentacles are luminescent, while experimental evidence has proved that the animal is extremely distasteful and well protected from certain fishes such as Pollack (cited, Poulton, 496).

Companies of the conspicuous black *Vanessa io* larvæ freely exposed on nettle leaves, or of the black and yellow *Hipocrita jacobææ* larvæ freely exposed on ragwort; the black, white, and red larvæ of *Porthesia auriflua* conspicuously feeding on the upper sides of hawthorn leaves; the similarly coloured larvæ of *Eriogaster lanestris* living gregariously on the same plant—these and many like examples will occur to the reader and are too familiar to need further mention. In reference to British species, Poulton has discussed the subject in his classical paper on the protective value of colour and markings in insects (494); and later literature contains innumerable references to the same point. Many further instances of this relation between aposematic appearance and habitual exposure will be found in the following pages, so we need not pursue the matter here.

VI. SLUGGISH BEHAVIOUR OF APOSEMATIC ANIMALS

Sluggish behaviour, combined with apparent indifference to enemies, is another characteristic of these animals. Every one who has seen aposematic grasshoppers such as the South African *Phymateus viridipes* in the field appreciates the striking manner in which their behaviour differs from that of active cryptic species such as *Acrida sulphuripennis*: the former courts observation and scarcely resists capture, the latter seeks concealment and is difficult to capture. Parallel differences between the habits of cryptic and aposematic species are observed in group after group of animals. For instance, when surprised in the open the East African Land Crab *Sesarma meinerti* stands its ground and puts up a vigorous defence; on the other hand, the cryptic Racing Crab *Ocypoda ceratophthalma* under similar circumstances rushes away at top speed, either avoiding capture by the skilful way in which it doubles and redoubles on its tracks, or by flying for refuge to the friendly breakers. In the case of lizards, the majority of desert-dwelling species depend for safety upon cryptic appearance, alertness, swiftness of foot, and burrowing habits; but in contrast to such forms, *Heloderma suspectum* and *H. horridum* stand out as striking exceptions. These ugly brutes, coloured respectively pink and black, and black and yellow, are notorious as the only poisonous members of the whole group; and correlated with the aposematic appearance and poisonous properties we find them as ill-equipped for speed as they are defiant and formidable in defence. Ditmars says of *H. suspectum*: 'At no time can the Gila Monster get over the ground at faster than a spry crawling gait, seldom raising the fat body entirely clear of the surface. . . . If annoyed while progressing in leisurely fashion, it stops immediately, evidently realizing the uselessness of attempted flight' (146). Similarly, aposematic frogs such as the South African *Phrynomantis bifasciata* and the South American *Atelopus stelzneri* are heavy in their movements, nonchalant in their manner, easily seen and easily captured: such forms stand out in striking contrast to cryptic species like the terrestrial agile long-leaper *Rana mascareniensis* or the arboreal acrobat *Chiromantis xerampelina*. Every naturalist knows how easily captured are the majority of aposematic insects, whether Hymenoptera, Hemiptera, Coleoptera, or Lepidoptera; whether in temperate or tropical regions. In general they are indifferent of escape; reluctant to fly, or flightless; sluggish on the ground and conspicuous on the wing, the flight being slow as in *Coccinella*, feeble as in *Hipocrita*, leisurely as in *Heliconius*, or noisy as in *Bombus* and *Sirex*.

VII. GREGARIOUS HABITS OF APOSEMATIC ANIMALS

Another habit of aposematic animals which serves effectively to heighten conspicuousness is the association or massing together of numerous individuals. The application in human affairs of this relation between aggregation and conspicuousness is familiar to every one.

Thus, by slightly modifying the words of an old song which appeals to man's gregarious instinct and associates merriment with numbers, we can give it a more truthful (and here pertinent) meaning, if we say:

> The more we are together, together, together,
> The more we are together, the more conspicuous we shall be.

The principle of conspicuousness in numbers is, of course, well known to every advertiser, whose rows of identical bills (which convert many small notices into one large one) weary the eye of the city dweller. The principle is employed, though probably quite unconsciously, by the angry crowd, out to air a grievance, with its aposematic neckties, its flaunted banners, and its noise all directed towards effective display: here, again, other things being equal, numbers count; they challenge notice; they command attention. The same principle had its war-time use (until comparatively recently) when soldiers, attired in aposematic uniforms, were drawn up in massed battle order.

In a simple form it is seen among animals in the close clustering together of numerous individuals on the same food-plant. Thus the notoriously evil-smelling Pentatomid bugs are frequently found crowded together on the surface of a leaf where they make a conspicuous patch. The same may be said of the gregarious larvæ of saw-flies like *Crœsus septentrionalis*, and of grasshoppers such as the aposematic *Zonocerus elegans*, whose black and green nymphs, when massed together on the food-plant, form glaringly conspicuous patches of colour.

Major R. W. G. Hingston records (265) a striking example of this type of behaviour from British Guiana. He found on a low tree a large family of Hawk-moth caterpillars, belonging to the genus *Isognathus*—various members of which are almost unrivalled even in the tropics for conspicuous coloration. The species observed by him had the head and the tail ends red, the body striped in white and black, and the long flexible whiplike 'tail' jet black. Now this is what Major Hingston says: 'Their habit was to rest in a compact cluster, a dozen or more on one leaf. They arranged themselves parallel to one another, all full length side by side, and facing in the same direction. All head ends were in one line and tail ends in another line. There was an aspect of military precision in the ranks.'

The Rev. A. Miles Moss had previously described gregarious habits in certain aposematic Sphingid larvæ observed by him at Pará, namely, in *Protoparce albiplaga*, whose conspicuous caterpillars are bluish-white in ground colour, marked with a bold black and cadmium-yellow design. Now it is very significant that, as Mr. Moss points out, gregarious habits among Sphingidæ, at any rate in his area, are quite exceptional, and that among 47 species which he has studied at Pará, the only other gregarious species was *Pseudosphinx tetrio* (Fig. 50), whose glaringly conspicuous larvæ are immense creatures—black-bodied, with yellow rings and red heads.

To take another case, from a different group of insects—the larva of a handsome grasshopper, *Zoniopoda tarsata*, from La Plata, is noteworthy for its gregarious habits and aposematic behaviour, vividly described by W. H. Hudson (276). The adult insect is cryptically coloured brown and green, lives in concealment, and is solitary and shy in its habits. In marked contrast: 'The young are intensely black, like grasshoppers cut out of jet or ebony, and gregarious in habit, living in bands of forty or fifty to three or four hundred.' So closely do they keep together that the bodies are in contact, and clustering thus on the summit of the weed where they happen to be feeding they are exceedingly conspicuous. Moreover, Hudson says that when changing their feeding-ground they deliberately cross wide roads, and open spaces barren of grass, where 'they look at a distance like a piece of black velvet lying on the ground'. Yet, though they thus expose themselves and seem to invite attack, this author never detected birds preying upon these 'black societies', one of which he had under observation for several days in places which were the resort of Icterine and Tyrant birds, Guira Cuckoos, and other grasshopper-hunting species.

FIG. 50.—Final instar of *Pseudosphinx tetrio* as an example of warning coloration. (*After* A. MILES MOSS)

Even more remarkable—because they are quite independent of feeding or breeding habits—are the gregarious resting instincts of butterflies. Numerous observations, which have been collected and discussed by Sir Edward Poulton (519), show that certain members of the aposematic Danainæ, Heliconinæ, and Acræinæ instinctively seek out dead or leafless twigs on which to settle for the night, and thus exposed, form sleeping assemblages of many individuals clustered closely together. From his careful studies of *Heliconius charithonia* in Florida, Professor F. Morton Jones concludes that the group-sleeping habit is unconnected with mating, as it is (obviously) unconnected with food: 'If Heliconia is protected by a nauseous odour or taste, advertised to its daytime enemies by conspicuous readily-recognized colours and colour-patterns, *then* its degree of protection, at night, when these warnings are not so apparent, may be increased by the close proximity of large numbers, under these conditions readily recognizable by form, colour or *scent*, as identical in kind and inedible ; for thus the injury or destruction of one of the group might conceivably work for the protection of the many.' It is significant that this species has been observed to exhibit the same gregarious resting instinct at noon on a dull day.

Various Danainæ, such as *Danaida plexippus*, possess similar gregarious-resting instincts. Referring to the Heliconinæ and Danainæ, Sir Edward Poulton concludes : ' . . . the striking fact remains that species of two distasteful, much-mimicked groups—the Danainæ among the more specialized of the Nymphalidæ and the Heliconinæ among the least specialized—both exhibit the same gregarious resting instinct combined with the instinct to seek dead or bare twigs. It is reasonable to suppose that the similarity in the behaviour of the two groups has been independently developed to meet a similar need—the need for an enhanced aposematic advertisement during periods of rest no less than in periods of activity, when it is manifested by display, flight, etc. This hypothesis . . . offers a reasonable interpretation of facts which, in the present state of our knowledge, are otherwise inexplicable.'

Finally, it has been shown by Professor Hale Carpenter that various species of the distasteful *Acræa* increase the force of their warning attributes by the like formation of sleeping assemblages in Portuguese East Africa.

If conspicuousness and easy recognition by foes is a vital factor in the lives of different ' protected ' species, then it is the young and relatively small insects which may be expected in particular to benefit from the habit of feeding and resting in assemblies. And it is significant that this method of making a display is frequently found in such cases. The massing together of the nymphs of the African *Zonocerus elegans* and of the South American *Zoniopoda tarsata* have already been mentioned. In his Presidential Address to the Royal Entomological Society, 1934, Sir Edward Poulton cites a similar case described by Dr. F. Morton Jones. The North American Acridian *Rhomalea microptera*—a large, clumsy, gaudily-coloured grasshopper which is incapable of flight—is protected by the pouring out of distasteful secretions, accompanied by a hissing sound when disturbed. In its earlier stages it ' has the habit of feeding and sleeping in massed assemblages, thus increasing its conspicuousness while the individuals are small ' (525).

And now, before I leave this aspect of warning coloration, I must refer to an extremely interesting example from a widely different class of animals. In a valuable paper which is full of original field observations, Mortensen (417) describes the case of a small aposematic Silurid fish whose habits beautifully illustrate the same principle. He says : ' On the flats of the coral reef at Little St. Cruz Island in the Strait of Basilan, near Zamboanga, my attention was attracted by a very conspicuous black thing moving about in the shallow water. On coming close to it I saw it was a mass of small fishes, black, with two longitudinal white stripes on the sides of the back. They swam very closely together, making thus a large ball; by the constant movement of the small fishes among one another the ball seemingly rolled along over the corals, making an exceedingly conspicuous object. It was quite easy to catch nearly all of them with a single stroke of a handnet. In order to preserve some specimens of them I started to take them with the hand from the net. The first one I touched stuck to my fingers, producing a most intense pain, and on trying to get it off, I had it hanging in my other fingers. It was exceedingly painful, the pain lasting quite a while after I had succeeded in getting it off. After this experience I avoided, of course, most carefully to touch any specimen of this fish, and when I had succeeded in getting some of them preserved I kept carefully away from these black, rolling balls.' Mortensen aptly refers to the significance of the swarming habit as follows: 'On account of the small size of the fish the coloration, though very conspicuous in itself, would hardly be of any use for the purpose.' He describes the fish, which is known to science as *Plotosus anguillaris*, as swimming together 'by the hundreds', and expresses the opinion that no predaceous fish or bird or other would-be enemy, man included, will venture to touch them more than once.

It is interesting to find that certain aposematic fishes belonging to the unrelated Diodontidæ have independently resorted to the same habit of massing together for additional mutual protection (see p. 210).

VIII. DIURNAL AND SEASONAL ACTIVITY OF APOSEMATIC ANIMALS

Above we have been dealing briefly with the *place of activity*, and the *nature of activity* of aposematic animals. A third important consideration is the *period of activity*—both in relation to daylight and in relation to the seasons. We have seen that many cryptic insects and other animals either hide away, or else rest motionless in special cryptic attitudes by day—that is, during the time of greatest activity by predatory enemies—only coming out to feed under the friendly shades of darkness. Now if warning colours really have a warning function, we might reasonably expect their possessors—unlike related cryptic species—to pursue their active business in daylight, that is when the colours can be seen by potential enemies. A little investigation shows that this is normally the case. The point is beautifully illustrated in certain families of homopterous bugs. The great majority of Cicadidæ are cryptic in their coloration and nocturnal in their habits. Is it then mere coincidence that the brilliantly coloured *Huechys sanguinea* of Malaya, clad in black and scarlet, is diurnal, and unlike other species flies about in full daylight among bushes in the open (7)? Similarly among Membracidæ, warning coloration is exceptional, the majority of species being brown or green and more or less cryptic in appearance and habits, while some are highly specialized for concealment, resembling such natural structures as bark-nodules, seeds, thorns, leaf-stipules, or buds. Is it then by mere coincidence that, as pointed out by Mrs. Brindley, the relatively few conspicuous species in British Guiana, such as *Darnis partita* and *Heteronotus armatus*, feed openly in conspicuous places?

The latter, with its black and yellow prothoracic mask, resembles a wasp in coloration and behaviour, being lively and active, frequenting open sunny places, readily taking wing, and flying with 'a noisy buzzing sound' (232).

Among Lepidoptera, a closely similar state of affairs is found in different families. For instance, to mention but one case, Hawk-moths (Sphingidæ) are typically nocturnal insects, with highly developed cryptic habits and appearance. But certain members of the group, such as the Broad-bordered, and Narrow-bordered Bee Hawk-moths (*Hemaris fuciformis* and *H. tityus*), diverge markedly from type, resembling more or less closely members of the day-flying and conspicuous Hymenoptera. These mimetic species differ from others of their own group, and resemble those of another order, not only in their conspicuous appearance, but in their diurnal habits. Here, of course, we have a case of true mimicry, but this aspect need not concern us at present: the point which I wish to stress is that conspicuous appearance (whether for warning—as in the (aposematic) hymenopterous models, or for false warning—as in the (pseudaposematic) lepidopterous mimics, is associated with appropriate (diurnal) activity.

The same point is very clearly illustrated in the case of Anura. Broadly speaking, frogs and toads and tree-frogs are more or less cryptic both in appearance and habits, and they tend in active life to be mainly crepuscular or nocturnal. It is therefore significant to find that among several families the most highly conspicuous species, such as *Atelopus stelzneri*, *Phrynomantis bifasciata*, *Dendrobates tinctorius*, and *Hyperolius marmoratus*, are diurnal, and parade their red and black and yellow pigments in the open in full view of daytime feeding predators. Many similar instances occur among aposematic lizards, caterpillars, butterflies, grasshoppers, and other animals.

A similar relationship between aposematic coloration and diurnal habits (as opposed to cryptic coloration and nocturnal habits) is found in certain Urodela, as indicated, for instance, in a comparative study by Hubbard (274) of the protective devices in the Californian salamanders *Batrachoseps attenuatus*, *Plethodon oregonensis*, and *Diemyctylus torosus*. At one end of the series we have *B. attenuatus*, which yields comparatively little poisonous secretion, and is eaten with avidity by snakes: this species is nocturnal, and was never found abroad in the daytime, which it spends hiding beneath boards and rotten logs. *D. torosus*, at the other extreme, possesses large and abundant skin glands, which yield a copious defensive secretion: this salamander is highly distasteful to, and well protected from, snakes, which apparently never take it as food; and it is significant that the animal, which is conspicuously coloured—being brownish-black above with the sides of the body, limbs and tail reddish-orange—is (in contrast to the other species) *diurnal* in its activities.

There are, of course, striking exceptions, notably among Musteline Carnivora such as the Skunk, Cape Polecat, Teledu, and others. But here the crepuscular habits are related, not to predators, but to prey, for these animals themselves come out to feed on nocturnal insects, worms, and other small creatures which are less readily obtained by day. Moreover, it is significant that the *white* element typical of the coloration of such animals is just the colour most conspicuous under conditions of poor lighting, so that these apparent exceptions support the view that there is a general relation between warning colours and the time of day when their wearers show themselves. An analogous case among insects is seen in certain large distasteful night-roving beetles (see Fig. 51), whose backs carry conspicuous white spots which, like the white gloves and coats worn by policemen on point duty, reveal their presence in the dark. The remarkable conspicuous coloration of certain large Carabid beetles such as *Anthia sexguttata*, which is not unlike a negative of the six of dominoes, must serve as a highly effective advertisement, whether by day or after dusk ; indeed, its rows of white spots call to mind the interrupted white marks which adorn our pavements and lamp-standards in war-time as an antidote to the black-out.

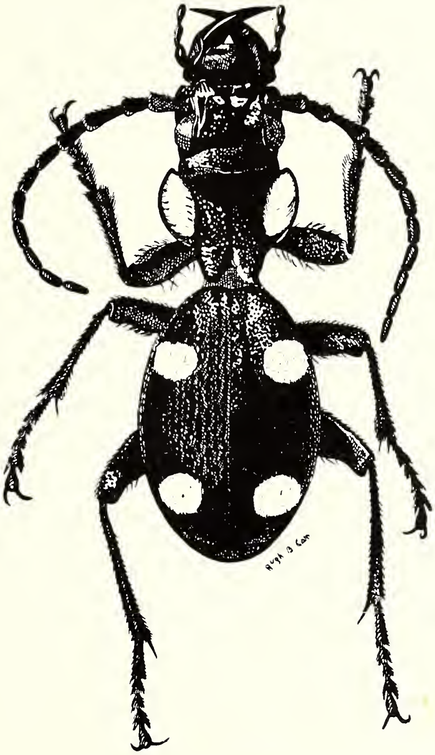

FIG. 51.—*Anthia sexguttata*

Turning now to the question of seasonal activity, Poulton drew attention many years ago to the scarcity of aposematic insects during winter, or during the dry season in countries with well-marked seasonal rainfall. In England warning colours are rarely seen during the winter months, when wasps, ladybirds, and other conspicuous insects seek retreat among dead leaves or beneath bark. Poulton (506) has made the interesting suggestion that the winter disappearance is due to the need for concealment at the time when insect-eating animals are hard pressed for food, rather than for escaping the cold, a view supported by the disappearance of such insects as the ladybird in early autumn when available insect life is diminishing, but before the onset of cold weather. A similar seasonal disappearance of aposematic species has been described by Mrs. Brindley (232) in the case of certain conspicuous bugs (*Nematopus indus* and *Brachystethus cribrum*) which appear in greatest abundance after the rains 'at a period of renewed activity and increased population'. There is reason to believe, therefore, that these and similar seasonal changes in the relative abundance of aposematic as compared with other insects is related to the stress of life in the critical periods of food shortage. This conception opens up an interesting field for further and more detailed ecological work, both in the tropics and elsewhere, not only with respect to insects, but other groups of animals.

2. WARNING DISPLAYS

> But all their works they do for to be seen of men: they make broad their phylacteries, and enlarge the borders of their garments.
>
> MATTHEW XXIII, 5.

In our review of the methods by which different aposematic animals reveal themselves to their enemies, we have hitherto been dealing with warning effects of pigment and pattern which are permanent, using that word in the sense that a fixed road-sign or the label on a poison bottle are permanent: that is to say, we have dealt with an advertising mechanism which does not involve any particular reaction or behaviour on the part of its possessor. The warning is always on view for any to see whom it may concern.

Now in contrast to these permanent effects, members of many different groups of animals have independently adopted for purposes of warning, or bluffing, a more or less elaborate, and often extremely interesting, mechanism, whose operation is *temporary*. This machinery is set to work at particular times, under special circumstances—*when its effect is needed*—for instance, when its possessor is in danger, in battle, or in love. If we liken the permanent warning sign of the Fire Salamander (*Salamandra maculosa*) or Cinnabar larva (*Hipocrita jacobææ*) to the aposematic road sign 'SLOW—MAJOR ROAD AHEAD', then we can compare the *temporary display* of the Fire-bellied Toad (*Bombinator igneus*) or Puss Moth larva (*Cerura vinula*) to the green-lettered sign 'GO' which, when occasion arises, is converted into the red-lettered 'STOP'.

The display itself may have a different function in different animals, or more than one function in the same animal at different times: for it may be directed towards a predator; or towards a rival; or towards a mate; or towards a friend—as a warning, a bluff, or an impersonation; as a threat; as an expression of sexual desire, or as a mark of recognition. Since I have confined myself in this work to the interspecific, as opposed to the intraspecific, relationships of animals, we are mainly concerned here with these advertisements in so far as they appeal to a special class of the animals' 'public', namely, to predatory enemies.

It is interesting to notice here an analogy between aposematic and cryptic animals, for with the latter, as with the former, *special reactions and special behaviour are often correlated with the adaptive colour-scheme.* In each class of cases the reaction involves a *change of appearance* which enhances the effectiveness of the adaptation: in each the reaction occurs in *special times of stress or danger*, i.e. on the approach of an enemy: but the nature and function of the change itself is in the two cases diametrically opposed; for on the one hand, we have an *aposematic display* (involving exhibitions of colour, movements, sounds, smells, etc.): on the other hand, we have *cryptic habits* (involving concealing attitudes, stillness, silence, death-feigning, etc.). As an example of these opposite, yet comparable, types of reaction, we have only to consider the protection behaviour of a Porcupine and a Frogmouth when hard pressed by an enemy. The one makes splendid use of his advertising equipment—he stamps and squeals, he rattles and he stinks. The other makes no less remarkable use of his concealing apparatus—remaining still and silent, and adopting a cryptic attitude, he melts into the landscape.

Finally, we have to remember that intimidating contrivances for display have been developed in many animals which have no power to support the warning with defensive action. With such animals the attempt is to bluster and bluff rather than to intimidate enemies. Such cases grade into examples of Batesian Mimicry, or false warning colours, where an animal masquerades in aposematic raiment, though it lacks the defensive attributes possessed by the animal whose uniform it wears. This, however, is an important aspect of adaptive coloration to which we shall return later. What I am dealing with here is the nature and mechanism of the displays themselves, and the question as to whether they represent genuine warning, mere bluff, or mimicry need not at present concern us.

I. DISPLAYS DEPENDING UPON AN INCREASE IN SIZE

An important element in the display mechanism, which has been adopted independently by animals belonging to widely different groups, is the power suddenly to *increase in size*. This increase may be *actual*, as when a poisonous Puffer-fish (Tetrodontidæ) inflates its body until it resembles a balloon (Fig. 52), or it may be merely *apparent*, as when a Baboon erects the hairs of its mane; or it may depend upon a combination of both physical and psychological elements, as when a Chameleon blows up its body with air, and then orientates it so as to present to an enemy its greatest surface—when the actual increase in size is augmented by a further apparent increase depending upon the relative positions of enemy and prey.

We may now consider briefly these two classes of cases, and show how the change in bulk, or the illusion of change, is brought about. (1) Objective enlargement of the body is achieved in many animals by distending the lungs or the alimentary canal with air or water. Famous examples are the conspicuously coloured Puffers or Globe-fishes (Tetrodontidæ), and the related prickly Porcupine-fishes (Diodontidæ). The former are protected by highly poisonous flesh, the latter by a spiny and almost continuous coat of mail. When irritated, members of both these families inflate the body until the skin is tightly stretched and the form almost globular. Among reptiles, several lizards illustrate the same point. Thus, Chameleons (Chamæleontidæ) have remarkable powers of inflation. Certain Iguanid lizards likewise intimidate enemies in this way. For instance, Bryant (65) says of *Phrynosoma b. blainvillei*: ‘These lizards show great aversion to dogs. When angered by one, the lizard presents a very bristling appearance by elevating the enlarged scales of the back, opens its mouth and gives a hissing noise by quickly expelling the air from the lungs. At such times it stands well upon its legs and puffs itself up to nearly twice its natural size.' In snakes true inflation (as opposed to local spreading of hoods and throat-pouches) occurs at its best in the African Boomslang (*Dispholidus typus*), which can inflate both the trachea and lung ' until it looks like an enormous sausage ' (19).

The same device is practised by frogs and toads belonging to several families —Ranidæ, Bufonidæ, Brevicipitidæ, and others. Thus the South American ' Escuerzo ' (*Ceratophrys cornuta*) distends its body to a tremendous size under provocation, at the same time uttering broken cries of remonstrance. The same habit is highly developed in another South American species, the venomous Giant Toad (*Bufo marinus*), whose lungs can be blown up until they extend the flanks in swellings so as to render the animal discoid in form. Annandale has described similar behaviour in a toad (*Callula pulchra*) from Siam : in this case the body is inflated so as to become almost globular, and the effect of the display is enhanced by the exposure on the back of two broad yellow stripes which are normally hidden beneath folds of the extremely loose skin (7). In this place we must also refer to the familiar bristling of fur, or fluffing out of feathers, by means of which many mammals and birds achieve a sudden and apparent increase in bulk as a caution to would-be meddlers.

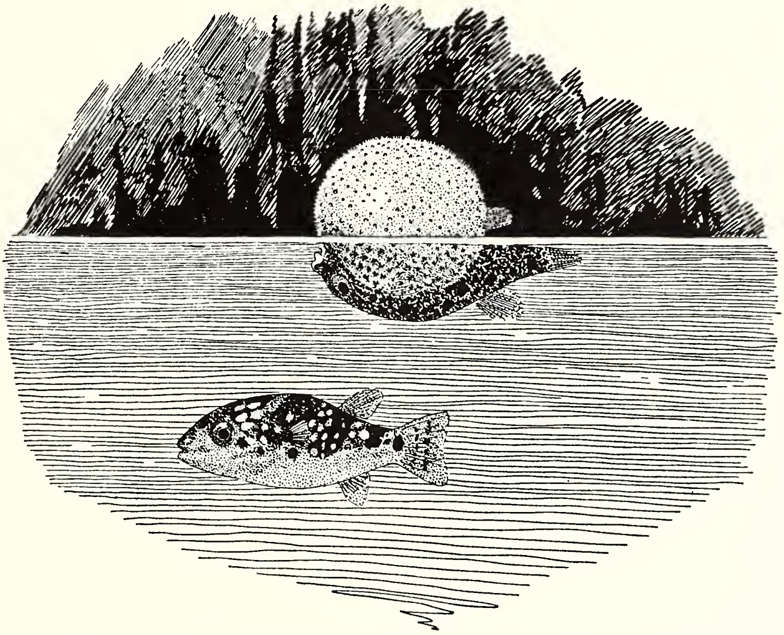

FIG. 52.—*Tetrodon fluviatilis,* showing the fish inflated and deflated

As a final example of this mechanism, I must mention a remarkable case in which protection is achieved not merely by individual inflation, but by the *bunching together of several individuals* into a compact and wellnigh impregnable unit. Norman (446) cites observations by Beebe which show that when threatened by a large Garfish, little Porcupine-fishes will thus mass together for protection 'giving the appearance of one large, round and prickly fish'. In this case, it was the formation which protected the individuals, for occasionally, when a single straggler became separated from the mass, it was promptly preyed upon.

Before leaving this class of warning or threatening display, I must draw attention to two points concerning its general function and significance. Firstly, there is no doubt as to the meaning of these swellings and puffings and inflations: they are known by actual observation in field and laboratory to be employed as a defence reaction against attack by enemies. Secondly, a word of explanation is needed as to the function which the reaction serves. Hitherto in my treatment of the subject, I have distinguished between the defences and the associated advertisements of aposematic animals. *The former operate as a physical factor in countering attack, the latter as a psychological factor in preventing it.* Now this distinction cannot be made in dealing with the phenomenon of inflation, for often we have there combined in the same act a means of defence and a means of advertisement. The reaction presents to a potential predator both a physical barrier and a psychological deterrent.

II. APPARENT INCREASE IN BULK BY ADAPTIVE ORIENTATION

In displays where the increase in bulk is apparent only, this, of course, is not the case: here we are dealing solely with a warning or threatening gesture, which does not in itself involve qualities of inedibility, although an intermediate condition is found in certain animals, where the optical effect depends upon the erection of such structures as spines, scales, or quills. That such illusory enlargements of the body may be highly successful in warding off attack (even in cases where the display is sheer bluff) will be shown later—but here we are concerned with their mechanism and function only, rather than with proof of their effectiveness.

In certain of these cases the aposematic equipment involves the erection of generally distributed integumentary structures—hair, spines, quills, or feathers. For instance, Wolves, Dogs, Jackals, Civets, and other carnivores erect the hairs of the body, thus appearing to swell visibly: Cats bristle up their fur and accentuate the display of bulk by arching the back: of the Mongoose, Hingston says: 'When it faces a serpent it does in actual reality swell to twice its normal size and its tail expands into an immense brush': a similar effect is brought about in porcupines and hedgehogs by elevating the quills. In birds a similar end is achieved by fluffing out the feathers, as seen in the intimidating displays of Turkeys, Cockatoos, Owls, and many others. In certain lizards, such as *Phrynosoma,* inflation of the body causes partial erection of scales, and adds to the menacing effect.

In a somewhat different class of cases, there is an erection or expansion of specialized local structures—manes, crests, frills, hoods, throat-pouches, fins or appendages. Although cases in this second category intergrade with those in the first, typically they differ in an important respect. The special structures concerned are of such a nature that when expanded they tend to be disposed more or less in one plane. This plane of expansion may lie, in relation to the axis of the body, in one of three directions: (1) transversely, as in the case of the Elizabethan ruff of the Australian Frilled Lizard (*Chlamydosaurus kingii*) (Fig. 55); (2) horizontally, as in the case of the hood of a Black-necked Cobra (*Naia nigricollis*); and (3) vertically, as in the case of the gular expansion of Kirtland's Tree Snake (*Thelotornis kirtlandii*). Now, in order to obtain the maximum effect, mere expansion of the frill or hood or pouch is not enough: the expanded surface must be directed towards the aggressor. It is therefore extremely interesting to find that in general displays of this kind are in fact enhanced by appropriate attitudes; adaptive structure is correlated with adaptive behaviour. Moreover, this habit of presenting the greatest surface towards the enemy is shared by such totally unrelated animals as lizards and lions, baboons and parrots, chameleons and grasshoppers—a striking fact which in itself testifies to the significance of the display, while, as we shall see later, observations confirm the view that these displays have in actual fact a warning significance, by proving their effectiveness when used 'on active service'.

This principle of adaptive orientation is nicely illustrated in the case of *Chamæleon dilepis* and *Bufo marinus*, whose habits I have had occasion to study in the Zambesi and Amazon valleys respectively. The Chameleon, on being approached by a rival or enemy, enormously inflates his lungs until his body appears to be almost at bursting-point. At the same time the yellow gular region is displayed, and one or both occipital flaps are raised. During this performance the animal inclines his body so as to present its broadest aspect towards his opponent. When thus displaying before a rival stationed on a branch above, the body is sometimes thrown over in a list almost to the horizontal—in which position, with lungs and throat fully inflated and occipital flaps erect, he doubtless presents a much more formidable and terrifying spectacle, as seen from above, than would be exhibited by the normal upright posture.

Now in the case of the Giant Toad, the same result has to be obtained in a different way. This animal flattens out and widely distends the body with air on being disturbed. Like the chameleon, he, too, inclines his body towards an enemy—though here, since the body is depressed in form, it is the *dorsal* rather than the *lateral* aspect which is exhibited. On being approached from the side, the toad will assume a most comical attitude (Fig. 53), with the near flank squeezed closely to the ground, and the further fore and hind limbs straightened so as to raise and tilt the body over to the desired angle. In order to test this display reaction, which is performed in the most deliberate and purposeful manner, I have more than once walked round and approached the animal from the opposite side, when, like a little ship rolling heavily on the ocean swell, the body is made to rock over until it is again orientated at right angles to the observer. This behaviour affords an interesting example of similar instincts which have been evolved independently in unrelated animals for the same purpose, namely, in this case, to dishearten or terrorize enemies by an increase in size—an increase which is partly real and partly due to an optical illusion. Parallel phenomena occur in the case of such unrelated creatures as zorillas and grasshoppers, where deliberate leaning postures are correlated with the display of patches of conspicuous colour, rather than with size alone. It is also to be noted that, as so frequently happens with adaptive phenomena, almost identical arrangements have been evolved independently in different groups. Among snakes, for instance, the expansion of the neck region may be horizontal, as in the Hog-nosed Snake or 'Spreading Adder' (*Heterodon*) and Cobras (*Naia*); or it may be vertical, as in the Mamba (*Dendraspis*) and Kirtland's Tree Snake (*Thelotornis*).

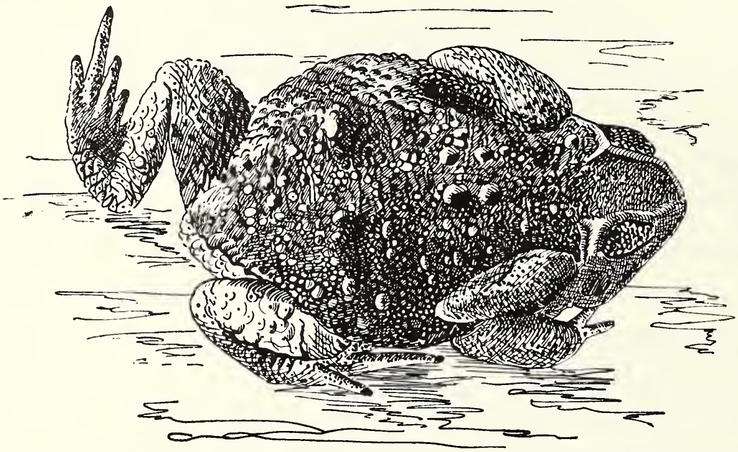

FIG. 53.—Warning display brought about by inflation combined with adaptive orientation in the Giant Toad (*Bufo marinus*)

Among insects, the same orientation phenomenon is seen in the intimidating behaviour of *Idolum diabolicum*, which has been described by Carpenter. When at rest this animal is extremely cryptic. On being alarmed, however, it assumes a threatening attitude, the body being reared up and the front legs extended so as to exhibit the large conspicuous area of the much-expanded coxæ, which normally lie in a vertical plane with the strongly contrasted coloured surfaces facing inwards. In bringing about this striking change of aspect, the coxæ are rotated through a right angle and are thus directed fully towards the enemy. In this attitude the insect will deliberately wheel round so as to present the advertisement directly towards its adversary (79). Similar swinging or wheeling movements are made by another mantis, *Pseudocreobotra wahlbergi*. Now it is extremely interesting to find that precisely similar habits of adaptive orientation form an essential part of the *cryptic* display of animals such as the Bittern, which is likewise known to wheel round so as to face its adversary, thereby presenting its *concealing colours*. In these different cases the movements are essentially the same, but their function and effect is in each case the very opposite—in the one they make for self-advertisement, in the other for self-effacement.

Terrifying attitudes of this kind are widespread throughout the animal kingdom, but here we can only mention a few before passing on to the next class of display phenomena. Among birds expansion displays—as different as the species which exhibit them—are common. Although in general they are correlated with rivalry or courtship or signalling, they are in many cases also used to intimidate enemies. A striking instance of this kind is presented by the Blue-fronted Amazon Parrot (*Amazona æstiva*). When alarmed or in danger this beautiful species throws its body forward into a horizontal position, partially spreads the wings in a horizontal plane, and widely fans out the tail, at the same time elevating its cobalt blue frontal fringe and green throat ruffle. This attitude effects the display of brilliant red areas on flight and tail feathers, which are normally concealed by a cryptic garment of green. Simultaneously in its excited mental condition the bird begins to quiver, so that the feathers, like the quills of a porcupine, are set a-trembling, and produce a rustling sound; the pupil contracts, and the iris flashes forth hues of orange and red—messages of hate or fear; finally, when the display is at its climax, the bird utters a staccato, high-pitched note of warning, somewhat resembling the radio time-signal!

III. SUDDEN EXHIBITIONS OF CONSPICUOUS COLOUR

In the warning or threatening displays of different animals an important element—different from, though often associated with, a local increase in size of the body—*is the sudden exhibition of bright colours which are ordinarily hidden from view*. Functionally, this element in the display mechanism is extremely interesting. (1) It renders possible in one and the same animal a combination of concealing and revealing coloration; if concealment fails to prevent detection, warning or bluff displays may yet prevent attack: it illustrates in action Hingston's principle of 'Colour Conflict' discussed at length in his stimulating work on 'The Meaning of Animal Colour and Adornment'. (2) The *sudden appearance* of colour previously hidden introduces in itself a new alarming factor, which has a psychological effect independent of its mere *exhibition*. What this effect is on the reactions of different predators is not clearly understood: indeed, we have here an almost untrodden field for future research. However, such direct evidence as is available—besides the indirect evidence afforded by the mechanism of the displays—testifies to its value as a means of defence.

I have frequently drawn attention in this book to the significant fact that in dealing with various types of adaptive coloration, we find that the same, or similar, ends are often attained by very different means in different animals. This point is well illustrated here, and it will therefore be interesting now to consider some of the varied ways in which this sudden change in the appearance is brought about.

(1) **By Displaying the Ventral Parts**—Certain animals which wear local conspicuous colour on the under parts of the body have the remarkable habit of turning over on their backs or otherwise exposing the ventral surfaces when in extreme danger. This habit, which occurs independently among such unrelated groups as snakes and amphibians, spiders and caterpillars, and which is used only under special circumstances and so as to expose the specially conspicuous areas, can only have one meaning. It is a warning to enemies. In the case of the Hog-nosed Snake (*Heterodon platyrhinus*), should the preliminary hissings, mouth-openings, and inflation fail in their effect, the animal turns over on its back and lies motionless, as if dead, revealing its black belly markings. Barbour states that if then turned over, it flops back again into the same position. Both the Fire-bellied Toad (*Bombinator igneus*) and the American Toad (*Bufo americanus*) exhibit the same belly-exposing habit, and in both the aposematic colouring is worn underneath. In other cases, the demonstration of conspicuous under parts is effected by rearing the body upwards before an enemy—a habit shared by many snakes belonging to different groups. In these cases the animal rears itself up before a foe, and exhibits its ventral shields, whose coloration is of a type so widely associated with warning displays—black, in the Black-necked Cobra (*Naia nigricollis*) ; black and white, in the Spitting Cobra (*Sepedon hæmachates*) ; bluish-white brilliantly marked with red, in *Coluber couperi* ; black, in *Coluber quadrilineatus* ; yellow or red with black spots, in *Macroprotodon cucullatus* ; red and orange with black spots, in *Zamensis hippocrepis* ; red with black spots, in *Zamensis asianus*. Among mammals an essentially similar mechanism is seen in the Mottled Polecat (*Putorius sarmaticus*) : in this creature the conspicuous coloration is likewise on the belly, which is glossy black, and Hingston states on the authority of Mrs. Yates (266) that ' it will face man or dog, attacking with calm self-possession, and rearing itself up on its hind legs ', thus exposing its aposematic surface to its enemy.

In certain Lepidopterous larvæ, such as the Sphingid *Leucorhampha ornatus*, a sudden rearing up and exposure of the ventral surface, with its terrifying eye-spots, is an essential part of the display. The following vivid account of the display in this species is quoted from the Rev. Miles Moss's beautifully illustrated monograph on the Sphingidæ of Pará. ' The larva ', he writes, ' is quite one of the most remarkable of living creatures that I have ever seen, a perfect Aaron's rod, combining in the most novel and striking way the principles of protective resemblance with an aggressive snake-mimicry. When at rest as an adult caterpillar, it hangs by two pairs of claspers in the vertical from the stem of its food-plant, and appears to be nothing but a broken branch covered with a dull, creamy white lichen. A strange black chequered dorsal design, with a gradual intensification of the grey on certain segments, completes the deception. The wonder, however, is if possible exceeded when, on being disturbed, this marvel of creative evolution endeavours once more to deceive by turning into a snake. . . . Though this wonderful transformation wants to be seen in life to be fully appreciated, I may explain briefly that the effect is produced by the creature turning itself over and exhibiting its ventral area, which is adorned by a broad band of dark olive-green with the three anterior sets of claspers completely with drawn and scarcely visible. The thoracic segments, which are always swollen, become puffed out laterally to an exaggerated extent; a pair of black eyes on segment 4, hitherto concealed and situated behind the now recumbent and wholly inconspicuous legs, open out; the cheeks appear to be adorned by yellow scales with black edges; and the fraudulent notion that one is beholding merely the head and neck of a formidable, if small, snake is carried to a nicety by the rigidity of the curve adopted. Then, as if to mesmerize, a swaying side-to-side motion is kept up for an appreciable number of seconds, before the creature, seeming to realize that an attack is no further contemplated, gradually closes its false eyes and relapses once more into diurnal slumbers.'

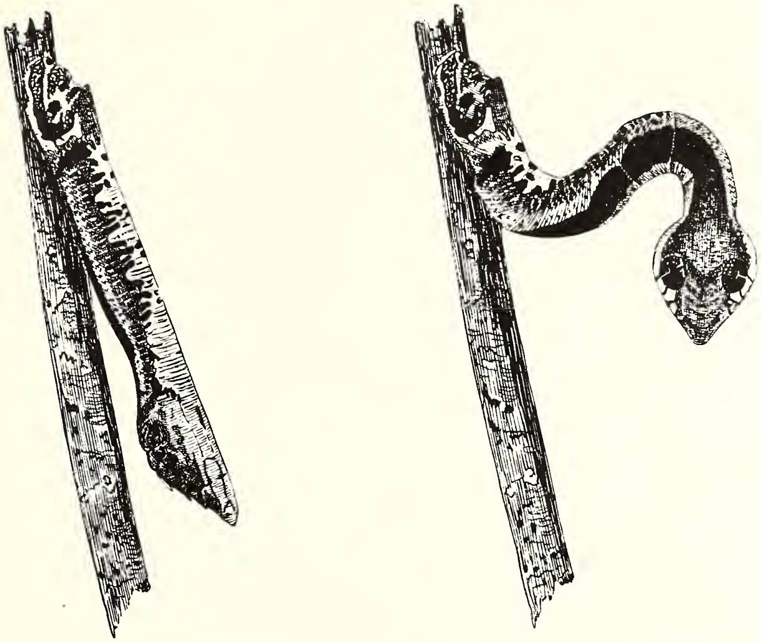

FIG. 54.—Larva of *Leucorhampha ornatus*: 1 Cryptic resting attitude; 2 'Terrifying' attitude. (*After* A. MILES MOSS)

In the poisonous Indian spider *Pœcilotheria*, which has been described by Pocock (476), we have another instance of a display of a conspicuous ventral surface. This creature has the upper surface of the body and limbs inconspicuously coloured with tones of brown and grey, but the body beneath is chocolate brown or black and the limbs whitish or lemon yellow, ornamented with black bands. When molested, it rears up on its hind legs, and brandishes the fore limbs and palpi in the air—thus adopting an attitude in which the aposematic surfaces are exhibited to great advantage.

In these and similar cases the significant facts will be noticed: (1) that the conspicuously coloured surfaces are normally hidden against the ground: (2) that the aggressive display posture is adopted only under special circumstances—that is, when the animal is in danger of attack: (3) that the attitude is correlated with the disposition on the body of the conspicuously coloured surfaces—that is, it is such as to exhibit these to the best advantage before the enemy.

(2) **By Uncovering Sematic Surfaces**—A relatively simple exposure apparatus, reaching its highest development among certain Lepidoptera and Orthoptera, consists in the *uncovering* of the conspicuous surface—which ordinarily lies concealed behind a cryptic masking element. For instance, the displays of the two grasshoppers *Phymateus viridipes* from Africa and *Acridium violescens* from Ceylon depend upon this principle, though in each case the details of the mechanism differ. The first, by erecting its fore wings, exhibits the black and crimson of its fanned-out hind wings; the second, by lifting up its hind leg, exhibits a row of lateral grey and black eye-spots on its abdomen. In a third case, that of the African Mantis *Idolum diabolicum*, the display is produced by extending the enlarged coxæ of the fore limbs—which carry the threatening pigment—so that they project clear of the flattened thoracic expansions that cover the brightly coloured areas when this remarkable insect adopts its normal cryptic attitude. The same principle is illustrated by a stone-like locust nymph of North Africa, which exposes in display the bright yellow inner surfaces of its hind femora.

The habit of displaying sematic surfaces has been evolved independently in several families of moths. The Zygænid *Neurosymploca xanthosoma* raises its wings so as to expose the bright yellow abdomen—a display which effectively deterred Carpenter's monkey from further advances (79). In the white Lymantriid *Arctornis producta* the tip of the abdomen, which is surrounded by yellow hairs, is protruded dorsally between the edges of the wings when the moth is disturbed (79). The Arctiid *Rhodogastria leucoptera* separates its wings and spreads out the legs so as to uncover the abdomen, which is bright rose-pink in colour, at the same time emitting from the thorax a copious acrid yellow froth (86). In the Sphingid *Smerinthus ocellatus* the fore wings are raised so as to exhibit the eye-spots on the hind wings.

(3) **By Spreading Out Folds of the Integument**—Another mechanism consists essentially in the spreading out of loose areas of skin in whose folds the coloured warning sign is normally tucked away out of sight. In some cases it is merely the loose skin of the body which conceals the sign. For instance, in the Siamese Toad *Callula pulchra* we have already seen that dilation of the body stretches the skin so as to reveal two broad yellow dorsal stripes. A parallel case is provided among lizards by *Liolepis belliana*. This animal wears a cryptic coat of brown, but concealed along each flank is a series of purple bars separated by yellow spaces. When taken in the hand, Annandale (7) found that the lizard, in its anger, flattens the body so as to bulge out the purple bars conspicuously. Moreover, it is very interesting to note that the same mechanism has

been evolved in certain insects, especially among caterpillars. In *Leucorhampha*, *Chærocampa*, and others, startling or terrifying effects which include the sudden production by an innocent-looking insect of huge snake-like eyes depend upon this principle. These creatures are nature's conjurers! A fine example has been described by Annandale (7) in the case of a large Lymantriid caterpillar. The body of this creature was covered with pale lemon-yellow hairs: but between the fourth and fifth segments was a black bar 'of a peculiar velvety appearance' which extended across the body and was surrounded by 'a kind of white halo'. When the caterpillar was feeding or walking the bar was concealed; but when irritated the animal 'suddenly bent the anterior and posterior regions of the body together, thus causing the black bar on the back to become stretched and continuous, and to appear like a gaping, cavernous mouth, of which the bunches of hair behind and before formed the jaws'.

(4) **By Opening Fans**—A similar, though more elaborate and specialized type of mechanism consists in the expansion of definite fan-like structures whose open folds reveal the warning sign.

Many New World lizards of the genus *Anolis* possess gular sacs, which are normally folded up inconspicuously beneath the throat, but which, when fanned out in display, exhibit the most brilliant hues of red, yellow, or blue. I came across one of these arboreal species (*Anolis ortonii*) at Obidos, on the Lower Amazon. Found resting on a lichen-patched branch, the beast was a fine example of cryptic resemblance, its variegated grey tunic harmonizing well enough with surrounding twigs. But when I approached to take it up, there was a transformation scene: with a startling flash, the throat-pouch flew open, to reveal a wide expanse of red, orange, and white pigment previously hidden within its folds. This type of intimidating equipment reaches its highest development in the frill of *Chlamydosaurus kingii* (Fig. 55), where an elaborate structure for the exhibition of threat has been developed. The striking appearance of the suddenly expanded gorget is further emphasized by open-mouthed and hissing demonstrations of ferocity—demonstrations in this instance which are pure bluff, for when escape is possible the lizard, who is a highly specialized runner, considers discretion the better part of valour, and makes off on its long hind legs with rapid strides.

Among certain fishes, fins perform the same duty: Doflein (cited Mortensen, 417) observes that *Trigla kumu* and *Leptotrigla Bürgeri* suddenly spread out their large, magnificently coloured pectoral fins, thereby frightening predators and warning against their poison spines. A closely parallel instance among insects is seen in the display of the Acridiid *Phymateus viridipes*, which erects the tegmina and spreads out fan-wise the vivid purple and black wings—a device which is known to be successful in preventing attack by enemies (see p. 306).

In the above cases the mechanism is like that of a paper-fan, whose pattern is only displayed when the fan is open. Such instances lead on to another device, which may be compared to a feather-fan—a type utilized in the crest, ruff, wing, and tail displays of different birds, including Herons, Storks, Blackcocks, Turkeys, Frogmouths, Parrots, Cockatoos, Owls, and many others. We cannot here discuss these cases further, beyond pointing out that such displays are by no means always associated with rivalry or courtship. Often they come into operation against predatory enemies, and as such must be regarded as warning (Aposematic) or false warning (Pseudaposematic). For instance, the intimidating machinery of a wounded Heron or of a Macaw is well known. And every one is familiar with the bluffing tactics of the Blackbird, who fans out and repeatedly jerks his tail upwards, at the same time uttering his wild alarm notes, when mobbing a marauding cat; and a similar attempt at bluff is made by the Hoopoe, when, according to Hingston, it 'makes its crest into a splendid fan' on being attacked by a hawk.

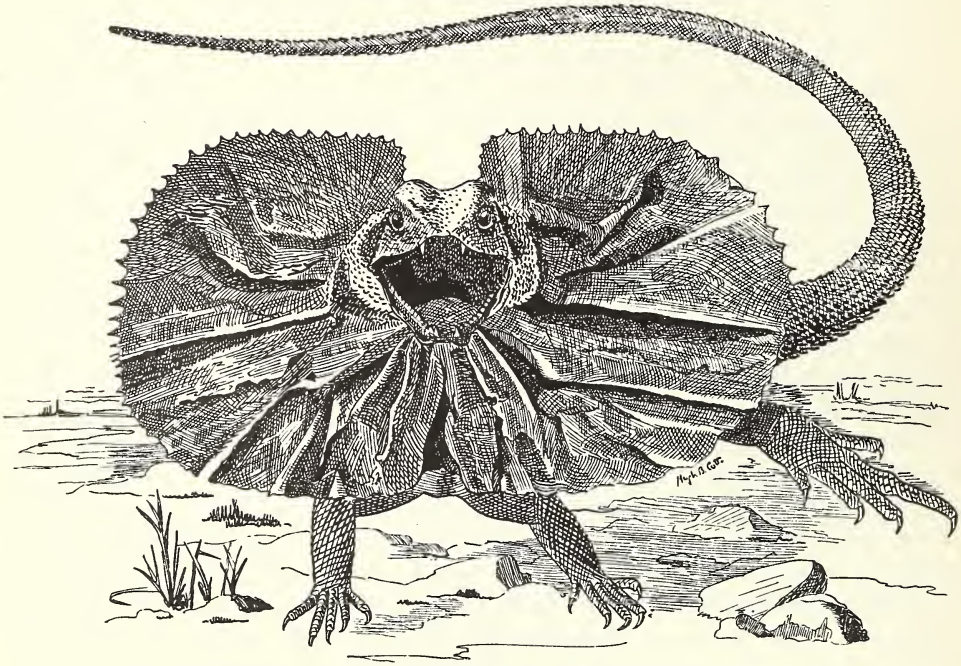

FIG. 55.—Warning display of the Frilled Lizard (*Chlamydosaurus kingii*)

The Australian Frogmouth (*Podargus*) likewise uses its head-feathers in display (555), but in this case the fan is erected laterally rather than longitudinally—the effect being somewhat analogous to the menacing attitude of the Australian Frilled Lizard (*Chlamydosaurus*). Other striking displays, in which the wings and tail are used as fans, have been independently evolved as threatening gestures by the Painted Snipe, Sun-Bittern, Long-eared Owl, and several other totally unrelated birds.

(5) **By the Erection of Hairs**—Dr. Julian Huxley has recently drawn my attention to a very remarkable display mechanism in the Crested Rat (*Lophiomys ibeanus*), in which the general effect—that of exhibiting conspicuous but pre-

viously hidden lateral stripes—may be compared to the display of the toad *Callula pulchra*, though the actual method by which it is achieved in the two cases is so utterly different. When alarmed, this rodent erects the hair of its back and lowers those of its flanks, in such a way as to form a wide and clearly defined parting or furrow extending from the ear to the hip, that is, nearly the full length of the body. This furrow is potentially lengthened before and behind by the forward and backward displacement of the fur in these parts. What makes the display so striking is the colour of the fur and skin thus exposed—the former being black at the base and whitish distally, while the skin is dark grey. The animal thus exhibits along each side a kind of trench, deep and black, more or less surrounded by a whitish border. By the kind permission of Mr. Seth Smith I am able to reproduce here a sketch taken from one of his photographs showing the animal in its remarkable display posture.

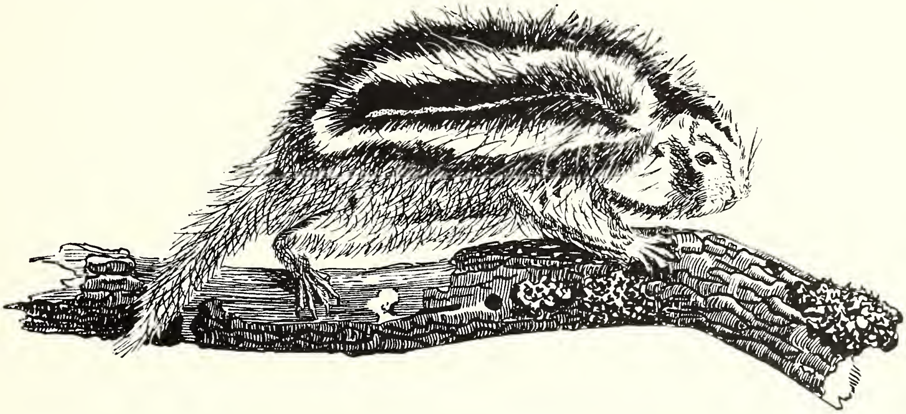

FIG. 56.—Warning display of the Crested Rat (*Lophiomys ibeanus*)

In the same category we have the less specialized displays of the North American Porcupine (*Erethizon*) and the South American Tree Porcupine (*Cœndu*). These forms lack the tail rattle of *Hystrix*, but when disturbed they raise their spines, displaying the red or white colour at their base.

(6) **By Stretching the Integument**—In a somewhat different category we have the sudden exposure of hidden colour due to lateral stretching of the integument, as seen in the displays of certain snakes. Sometimes the pigment exposed is on the area between the scales. Thus when irritated, *Natrix stolata* flattens and distends the neck so as to expose a blue and red pattern normally hidden between the scales (266); it is by this method that the green Indian Whip Snake, *Dryophis mycterizans*, displays on the fore part of its body a remarkable checkered pattern of black and white. Sometimes, on the other hand, the colour exhibited in display is situated on the overlapped area of the scales themselves, which is blue in the Indian *Dendrelaphus tristis* and greenish-blue in *Natrix himalayana* (266). An especially interesting case is that of

Thelotornis kirtlandii, in which both these methods are combined—for here elements in the display pattern extend unbroken across scales and skin. The display itself, which I have witnessed in wild specimens in Portuguese East Africa, is a remarkable performance. Normally this handsome snake, with its elongated vine-like body and extremely attenuated tail, its cryptic dress of greens and browns and greys, and its specialized arboreal habits, is recognizable in nature only with great difficulty. But when alarmed, the cryptic appearance is miraculously transformed. Suddenly, by the spreading and lateral compression of throat and neck, there appears a series of purplish-black bars of pigment strongly contrasted against a white expanse, where a moment before was what seemed the stem of a climbing plant. Simultaneously, to accentuate the effect, the vermilion, black-tipped tongue is thrust out fully extended.

(7) **By the Elevation of Appendages**—Another method frequently adopted consists in holding erect and displaying a conspicuously coloured appendage. In many unrelated animals the part thus displayed is the tail. Hingston has discussed the role of this organ in the intimidating mechanism, and has demonstrated that it forms an important element in the display of many unrelated mammals, including the Lynx, Lion, Cat, Dog, Wolf, Fox, Jackal, Mongoose, Stoat, Wart Hog, Skunk, Gnu, and others. Among mammals the tail erections, brandishings, swishings, and spreadings are mainly employed *as threats directed in rivalry against members of the same sex*; and as such they do not concern us here. Now it is very interesting to find that similar tail displays occur among other animals, such as snakes, where they are known to be used *as warnings directed in defence against enemies of different species.*

The poisonous Malayan *Doliophis intestinalis* is reputed by natives to travel about holding its tail in the air; and the truth of this has been confirmed by Barbour (19), who observed the species in Java carrying its tail erect, in such a way as to expose the lower surface, *which is red.* The quite unrelated and entirely harmless burrowing *Cylindrophis rufus*, from the Malayan Peninsula, reacts to danger in the same way, as witnessed by Annandale and Barbour. When brought above ground, it ‘ travels along with the tail bent sharply upward . . . and if the snake is touched the upturned tail snaps around in a threatening manner, precisely like a striking head ’ (19). Here, again, the under surface of the tail is brilliant red. In Brazil *Apostolepis* apparently has the same habit, but instead of being red-tailed, the whole snake is a vivid red, and the head and tail are black. In Mexico *Diadophis amabilis* rears up its tail when alarmed, curling it forward and giving it a spiral twist, thus exhibiting to advantage the red of its under surface. The Indian *Calophis trimaculatus* likewise curls its tail upwards when disturbed, thus exposing the coral-red and black warning of the anal region.

In this category we may also include the menacing display of the Land Crab *Sesarma meinerti*, whose habits at Beira I have described and figured elsewhere (108). *S. meinerti* is an extremely handsome animal, having a dark purple carapace, narrowly bordered with orange, and massive, powerful chelæ of a brilliant orange-vermilion hue. When encountered some distance from their burrows, with their line of retreat cut off, the crabs do not attempt to bolt for it: instead, caution is replaced by a bold, pugnacious demeanour and a fine show of temper. Standing their ground, armed and aggressive, they deliberately turn to face their adversary, and, with the carapace elevated, the huge red chelipeds extended upwards in the most formidable and menacing attitude, and the 'fingers' held widely open in the 'ready' position, they await the turn of events. These deliberate and defiant actions are most striking, and the meaning of the posture could hardly be made plainer if the crab were to hold aloft two red flags and exclaim 'Beware!'

We may mention here the threatening display of certain birds like the Sun-Bittern (*Eurypyga helias*), whose wings, upraised and spread so as almost to encircle the body, are presented towards an enemy. Such a display is of particular interest when we consider how closely analogous effects are produced by other animals very far removed in every way, namely, grasshoppers and mantids.

A beautiful example of the kind is furnished by the mantis *Pseudocreobotra wahlbergi*, to whose menacing attitude my attention was drawn by Mr. L. C. Bushby at Caia, in Portuguese East Africa. When alarmed this animal elevates its wing-covers above its back like two signal arms—each of which bears on the *dorsal* surface a conspicuous ocellus—assuming the remarkable posture shown in Fig. 81, thus directing towards the intruder a somewhat formidable, not to say astonishing, appearance.

With the above we may compare the behaviour of another mantis, *Eremiaphila braueri*, whose frightening attitude has recently been described by Dr. Roonwal (544). This insect, a desert species from Baluchistan, suddenly turns at bay when molested, unfolds its wings and stands up on its hind legs 'like a performing bear' so as to present the *ventral* surfaces of both fore and hind wings, which are brightly coloured—the former faint violet with a prominent blackish marginal streak, the latter black with a purple base. Roonwal states that when he moved round the insect in a circle, it turned round, always facing him, and maintained its erect poise for over twenty minutes.

Various other mantids are known to display, either when in danger, or, as sometimes happens, when confronted by large prey. Shelford (570) has given us a careful account of the *parade admonitrice* of *Hestiasula sarawaka*. When at rest this mantis appears cryptically clad in sombre brown and grey. Its front femora, widely expanded into flattened plates, are then held close together in front of the body. But when irritated a wonderful transformation of attitude and colour takes place. The prothorax is elevated; the front legs are spread sideways; the elytra and wings are opened; and the abdomen is uplifted. Each of the surfaces now exposed are highly coloured. The first coxæ are deep crimson on their internal face. The disc-like femora are brilliant yellow with a black border. The under-parts of the thorax are coal-black. The wings black, mottled with yellow. And as if to accentuate the effect, the insect sways over from side to side, at the same time uttering audible warnings by snapping the fore tibia down on their femora with clock-like regularity—also producing a continuous rustling sound with its wings.

The white and purple colours of the African *Idolum diabolicum*, once regarded as a floral simulator, almost certainly belong to the same category. On being disturbed, this cryptic, leaf-green mantis rears itself up on its two last pairs of legs, and extends the gaily coloured forelegs forwards, with their flattened coxæ held in the same plane as the broad thoracic expansions. Carpenter states that the effect of this large diversely coloured area being suddenly exposed in a threatening manner was extremely surprising both to him and to his monkey against which the display was directed. The monkey hastily backed away from the insect—which on this occasion saved itself by its terrifying attitude (79).

Dr. G. C. Varley, who has recently collected for review the available data relating to display in Mantidæ, himself observed another and very different attitude adopted by a Californian mantis of the genus *Stagmomantis*. He tells me that this insect rears up on four legs, elevating the thorax almost vertically, raising the tegmina, spreading the wings, and *turning sideways so as to direct the expanded surfaces* (which are framed beneath by the curved abdomen) *fully towards the observer*. In all these and similar instances, the close correlation between the disposition of the coloured surfaces and the manner in which they are displayed is very apparent (639*a*).

(8) **By the Extrusion of Filaments**—These examples lead us to a class of cases in which the advertising instrument is likewise brandished aloft, but in which it is solely a display structure that normally lies retracted within the body when not in use. Such structures are found in various larval Lepidoptera, and in certain Locustid and other insects. A well-known instance is provided by the two pink whip-like processes which the Puss Moth larva (*Cerura vinula*) can protrude from the hinder end of its body and brandish above its head as the disturbed insect assumes its terrifying attitude. A similar general effect, though different in detail, is seen in the display of an Indian Swallow-tail caterpillar (*Papilio demoleus*), which when disturbed can shoot out through a narrow transverse slit behind the head two red tentacles that diverge like a pair of horns. Hingston, who has described this display, says: 'They look raw and fleshy and their skin glistens, and with them comes out a pungent odour.' When not in use, these delicate telescopic tubes 'disappear into the slit which closes and hides them from view' (266). In both these cases the filaments are forced out by pressure from within. In another group, the Indian Lasiocampid caterpillars belonging to several species illustrate the same point. They react when touched by opening two slits on the back, just behind the head, and suddenly extruding a brush of velvety hairs. These processes are always brightly coloured, being black, orange, pink, and steel-blue respectively in four species. Hingston says: 'It is an abrupt and astonishing performance. The extrusion is so unexpected that it frightens one not a little, making one feel that with this kaleidoscopic creature it is advisable not to interfere' (266). It is very interesting to find similar intimidating devices in the quite unrelated Tettigoniid *Capnoptera* of Malaya.

When taken in the hand this animal lowers its head, so as to separate it from the thorax, and forces out through the cleft thus formed a vivid scarlet bladder, which is everted and projects behind the head like a hood.

(9) **By Displaying the Inside of the Mouth**—The mouth of a vertebrate provides an almost ready-made display mechanism; and accordingly we find, especially among birds, lizards, and snakes, that the mucus membrane and tongue are often brilliantly pigmented with black, pink, red, orange, or yellow; and that this internal coloration is associated with the habit of widely gaping the jaws before an enemy so as to show off the warning hues to good purpose. Whilst collecting reptiles in Portuguese East Africa different examples of this habit came to my notice. For instance, in the Amatongas Forest, there lives a fine arboreal lizard, *Agama atricollis*, of which several specimens were obtained. Like so many strictly tree-dwelling species, its colour-scheme beautifully illustrates the principle of cryptic resemblance. But on being interfered with, it puts up an impressive show of aggression—turning in a most threatening manner upon any one coming near it, arching the neck and raising the head, and throwing widely open the doors of its mouth so as to display before the enemy the brilliant orange-yellow interior decoration. An African Chameleon behaves similarly, exposing a blue-black mouth interior bordered by pink lips, while further examples are *Chlamydosaurus kingii* of Queensland, and *Phrynocephalus mystaceus* of India, where the colours exhibited are yellow and pink respectively. This habit is also known to occur in certain snakes, such as the American Hog-nosed Snakes (*Heterodon*), the Pike-headed Snake (*Oxybelis acuminatus*), and the Fer de Lance (*Bothrops atrox*); and is used as part of the threatening display by many birds. Referring to that beautiful green tree snake of India and Ceylon, *Dryophis mycterizans* (whose mouth is pink inside), Wall states that when much excited 'it opens the jaws widely, and expands the lower jaw laterally in a very remarkable manner, so that the jaw, naturally shaped like the bows of a slender boat, becomes shovel-shaped . . . and the edges of the lower lips are simultaneously turned down. While menacing, the neck and fore-body are much compressed, and the throat is pouched . . . Seen under these conditions with the head retracted and the fore-body thrown into sigmoid curves, the snake presents a most formidable aspect' (645).

(10) **By Sudden Physiological Colour Adjustment**—We have now to consider a singular display mechanism which differs fundamentally from previously described cases in that it depends, not upon a sudden exposure of surfaces normally hidden, but rather upon a sudden change in the appearance of a surface already exposed. For the following facts I am indebted to Mr. William Holmes, who has very kindly allowed me to see an account of his recent work, as yet unpublished, on the colour-changes and colour-patterns of *Sepia officinalis* (269).

Under strong disturbance or provocation, this cuttlefish undergoes a series of colour-changes as conspicuous and complete as they are rapid. The first of the successive patterns is one in which two large black spots appear on the dorsal surface of the mantle. Then follows a rapid and complete paling of the rest of the animal, while the black spots themselves become still more saturated and intense. 'Thus for a moment', writes Holmes, 'the two black spots stand out most vividly on the background of the iridescent white animal.' Sometimes this pattern is accentuated by marked flattening and expansion of the body—a change which brings the eyes into a somewhat dorsal position. At the same time a black crescent forms beneath each eye, the pupil dilates, and the edges of the fins become strongly outlined in black—the rest of the body remaining white.

Alternatively, the two-spot pallid phase may be followed by the animal shooting away, the rapid departure being accompanied by simultaneous darkening of the whole body. Further irritation may lead to total paling and the superimposition of four longitudinal black stripes on the upper surface. 'These lines flicker vividly over the pallid back, and then suddenly disappear, to be followed perhaps by a reappearance of the black spots, another total darkening, or a brief reappearance of the zebra pattern. All this time, the animal darts about rapidly, as if to avoid the irritation, and its final action when it cannot do so is to eject a cloud of ink. Then at once it becomes motionless, and hides below the black cloud which it has produced, and its colour can be observed no more.' Now it seems very probable, as Holmes suggests, that these changes are to be regarded as terrifying displays, calculated to produce avoiding or flight reactions in a predator. Particularly significant is the adoption of a colour-scheme, which, for reasons already mentioned, is one likely to produce the maximum effect on the eye of an observer. For here we have a combination of the most conspicuous tones—black and white; arranged in the most conspicuous manner—large spots on a flat field, whose outline is accentuated by a black border: and the whole displayed to advantage by the special flattened and expanded attitude of the cuttlefish, and especially since the whole effect appears and disappears with great rapidity. In short, these reactions appear clearly to represent a remarkable and highly specialized method of producing those sudden and striking alterations of appearance which in many analogous cases are known to afford protection, by intimidating would-be aggressors.

IV. ADVERTISEMENT BY MOVEMENT

In the earlier part of this book I have stressed how vitally important is immobility in the successful use of any concealing colour-scheme. Quite apart from *a priori* considerations, and from the experience of naturalists and sportsmen, it has also been shown experimentally that *movement* attracts the attention of animals. Moreover, we have seen that where concealment satisfies a vital need in the lives of animals, associated with cryptic coloration we almost invariably find cryptic habits, that is to say, *the instinct to 'freeze' or lie motionless on the approach of danger.* Now it is extremely interesting to find that in the case of aposematic animals, where the colour-scheme has precisely the opposite function, and where observation is courted, rather than shunned, there has been adopted as an important element in the aposematic make-up the appropriate, and opposite, habit, that is, *the instinct to move on the approach of danger.*

This principle is, of course, recognized by human advertisers, and its application may be seen at night in the ingenious illusory movements of electric signs displayed in almost any town. But moving advertisements are older than any of these towns where we see them displayed. This same device has long been employed in nature—in deserts and savannahs and forests, by Caterpillars and Birds of Paradise, by Snakes and Praying Mantids, by Iguanas and Fiddler Crabs —and was no doubt an established and recognized method of advertising ages before the appearance of man in the world.

When angered or in danger many Iguanid and Agamid lizards jerk the head up and down before their rival or enemy. The handsome black and yellow tree snake *Dipsadomorphus dendrophilus* of Siam makes a great exhibition of movement when driven to extremities—gaping, hissing, striking out wildly at anything near it, and drumming on the ground with its tail (7). Other snakes such as the Siamese *Xenopeltis unicolor*, the Ceylonese *Dipsas ceylonensis*, and the Indian *Dipsadomorphus gokool* elevate and vibrate the tail (266). The Bornean mantis *Hestiasula sarawaca* vibrates its antennæ when displaying. Certain Hymenopterous larvæ, such as *Crœsus septentrionalis*, whip the abdomen actively when disturbed, the effect of the writhings and wriggling being enhanced by the gregarious habits of this and related species.

Many Sphingid caterpillars, such as the Brazilian *Isognathus swainsoni*, and the Peruvian *Pholus labruscæ* (419), brandish and lash their whip-like ‘ tails ’ in the face of enemies, just as cats and lions do ; and the caudal filaments of the British *Cerura vinula* caterpillar are used in the same way. I have already referred (p. 200) to Hingston’s account of the remarkable gregarious habits in aposematic caterpillars of the genus *Isognathus* (Sphingidæ). As though to enhance the formidable display of colour presented by the caterpillar-cluster, the gregarious instinct is combined with instinctive movements. ‘ During the day they remained quite still with the caudal appendage erect and motionless. But the moment they were interfered with or made to move, the caudal whip was put into motion. It was waved about from side to side and carried in sweeps over the body.’ Hingston regards this as a ‘ frightening instrument ’ and suggests that the swaying and sweeping of the whip serve to frighten or brush away parasitic Hymenoptera. Whether or not this is its main function, there can be no doubt that movements of the kind which he describes add effectively to the aposematic equipment.

V. WARNING SOUNDS

Advertising sounds, like advertising appearances, serve a wide range of functions in different animals : indeed, considered in relation to their biological significance, sound and coloration are closely analogous phenomena. *Often the same end is attained by the one as by the other in different animals*—for both visual and auditory advertisements may be employed as a challenge to a rival ; as an attraction to a mate ; as a signal to friend ; as a warning to foes. *Often both are used for a common purpose in the same animal*—as when the rabbit, showing his white upturned tail as he makes for the burrow, thumps loudly on the ground before entering ; or when the cobra, spreading his hood, reinforces the display by hissing ; or when the porcupine erects his quills, grunts and shakes his tail-rattle in the face of the enemy ; or when the peacock spreads his plumed fan, and vibrates it with a sound like the rustling of leaves in the wind.

We see, then, that the biological uses of sound, like those of appearance, are both varied and interesting : in their different aspects they may be interspecific or intraspecific. There are the love-songs of Crickets and Toads and Nightingales, correlated with courtship, which serve to bring the opposite sexes together, or to warn rivals off occupied territory. There are the call notes of Owls and Hyænas, of Titmice and Tanagers, which, especially developed in nocturnal or forest-dwelling forms whose activities preclude the extended use of vision, serve to keep together members of the flock or family. There are the alarm signals of Blackbirds and Racing Crabs, which broadcast to friends the signal of a common danger, or caution intruders from entering an occupied burrow. And there are the rattlings and rustlings, the stridulations and stampings and cries by which insects, snakes, and other animals notify an enemy of danger.

The biology of animal-sound—its nature, its functions, and its origin—is a large subject, which provides material for a chapter of natural history as interesting as it is remarkable. But in this place we are not concerned with problems of sound, except in a special connexion, namely, in association with aposematic qualities and habits : or, in other words, in relation to self-advertisement as a means of self-defence.

In such cases, the notice ' You have been warned ' is not merely displayed : it is broadcast, in a simple warning language, which, like warning coloration, may be learned by predators in the stern school of experience ; and which, like railway signals and fog detonators, may each play a vital part in the recognition of danger.

As with visual colours and displays, sometimes the auditory sign represents a real warning, sometimes it is mere bluff—depending upon whether the threatening gesture is backed by the ability to inflict punishment. Rattlesnakes and Porcupines both possess rattles, and they both punish an aggressor. Here the warning is a genuine warning of real danger. On the other hand, chamaeleons and kittens distend themselves and hiss savagely at an intruder ; but the utterance, so like that of many poisonous snakes, is a mere puff of air, and nothing but bluff—just as the resemblance of a Hornet Clearwing Moth to a Hornet is bluff. In either case, the animal imitated is poisonous, and the imitator harmless. In fact we seem to have in such cases a kind of mimicry, organized on an auditory rather than on a visual basis.

The nature of the sounds uttered by different aposematic animals varies within wide limits. One thing, however, they have in common—generally speaking, none are very loud. The reason for this is not far to seek. Unlike a ship's fog siren, which must give out its message loudly and repeatedly whether danger is near or not, in the case of warning sounds emitted by animals, the utterance is only needed for use at close range and on special occasions, that is when attack is imminent. In this respect, aposematic sounds differ strikingly from love-songs and call-notes—from the warbling, churring, ringing, screeching, hooting, trilling and rattling tones of Blackcaps and Nightjars, of Bell-Birds and of Hyænas and Howling Monkeys, of Toads and Tree-frogs and a host of other creatures whose urgent messages, penetrating and repeated, are broadcast afar by night or day, through desert or forest.

Hissing—the sound produced by the issuing of a gas under pressure through an orifice—is commonly used for purposes of warning or intimidation by snakes and lizards. It must be remembered that the general coloration in both these groups is cryptic. But many species of both groups make menacing displays of colour when provoked, and these coloration threats are often attended by sound threats, of which hissing is the chief. Such gestures, which make a combined appeal to the sight and hearing of an enemy, constitute a second line of defence. Their value in poisonous forms like the Gila Monster, and many venomous snakes is clear. For poison is precious : it must not be wasted. Prevention is better than retaliation : peace than war. On the other hand, in non-poisonous species the sound can only have a deceptive significance, but there is evidence that at least sometimes the ruse is successful.

One needs a certain practical acquaintance with snakes in the field to appreciate the unpleasantly startling effect of this sound, especially when produced by the larger species, whose lung capacity is considerable, and which, in the words of Barbour, ' can hiss almost as loudly as escaping steam '. It is interesting to note that similar hissing threatenings and bluffings form a feature in the warning displays of many birds, such as the Wryneck and Painted Snipe, and like those of snakes, they are directed against general enemies (as opposed merely to rivals of the same species). The display of the Painted Snipe (*Rostratula capensis*) is both auditory and visual : so, as already mentioned, is that of the Blue-fronted Amazon Parrot (*Amazona æstiva*). When sufficiently alarmed or enraged, these birds spread both the wings and the tail—the former making a hissing sound ' like that produced by plunging a hot iron into water ' (172), the latter causing the feathers to tremble and produce a considerable rustling noise.

In addition to hissing, many snakes also make warning sounds with the other end of their bodies. This is due to the fact that when excited different species vibrate the tail. Sometimes this organ is elevated and shaken, as in the Old World *Xenopeltis*, *Dipsas*, and *Dipsadomorphus*, and may result in the rustling of leaves and disturbance of surrounding vegetation. In *Dipsadomorphus* the end of the tail is drummed spasmodically upon the ground. In the New World *Trigonocephalus* the tail is hammered against brushwood and stalks. This production of threatening sounds with the tail reaches its highest development in the specialized 'rattles' of *Crotalus*, where a definite sound-producing organ has been evolved. An entirely analogous case among mammals is heard in the tail-rattle of the Porcupine.

In other animals, sound-threatening is produced by a stridulating element, a method commonly used by, but not confined to, insects. It has been described in the case of a Bornean mantis *Hestiasula sarawaca* by Shelford (570) and of an African mantis *Idolum diabolicum* by Carpenter (79). In the former the sound is caused by snapping the tibiæ on the femora, and rustling the wings; in the latter it is made by rapidly drawing the left posterior leg along the outer edge of the left fore wing. In both cases this sound-threat forms part of the display. In a number of aposematic moths and grasshoppers, the emission of defensive froth is accompanied by 'sizzling' or 'rattling' sounds, for the production of which in certain Arctiid moths of the genus *Rhodogastria* there is a special thoracic stridulating organ (86).

Jobling has described an interesting case of stridulation in the butterfly *Parnassius mnemosyne*, which he observed in central Russia. In many cases stridulation among butterflies is known to be associated with the business of courtship, as are the musical activities of certain Orthoptera. But in the present species the sound is evidently a protective device, for it was only the fertilized females which produced the sound—when no males were present—while males and unfertilized females, which were more alert and more often on the wing, were not observed to stridulate (287). A somewhat analogous mechanism is brought into action by Horned Vipers of the genus *Cerastes*, which according to Barbour produce a sharp swishing sound by rubbing together specially modified lateral scales of the body (19). The large dung-beetle *Heliocopris mouhotus* squeaks like a bat when touched. Similarly, the large Dynastid beetle *Xylotropes gideon* emits a loud sharp hiss when picked up. Sphingid larvæ, such as the Indian *Langia zenzeroides* and the British *Acherontia atropos*, are also known to utter hissing or squeaking sounds under provocation. Certain highly poisonous spiders of the genus *Pœcilotheria* also possess a stridulating organ whose sounding forms part of the threatening display when the animals are molested (476).

Finally, voice frequently plays a part in these warnings, especially in the higher groups. Every one is more or less familiar with the growls and snarls uttered by Wolves, Dogs, and Jackals when encountering an enemy or spoiling for a fight. The Badger's warning utterance is a menacing snort. And as for the growlings, gruntings, and squealings of Skunks, Grisons, and Porcupines, when threatening enemies—we shall have occasion to refer to them on a later page

VI. WARNING SCENTS

In addition to elaborate and varied warning *appearances* and *sounds*, it has long been recognized that a third advertising medium is often employed, namely, a 'warning scent' which likewise can operate from a distance. From its very nature, such a character will be especially effective against enemies which hunt mainly by scent rather than by sight, and which, therefore, pay less heed to a visual warning.

Some animals possess a general offensive or advertising odour, just as aposematic forms possess a general advertising colour. But in its highest development, odour, considered as a means of defence, is essentially used as an olfactory '*display*': like visual displays of bulk, colour, and movement, the offensive discharge is reserved for *special occasions* of need. Often it is only released, as a last, desperate resort, in the face of the aggressor.

Like warning displays of colour and sound, this additional method of defence has been elaborated in many different groups of animals.

The intolerable stenches produced in special circumstances by Tree Porcupines (*Erethizon*, *Coendu*), Skunks (*Mephitis*, *Conepatus*, *Spilogale*), Zorillas (*Ictonyx*), Teledus (*Mydaus*), Ratels (*Mellivora*), Grisons (*Grison*), Shrews (*Sorex*, *Crocidura*), and Hedgehogs (*Erinaceus*) will claim our attention later.

Similar protective attributes are possessed by many snakes, such as the common Grass Snake of Europe and the Garter Snakes of North America, which discharge fetid milky secretions from glands in the cloaca. These unpleasant substances, though they cannot be projected at an enemy like the odious fluids of many mammals and insects, quickly besmear the body of any animal holding the writhing serpent, and are stated by Barbour to have 'a high value as a protective device' (19).

Analogous defences are possessed by many insects. Thus, Heteropterous bugs, especially the Pentatomidæ and various members of the Coreidæ and Reduviidæ, are notorious for the vile stenches which they emit, and most members of the group are supposed to be rendered unpalatable in this way. In South America, for instance, the Pentatomid *Brachystethus cribrum* and the Coreid *Nematopus indus* are both protected by a powerful odour, and both are conspicuously coloured in black and red. Many beetles possess similar attributes. Carabids, on being handled, emit an evil-smelling and acrid liquid from the tip of the abdomen; Coccinellidæ exude a pungent yellow oily fluid; the Lycidæ and Lampyridæ are evil-smelling and highly distasteful. Many hymenopterous and lepidopterous larvæ are similarly protected—in the hymenopterous *Crœsus septentrionalis* the discharge is from the everted ventral glands. In the caterpillar of *Porthesia auriflua* it is from the dorsal glands; in that of others, such as *Vanessa urticæ* and *Deilephila euphorbiæ*, the noxious moisture is dribbled from the mouth. Many butterflies, notably those belonging to the aposematic groups Danainæ, Heliconinæ, and Acræinæ, habitually exude evil-smelling secretions. The same habit occurs among different Orthoptera, such as the noxious grasshopper *Dictyophorus laticinctus*, which has been described by Carpenter as emitting from the thoracic spiracles a strongly smelling froth which is forced out with a hissing sound audible several yards away (86).

Various attempts have been made to describe these relatively potent odours. Thus Lydekker describes the peculiarly disagreeable smell of *Gymnura rafflesii* as of a somewhat oniony or garlic-like nature, and it has been elsewhere likened to Irish stew that has gone bad (Blandford, in Pocock, 481). The dreadful scent of the Tree Porcupines (*Erethizon* and *Coendu*) has been compared to that of concentrated human perspiration and of unwashed tropic humanity. In the Shrews the repellent odour is musky. 'A most pungent and disgusting smell of musk' is also given off by the little sea-snail *Bulla*, an aposematic form 'whose coat of emerald green, spangled with orange spots, attracts the eye like a meteor'.

Among aposematic insects, the exudation of *Heliconius charithonia* is said by Professor Morton Jones to suggest 'the rank sweetness of the Datura blossom' (520). The pungent odour emitted by *Heliconius h. hydarus* has been likened by Mr. P. L. Guppy to that of the acrid blistering oil derived from the shells of the cashew-nut (*Anacardium occidentale*); by Dr. G. B. Longstaff to that of acetylene—and later compared to witch-hazel (*Hamamelis*); and by Dr. C. L. Withycombe to the smell of carbylamine, which was replaced by a scent like sweetbriar on heating with distilled water and hydrochloric acid (520). The penetrating discharge of *Papilio machaon* has been compared to decaying pineapple.

The relation between gregarious habits and conspicuousness has already been considered. Now, just as the gregarious resting instinct serves (especially during daylight) to intensify conspicuousness, so the combined odour emanating from a resting butterfly assemblage will be effective in making for easier recognition by enemies and in eliminating attacks due to mistaken identity of the unpalatable insects. A comparable case, from the Hymenoptera, is that of the gregarious sawfly larvæ of *Crœsus septentrionalis*, whose habits have been referred to by Sir Edward Poulton as follows: 'When disturbed, the body is turned forward over the head, and the glands are everted so that their secretion escapes into the air. The meaning of the gregarious habit is very clear in this and parallel cases; for when many individuals combine to discharge an unpleasant odour, they become surrounded by an atmosphere which acts as a most effective barrier' (496).

The special protective value of these odours, like that of warning appearances and warning sounds, is that they render possible recognition from a distance—that is to say, *before* the insect has been attacked and tasted. In this respect they differ from, and are not to be confused with, the various unpalatable properties which could not of themselves prevent experimental tasting, and of which the aposematic attributes above mentioned are the outward and visible sign. Thus, by exuding juice from its thorax on the approach of an enemy, the African aposematic *Acræa buxtoni* can 'show its nauseous qualities without necessarily having to be injured . . .' (395).

That such evil odours *do* afford an efficient protection against predatory attack is clearly proved by Dr. Myers' observations on the food of the Coati *Nasua nasua* (433). In his list of Arthropods summarily refused, the following evil-smelling insects 'were all sniffed once, and at once rejected': Green lacewings or 'stink-flies'—*Leucochrysa lateralis* and *Chrysopa* (Chrysopidæ); fireflies—*Photuris vittipennis* v. *conformis* and *Pygolampis* sp. (Lampyridæ);

bugs—*Edessa* sp. (Pentatomidæ), *Acanthocephala angustipes* (Coreidæ). What is significant here is the rejection of aposematic insects by an animal which hunts almost exclusively by scent, and on whom the additional attribute of warning colours can (when present) make little or no impression. In this case the evil odour alone was a sufficient deterrent—a result all the more remarkable in an animal which, as Myers aptly remarks, 'is by no means particularly delicate about its food'; for his Coati would even tackle the poisonous toad *Bufo peltacephalus*, whose secretions are well known to operate effectively against dogs.

Such offensive odours in insects, associated as they often are with conspicuous coloration and exposed habits, appear extremely interesting when it is realized that parallel phenomena have been evolved in the plant kingdom, where we find developed those wonderfully elaborate and efficient structures (I refer, of course, to insect-pollinated flowers) which likewise serve to advertise their owners by conspicuous and freely exposed displays of colour and by penetrating perfumes. But here the analogy ends: for the phenomena have in plants a precisely opposite meaning and function. In the one, the scent is attractive; in the other, it is repellent. The gaily coloured and sweet-scented floral advertisements appeal to a different 'public' and for a different reason. Their object is not to warn enemies away from an unpalatable mouthful, but rather to invite friends to the banquet: their effect is to confer the benefit, not of safety from an insectivorous predator, but of cross-fertilization by an insect. It will be noted that in both cases the scent is made use of *at appropriate times*. For, on the one hand, the wonderful floral mechanisms are adapted in this, as in other respects, to the habits of their insect visitors: thus Hymenoptera-flowers, such as Clover, are diurnal, while Lepidoptera-flowers like the Evening Primrose, Night-scented Stock, and Honey-suckle smell sweetest and strongest at night when the moths which pollinate them are on the wing. On the other hand, stinking aposematic mammals and insects in general conserve their diabolical sprays and discharges, resorting to malodorous measures when they are especially needed, that is, when the animals are disturbed or in danger. We find, then, on considering the adaptive odours produced by these two very different classes of organisms, that in each case there is an advertisement which can appeal from a distance to certain recipients through the sense of smell; that in each case the advertisement is operated at its best at times when it is especially required; and that in each case both the advertiser and the recipient have something to gain if the advertisement is heeded.

In this section I have dealt with the methods by which different animals are rendered conspicuous in nature. The subject is a large one. In the space at my disposal I have attempted to stress general principles rather than to catalogue instances. I have, however, given what I consider to be sufficient examples of each type of phenomenon to make my meaning clear and to enforce my argument. It will be convenient here to review the evidence derived from a study of the appearances and habits of aposematic animals, and to see in what direction this evidence points.

(1) Considered from the aspects of physical optics, and the physiology of colour vision, the brilliant pigments (black, white, red, orange, yellow) and bold patterns (spots, ocelli, rings, bars, stripes) generally worn by aposematic animals are such as to render them highly conspicuous in nature. This conspicuous livery is typically associated with attitudes, attributes, and habits (including free exposure in the open; gregariousness; special displays of colour, of bulk, and of movement; production of sound; emission of odour; aggressive behaviour), all of which increase the effectiveness of the advertisement, and thus as far as possible attract the notice of predatory enemies.

(2) General warning coloration—and warning displays (which represent a special application of the principles of warning coloration)—have been evolved independently in many unrelated groups of animals: they are found in almost every inhabited part of the globe; they occur in almost every type of environment: that is to say, their distribution is extensive whether considered from the viewpoint of taxonomy, zoogeography, or ecology.

(3) The essential character of *displays*—a sudden and conspicuous exhibition of colour—is achieved by very diverse means: the surface displayed may be part of the integument; it may be an internal membrane; a modified appendage; or a specialized fan or filament: it may normally lie concealed beneath the body, within the body, or about the body: it may be exhibited by orientation, expansion, extrusion, or illumination, by uncovering, opening, stretching, or erecting structures.

(4) The pigments and patterns of the specially displayed areas (like those of the generally exposed areas of aposematic animals) are typically vivid tones and saturated hues; and almost irrespectively of the group of animals wearing them, or of the part displayed, we find these transitory advertisements associated with exhibitions of black, white, vermilion, orange, chrome, or pink, or some combination of these colours. Moreover, generally speaking these special areas differ markedly in this respect from the subdued, cryptic coloration of the parts normally exposed when the animal is walking, feeding, or at rest.

(5) There is an essential correlation between the attitude adopted in display and the disposition of the highly pigmented surfaces: the mammals, reptiles, and amphibians which rear up on end, or turn over on their backs, have the breast or belly vividly coloured; the birds, lizards, and snakes which threaten by mouth-opening have the mouth-interior vividly coloured; the forms which unfold dermal creases, membranous wings, fins, frills, gular fans and feather fans have these areas vividly coloured; the insects which extrude filaments or uncover appendages, the mammals which erect the hair, the snakes which stretch apart the scales or elevate their tails—all tend to have these several regions vividly coloured.

(6) The conspicuous surfaces are thus normally hidden, except when in use. *Then* the changes in appearance, which are brought about in so wide a range of animals, both vertebrate and invertebrate, are such as to convert a relatively or highly cryptic colour-scheme into one that is glaringly conspicuous:

the transfiguration is often sudden and rapid; striking and extensive; startling or even terrifying: it occurs typically under special circumstances, namely, in times of danger—that is, *when* it is needed; and it is directed in a special manner, namely, towards the enemy—that is, *where* it is needed.

(7) The phenomena we have considered are mainly and essentially optical—that is, they concern the *appearance* of things. If, as we have reason to believe, they have an advertising function, that is what we should expect in view of the overwhelming importance of vision in the hunting and selection of food by active predatory vertebrates. But it is significant that in general the same animals whose appearance and habits make for conspicuousness and easy recognition by sight also possess sound- and smell-producing apparatus and habits which appeal as advertisements to the ear and nose of enemies just as the appearances appeal to the eye.

(8) The different methods used by widely different animals for visual, auditory, and olfactory advertisement cut right across the classification of the animals themselves: a toad and a lizard may display in one way; a frog and a fish in another; one means may be used by a mantis and a crab; another by a cobra and a caterpillar; another by a cat and a gecko; another by a chameleon and a nightjar; another by a rattlesnake and a porcupine; another by a skunk and a grasshopper—illustrating in a very remarkable manner the principle of adaptive convergence. Conversely, within a single natural group of animals we find wide adaptive radiation in the nature and mechanism of the display, as illustrated, for instance, by birds, or by snakes, or by orthopterous insects.

(9) Taken together, these classes of evidence—of physical optics, of systematic and geographical distribution, of field ecology, of comparative morphology, and of comparative behaviour—all point to the conclusion that *aposematic appearances are adaptive*: that they tend to satisfy a vital need in the struggle for life, *the need for recognition by predatory enemies as something unwholesome, something unwelcome, and something to be avoided.*

3. ADVENTITIOUS WARNING COLORATION

> We lose a vast amount of the enjoyment of life in the non-appreciation of colour in its infinite varieties and combinations.
>
> ALFRED EAST

Masks of adventitious material may serve a variety of purposes—protective or aggressive, alluring or warning. It is with the last of these functions that we are now concerned. A number of relatively defenceless and palatable animals are known habitually to associate themselves with others which are specially protected and conspicuous, and thus to share the protection from enemies which the latter enjoy. ‘ Such a method of defence ’, writes Poulton, ‘ bears the same relation to Warning Colours as the examples of Adventitious Protection and Colouring bear to true Protective Resemblance ’ (496). Instead of borrowing a cryptic uniform which makes them *appear* inedible and *unattractive* to enemies, they borrow an aposematic one which *is* inedible and positively *repellent.*

I. INTIMATE PARTNERSHIPS BETWEEN CRUSTACEA AND APOSEMATIC ANIMALS

Many crustaceans are closely associated with sea-anemones, sponges or tunicates, and trade upon the unpalatable reputation of their partners. Among the Hermit Crabs (Anomura) especially is the instinct to associate with other organisms strongly developed—Zoanthids (*Epizoanthus*, *Palythoa*), Actinians (*Adamsia*, *Actinia*), Hydrozoa (*Hydractinia*, *Hydrissa*), Bryozoa (*Conopeum*, *Cellepora*), and sponges (*Suberites*, *Ficulina*), all being attached by various Hermit Crabs to the gastropod shells they inhabit (14).

(1) **The Nature of the Relationships**—In certain cases the association is very regular, different crustaceans showing marked attraction for particular species of stinging anemone or stinking sponge. For instance, *Eupagurus prideauxi* is almost invariably associated with *Adamsia palliata.* Verwey (643) states on the authority of Cotte that this hermit and anemone are only to be found without each other when very young. Again, it is stated that *Eupagurus cuanensis* always has its lodging covered with the aposematic sponge *Suberites domuncula.* Similarly, *Hepatus chilensis* and *Antholoba reticulata* are regular associates. Among sixty specimens of this crab collected by Bürger (69), only four were found without their anemone ; though it must be added that the anemone is less dependent upon the crab, and, as in many similar cases, may occur without its partner.

(2) **Modifications of Instinct and Structure Involved**—A point of great interest is the deliberate manner in which the crustaceans obtain and attach their

protectors. This is no less striking than the corresponding behaviour of masking-crabs such as *Maia* and *Hyas* when attiring themselves with natural drapery (page 359). For example, *E. prideauxi* itself loosens its anemone from the bottom, and fixes it to its house (643). Later, when obliged by growth to shift into more roomy quarters, the hermit crab transplants its partner from the smaller shell and holds it in position against its new residence, until the *Adamsia* is firmly attached by a good broad base. The actual process has been described by Gosse (211) as follows: 'No sooner did the crab touch the *Adamsia* than he took hold of it with his claws, first with one, then with both, and I saw in an instant what he was going to do. In the most orderly and expert manner he proceeded to apply the *Adamsia* to the shell. He found it lying base upward, and therefore the first thing was to turn it quite round. With the alternate grasps of the two pincers, nipping up the flesh of the *Adamsia* rudely enough, as it seemed, he got hold of it so that he could press the base against the proper part of the shell,—the inner lip. Then he remained quite still, holding it firmly appressed, for about ten minutes; at the end of which time he cautiously drew away first one claw, and then the other; and, beginning to walk away, I had the pleasure to see that the *Adamsia* was once more fairly adhering, and now in the right place.'

The Sponge-Crab (*Dromia vulgaris*) and other members of the family Dromiidæ have the last pair of legs modified in relation to the commensal habit. These appendages are short and carried up over the back, and are used to hold a mass of living sponge in place on the back. The coral-haunting crab *Melia tessellata*, from Mauritius, invariably grasps two anemones, one in each claw—employing them both for defence and for feeding. Borradaile states that if the crab is assailed it thrusts the polyps towards the enemy and thus wards him off with their stinging tentacles, but if the polyps capture food, the crab takes the morsel from their grasp with one of its legs and transfers it to its own mouth. In this case the chelæ are specially modified in relation to their peculiar use, being small and consequently of little value as weapons, but furnished with recurved teeth, which enable the forcep-like fingers to hold firmly on to the anemone's slippery body (57).

Paguropsis typica carries the anemone *Mammilifera* like a hat on its back, without using a shell. In other cases the crustacean is entirely covered and hidden from above by its protective burden, as happens, for instance, with *Cryptodromia pileifera*, native to the Andaman Islands, whose partner and messmate is a cap-shaped sponge which fits neatly over the crab's back. An American Hermit Crab, *Eupagurus pubescens*, has for companion a colonial sea anemone belonging to the genus *Epizoanthus*, which after a time dissolves the protective gasteropod shell and remains thereafter as a sort of expansible greatcoat enveloping its body.

(3) **The Aposematic Function of the Partnership**—Such associations must undoubtedly be of great service to the more active and defenceless partner. Hermit Crabs, like other crustaceans, are much sought after for food, as is proved by their occurrence, shell and all, in the stomachs of Gurnards and other fishes. Sea-anemones, on the other hand, are well known to be highly distasteful—being

effectively protected against the attacks of most predatory animals by the possession of poisonous stinging cells, the nematocysts, which act like microscopic hypodermic syringes. Anemones are, in consequence, generally avoided by fishes, and will not serve for bait. The same is true of sponges.

The protective value of such associations has been confirmed experimentally by Poulton (509). Small pieces of *Sagartia parasitica*—the anemone usually carried by *Eupagurus bernhardus*—when offered to fish in an aquarium tank, were instantly and violently rejected by those individuals which mistook them for the pieces of meat which they were accustomed to take. On the other hand, when a hermit crab, deprived of its protector, was offered, ‘ there was a wild struggle, and the fortunate captor swallowed him in a moment ’.

Garstang states that this hermit, when *not* associated with an anemone, is very frequently found in the stomachs of Cod and Haddock ; but that he does not know of a single instance of its having been found in the stomachs of the same fishes when associated with one (203). He also cites an interesting observation by Eisig that an *Octopus* would instantly retreat from an attack upon a hermit crab, upon being touched by the stinging cells of the associated Actinian.

Similar results are reported of the sponge *Suberites domuncula*, which is ‘ full of flinty needles, has a strong odour and a disagreeable taste ’, and was found by Garstang to be intensely disliked by fishes. ‘ I have never succeeded ’, he writes, ‘ in inducing any species to swallow a fragment of the sponge ’ (203) ; and he adds that he knows of no fish capable of extracting the hermit crab from its retreat. ‘ It is obvious ’, he writes, ‘ that the allosematic method of protection is all but perfect, since it is largely free from the loss due to experimental tasting attendant upon the method of a purely warning appearance.’

II. PERMANENT ASSOCIATIONS BETWEEN SPIDER CRABS AND SEA ANEMONES

The associations between sea anemones and various marine animals which derive adventitious protection from them show different degrees of closeness. Among the most remarkable are cases in which the anemone is not carried about by the more active partner, but is itself fixed and used regularly as a place of refuge. Although this type of partnership is more loose than that previously considered, it is one which includes some of the most ideal instances of commensalism yet investigated.

Thomson (621) has studied the case of the Long-legged Spider Crab (*Stenorhynchus phalangium*), which is said always to be found in the neighbourhood of *Anemonia sulcata*. ‘ Usually the crab takes up its position close to the column of the anemone, so as to be more or less concealed by the tentacles, only the rostrum and the first pair of walking legs being visible from above, whilst the legs of the fourth pair may reach backwards to grasp the anemone. But at times, and especially when disturbed, the crab climbs backwards right on to the crown of the anemone ; and one specimen, a female bearing eggs, repeatedly worked its way right under the base of the anemone, so that only the tip of the rostrum and the limbs could be seen. The anemone makes no attempt to seize the crab, but if the crab dies its body is soon lifted up and devoured. It is clear that the crab must be well protected by the anemone, which does not retract its tentacles when disturbed.'

That the association is not merely accidental was shown by the fact that when crabs were removed to a distance of over three feet, they 'returned time after time to an *Anemonia*, passing on the way anemones of various species, as well as all manner of objects which might conceivably afford shelter'. Of fifteen crabs observed by Thomson during three summers, every one to a greater or less degree showed the same tendency. The anemones also benefit from this curious partnership; for food which is found by the crab and dragged to its shelter to be devoured is snatched by the tentacles of the anemone from the crab's grasp and swallowed.

III. PERMANENT ASSOCIATIONS BETWEEN DAMSEL-FISHES AND SEA ANEMONES

We may compare with the above the close commensal association found on the coral reefs of the Indo-Australian Archipelago between Damsel-fishes of the family Pomacentridæ and certain large Actinians. It has been known for many years that a close partnership exists between species of *Amphiprion* and *Premnas* and sea anemones of the genus *Stoichactis*, among whose stinging tentacles the fishes find shelter. Little, however, was definitely known about the real nature of these associations before the publication, in 1930, of Verwey's careful investigations, which serve to confirm and extend those of Sluiter in 1888 (576).

In the Bay of Batavia, Java, Verwey found five species of Damsel-fishes—*Premnas biaculeatus*, *Amphiprion ephippium*, *A. polymnus*, *A. percula*, and *A. akallopisus*—living with anemones, and from his interesting and significant observations, the following facts may be mentioned.

The Damsel-fishes are apparently unable to exist without their anemones, upon which they depend absolutely for protection from predators. They move slowly, and in the absence of their partners are incapable of maintaining themselves against the attacks of more active fishes of prey, such as *Lutianus*, *Epinephelus*, and *Scorpænopsis*. Both Verwey and Sluiter found that if deprived, in aquaria, of their living refuge place, they are immediately captured and eaten, one after another, by these predators. On the other hand, when afforded the protection of an anemone, they may survive such dangers in the confined space of an aquarium for more than a month (576).

Without going into details, it may be noted that in nature the Damsel-fishes never occur without their anemone. Moreover, the different species exhibit definite preferences for distinct species of sea anemone—for example, *Amphiprion percula* is always found with *Stoichactis kenti*, and *A. bicinctus* (*polymnus*) with *S. haddoni* (554).

As with many birds in the breeding season, the instinct to guard and maintain territory is strongly developed. Verwey states that on visiting the reef one generally finds that each anemone, or each group of anemones living close together, is attended by two fishes, male and female.

The pair never venture far from the forest of sheltering tentacles, but invariably keep within easy reach of their refuge, ranging from 5 to 15 cm. away in the case of smaller individuals, and up to several metres in the case of large individuals needing to explore a wider area for food.

When approached, they dive in among the stinging tentacles, where Verwey states that they distinctly show that they feel quite at home. So marked is the sheltering instinct in these fishes, that they may even lie down between the tentacles or on the oral disk and remain there while the anemone is loosened and taken out of the water.

We need not concern ourselves here with the advantage to be derived by the anemones from this strange partnership, though it may be noted in passing that they are themselves more or less dependent upon the fishes, who fetch them their food and care for them in various other ways.

IV. NESTING ASSOCIATIONS BETWEEN BIRDS AND ACULEATE HYMENOPTERA

A number of naturalists have recorded from tropical countries of both New and Old Worlds that certain birds habitually build their nests in close proximity to the nests of venomous and aggressive Hymenopterous insects—wasps, hornets, bees, and ants.

These nesting partnerships between birds and aculeates have been investigated by Dr. J. G. Myers in South America and the West Indies, and this observer has reviewed the whole question in an extremely interesting paper published in 1935 (434).

It appears that the associations are more widespread and more regular than has generally been supposed. They are known from America, Africa, and Asia; they are recorded of many species of birds belonging to a number of different families; and in certain cases their occurrence is of an intimate and very regular, almost obligate, nature.

Now it seems quite clear from the evidence that the facts cannot be explained as due either to chance proximity of nesting sites, or to ' a mere random gregarious impulse '; but that the birds deliberately select sites near to the insects upon whose protection they appear to trust.

Myers has given evidence both in the present, and in an earlier, paper (432) to show that the birds discriminate in the selection of protected sites. For instance, where the partners are wasps, it is the insects and not the birds who first become established. To quote a single example, he states: ' In the Orinoco Delta a colony of *Cacicus cela*, of nine nests, mostly still in process of construction, with many fibres still green—thus an obviously new colony—was grouped round a gigantic nest of *Polybia rejecta*, at least 2 feet long and 14 inches in diameter, and thus evidently of considerable age.'

Cases of close proximity, in the same tree and on the same branch, of birds and wasps, while neighbouring trees are available but unoccupied, likewise add weight to the view that the birds deliberately seek the company of the wasps. Among fifteen colonies of *Cacicus* observed by Myers in Trinidad, the Guianas and Amazonia (434), twelve were associated with nests of wasps or ants. Sometimes the nests are built so close, that ' the homes of insects and birds rattle against each other when the wind blows ' (39). Yet the wasps, which are quick enough to attack an intruder from outside, do not molest their handsome neighbours.

Among examples illustrating the proximity of the nests, and indicating the protection likely to be enjoyed by the birds, we may mention here the following cases given by Myers : ' At Liguanea, Jamaica, a nest of *Cœreba* in a very prickly *Acacia*, the bird sitting, surrounded within two feet, by no fewer than ten *Polistes* nests, a good proportion of which were old and abandoned, indicating an old colony ; in the same locality, in a *Melicocca bijuga*, a *Cœreba* nest completely surrounded by 57 medium-sized and small *Polistes* nests, *all occupied*, so that it was quite impossible to approach the nest ; in both the above cases there were *no* wasp-nests in the adjacent trees ; on La Gonave Island, Haiti, a *Cœreba* nest high in a prickly mesquite (*Prosopis juliflora*), with *Polistes* comb, the only one in the vicinity, hanging a few inches in front of the entrance.'

Indirect evidence that these remarkable nesting arrangements are correlated with the need for protection is afforded by the kinds of Hymenoptera chosen as companions. For the species of wasps, bees, and ants frequented are typically among the most virulent and vicious members of the group, namely, species of *Polybia*, *Polistes*, *Apis*, and *Azteca*. For example, writing of *Polybia rejecta*, the usual wasp-associate of *Cacicus*, Rau remarks that ' the most vivid impression that these wasps left was their pre-eminent ability to sting ' (534).

Myers also points out that in the tropics the vast majority of small birds attain protection ' by a consummate art in hiding the nest, as any one who has bird-nested in a tropical forest will agree '. And he has drawn attention to the significant fact that the most regular frequenters of aculeates are species which build large conspicuous or untidy or colonial nests which could not well be hidden.

' It is significant again ', he writes, ' that all the eight regular neotropical ant- and wasp-associates and five of the less regular ones, as though conscious of a special need for protecting their conspicuous nests, adopt usually (or at least frequently) one or more of the following additional devices, (*a*) nesting in colony (*Cacicus*, *Textor*, *Crotophaga*), (*b*) nesting near human habitations (*Cacicus*, *Textor*, *Panyptila*), (*c*) nesting in isolated trees over water (*Cacicus*, *Fluvicola*, *Certhiaxis*), (*d*) suspending the nest from a branch (*Cacicus*, *Icterus*, *Rhynchocyclus*), (*e*) nesting in thorny bushes (*Cœreba*, *Textor*), (*f*) using thorny twigs in nest construction (*Synallaxis*), (*g*) using snake-skins in nest construction (*Heleodytes*, *Certhiaxis*).'

Of the genus *Cacicus*, Myers states that he never found a colony which was not either in a tree isolated by water or swamp ; very close to a house ; associated with aculeates ; or showing some combination of these groupings. Similar observations have been made by Beebe (39), who comments upon ' the real intelligence in the selection of a site ' shown by the additional precautions taken to build near a human habitation or near a great wasps' nest.

Taken together, the evidence indicates that we have in these forest-dwellers a highly perfect and singular instinct correlated with the need for protection from enemies—an instinct which appears none the less remarkable when we remember that it is not unique ; for it has its parallel, as we have already seen, in the waters of coral reefs, where stinging anemones, rather than stinging aculeates, play the role of protector to the defenceless creatures who solicit their company.

WARNING COLORATION IN REFERENCE TO PREY

4. THE NATURE AND FUNCTION OF WARNING COLORATION AS ILLUSTRATED BY THE MAMMALIA

> Thus the skunck, or stonck, is an innocuous and sweet animal ; but when pressed hard by dogs and men, it can eject such a most pestilent and fetid smell and excrement, than which nothing can be more horrible.
>
> GILBERT WHITE

I. PROTECTIVE ADAPTATIONS IN PORCUPINES

THE Common Porcupine (*Hystrix cristata*) is the well-known possessor of a set of large quill-like spines, which form a prickly protective armour covering the animal's back, flanks, and tail region. Although strictly nocturnal in its habits, the whiteness of the quills, which can be erected in a characteristic fan-like manner, render the animal conspicuous in the dark. Moreover, Mr. Pocock (477) tells us that its behaviour at night when prowling abroad is quite different from that of most nocturnal animals. For, instead of being silent in its movements, the Porcupine seems to make as much noise as possible, shaking the tail-quills, which are specially modified to form a rattle, and uttering hoarse guttural grunts, both of which sounds can be heard at a considerable distance. Writing of Porcupines elsewhere (478) this author states '. . . no one who has seen them in the dusk, can dispute that the whiteness of the quills makes them conspicuous. In addition to this they rattle and grunt and stamp, and appear to advertise themselves in all ways at their disposal, and are extremely unpleasant animals to deal with.' Striking indirect testimony to this last statement is afforded by the following observation: It appears that the Porcupine *Hystrix galeata* can put up a defence even against the most formidable adversaries, for Mr. Arthur Loveridge (362) examined an almost full-grown leopard which entered a hut at Tindiga, where it was shot by a native. He says: 'It was in a most frightful condition, covered with sores, from one of which I removed a broken portion of a porcupine quill. On its neck was a bare patch a foot in length and two inches broad in its widest part; the patch was hard dried skin and may have been made by the leopard clawing at some quill-stumps left in the skin.'

The actual method of attack has been described by Pitman (472), who writes from personal, and painful, experience. He was standing a few feet from a

Porcupine which had recently been dug out from its earth, in Mesopotamia, and talking to a youngster who had assisted in its capture, when suddenly he received a terrific blow on his shin which all but knocked him over. The animal, which weighed over 25 lb., had launched itself backwards with lightning speed, hurling its hindquarters against him so as to strike a blow with the bunch of stout white quills above its tail. The effectiveness of this method of defence is remarkable: 'It was exactly as if I had been dealt a severe blow with a pick helve or stout wooden cudgel—and fortunately for me I was wearing thick puttees and riding breeches, and two pairs of socks at the time, but even then a few of the animal's quills penetrated nearly half an inch into my leg and for a short while the pain was agonizing. For many days my leg was very stiff and sore and I carried a large bruise for over a fortnight to remind me of the incident.'

Instead of retreating when attacked by a dog, the Porcupine faces about and runs backwards *at* the enemy, in whom he leaves a few quills to discourage his further attentions. In one such encounter witnessed by Morris (415) a porcupine, which was being chased, met the dog's onslaught by abruptly standing still. The unfortunate animal in its recklessness leaped right on top of his prickly quarry, who 'then went on its way, leaving the dog riddled with quills'.

Besides being able to put up a good fight, the porcupine agrees with other well-protected animals in being extraordinarily tenacious of life. Loveridge (362) says that it does not succumb to wounds that would kill any other animal, and describes how one specimen which he shot through the head with a ·22, and which was supposed to be dead, subsequently drove four quills into the palm of a native who reluctantly ventured to take hold of it!

In the case of the Canadian Tree Porcupine (*Erethizon*) there is no tail rattle, but the animal is conspicuously coloured when the spines are erected, and, possibly as an additional protection, the creature 'possesses a strong and unpleasant odour recalling that of concentrated human perspiration' (478). The Brazilian Tree-Porcupine (*Coendu*) is similarly endowed with a foul odour which was described by Charles Kingsley: 'More than once we became aware of a keen and dreadful scent, as of a concentrated essence of unwashed tropic humanity, which proceeded from that strange animal, the Porcupine with a prehensile tail, who prowls in the tree-tops all night, and sleeps in them all day, spending his idle hours in making this hideous smell. Probably he or his ancestors have found it pay as a protection; for no Jaguar or Tiger-cat, it is to be presumed, would care to meddle with anything so exquisitely nasty, especially when it is all over sharp prickles' (478).

II. PROTECTIVE ADAPTATIONS IN MUSTELINE CARNIVORA

In the case of certain of the Musteline Carnivora there is also found the association of an advertising livery with formidable means of defence. The coloration and bionomics of these animals have been discussed in an illuminating paper by Mr. R. I. Pocock (478), to whom I am indebted for many of the facts referred to below.

The Skunks of America (*Mephitis*, *Conepatus*, and *Spilogale*) are notorious for the repulsive and persistent odour of the fluid which they eject from their anal glands when attacked. Nocturnal in their habits, they roam about at dusk in search of insects and other small animals which constitute their diet. They move in a nonchalant, leisurely manner, as though well aware of their ability to defend themselves. So long ago as 1874 Belt (45) described the conspicuous black and white coloration of the skunk, which ' goes leisurely along, holding up its white tail as a danger-flag for none to come within range of his nauseous artillery '.

Referring to the special means of defence in *Mephitis*, W. H. Hudson (276) speaks of an effluvium ' after which crushed garlic is lavender, which tortures the olfactory nerves, and appears to pervade the whole system like a pestilent ether, nauseating one until sea-sickness seems almost a pleasant sensation in comparison '. With its gas attack, it is well able to defend itself, as Gibson has shown, from powerful birds like the ' Carancho ' or Carrion Hawk (*Polyborus tharus*) when they commit the blunder of attacking it. Hudson gives an amusing account of the behaviour of dogs when in the presence of *Mephitis*. One moonlight night he went out at his home to where the dogs, twelve in number, were sleeping. While he stood there a Skunk appeared and deliberately came towards him, ' passing through the dogs where they lay, and one by one as he passed them they rose up, and, with their tails between their legs, skulked off '.

The South African Zorilla or Cape Polecat (*Ictonyx*) is another black Musteline, bearing on the back a set of broad conspicuous white longitudinal stripes. If interfered with, it enhances its conspicuous appearance by erecting the body-hairs and brandishing the bushy white brush, at the same time uttering shrill squeaks of anger and ejecting the intolerable acrid anal secretion. Mr. M. Versfeld tells me of an interesting observation which shows that this animal will deliberately display in the face of an enemy, making the utmost use of the white warning dorsal stripes. In the course of a walk some men came suddenly upon a Cape Polecat. When first seen, the beast appeared to be shamming dead: it lay on its side, with its legs stretched out on the ground towards them. However, on their looking back, having momentarily turned aside, it was noticed that the animal had turned over, *so that its back was now directed towards them*. Interested in this, they walked round the animal, pretending to take no notice of it, and on again looking round at it, the polecat was found to have turned over, so that once more the stripy back was directed towards them. They then repeated the process two or three times and on each occasion the creature turned over, presenting to full view the conspicuous black and white warning livery.

The Teledu (*Mydaus*) of Indo-Malaya is another warningly coloured member of this family. It is blackish-brown in colour, with a single white band extending from the top of the head down the spine to the tail. Like the Skunk and Zorilla, it is nocturnal, slow in its movements, and largely insectivorous: like these animals also, it possesses stink-glands which exude a fetid liquid. So repugnant is this material, that Horsfield (478) states ‘ the entire neighbourhood of a village is infected by the odour of an irritated Teledu, and in the immediate vicinity of the discharge it is so violent as in some persons to produce syncope ’.

In the case of the Ratels (*Mellivora*) of India, Arabia, and Africa, the back and head, sometimes white, is as a rule iron-grey, the muzzle, legs, and under parts being jet black. These animals likewise defend themselves by emitting an offensive suffocating odour from the anal glands. Moreover, when attacked they fight desperately and are extraordinarily tenacious of life. According to Sclater the African species is very difficult to kill, ‘ . . . only, it is said, by actually crushing its skull or by stabbing to the heart can this be effected ’.

Another animal coloured somewhat like the last is the Grison (*Grison furax*) of South America. The upper parts of the body and head are greyish and the under parts and legs black, while across the forehead and along each side of the head where the grey and black join there is a conspicuous whitish band. When fighting, or when disturbed, they emit a disgusting stink. The animal is reported to be extremely savage, fearless, and a most formidable antagonist. It sits up ‘ grinning and chattering at the passer by ’ with an expression on its face which Hudson describes as ‘ malignant and bloodthirsty beyond anything in nature ’.

The European Badger (*Meles meles*) is similar in style of body coloration, being hoary grey above and black below, the head white with a broad black band on each side extending from muzzle to ear. The Badger also possesses stink-glands : it is slow and leisurely in its movements ; fearless and indifferent in its manner ; notoriously savage when attacked ; and very tenacious of life.

III. THE HABITS AND ATTRIBUTES OF APOSEMATIC MAMMALS

Now if we consider the bionomics of the rodents and carnivores already mentioned in this chapter—we find certain characters which they tend to have in common, and these characters throw an interesting side-light on the object and effect of the warning colours which they wear.

(1) Their coloration is such as to make them extremely conspicuous in nature, due to the use of a black and white, or dark and light, livery, the latter element in the colour-scheme being particularly effective in animals of nocturnal habits. The effect is doubtless intensified by the reversed disposition of dark and light markings—for, unlike the majority of mammals, these have the light fur on the upper surface and the dark beneath. Such an arrangement is the opposite of the usual style of coloration, whereby under a top lighting, according to Thayer’s principle, reflected lights on the back are toned down by the darker coat-colour, and shadows beneath are obliterated by the lighter colour of the belly.

(2) A second, and perhaps the most striking, feature is the possession of a formidable and potent method of defence—by means of spines or stinking secretions—which must confer a measure of immunity from attack.

(3) Associated with these warning colours and potent means of defence are a number of characteristics and habits which support the view that it is

advantageous for these animals to be seen and recognized as quickly and as easily as possible. When they emerge to feed they are typically slow and deliberate in their movements: they court observation: their manner is fearless and indifferent: in short, their behaviour is in keeping with the view that they have little to fear from predatory attack.

(4) The absence of the hiding instinct in the young is another feature bearing upon the question of immunity. Writing of *Grison furax*, W. H. Hudson (276) says: 'I once surprised a weasel in the act of removing her young, or conducting them, rather; and when she was forced to quit them, although still keeping close by, and uttering the most piercing cries of anger and solicitude, the young continued piteously crying out in their shrill voices and moving about in circles, without making the slightest attempt to escape, or to conceal themselves, as young birds do.' Belt (45) refers to the fearlessness of the young Skunk in the following passage: 'The only animal we met with was a black and white skunk, with a young one following it. The mother ran too fast up a rocky slope for the young one, which was left behind, and came towards us. It was very pretty, with its snow-white bushy tail laid over its black back. We were, however, afraid to touch it, fearing that, young as it was, it might have a supply of that fœtid fluid that its kind discharge with too sure an aim at any assailant.'

(5) When interfered with or attacked the effect of the aposematic coloration is enhanced by special warning or threatening displays, including the erection of dorsal crests, an apparent increase in size by the erection of the hairs of the body, display of the dorsal stripes, elevation of the tail, and so forth. And further, these effects are supported by warning sounds—the rattling of quills, the uttering of hoarse grunts, or of shrill or chattering cries, and the stamping of feet.

(6) Another characteristic shared by these animals, and one which has an important bearing upon the aposematic uniform, is their savage disposition when attacked, their toughness, and their remarkable tenacity of life when injured. Conspicuousness courts not only attention, but attack, by an enemy that has no experience of the unpleasant consequences. Predaceous foes have to learn by experience in these matters, and it is obviously a vital advantage to the Skunk or Zorilla or Porcupine to be so constructed that in addition to inflicting a punishment on its adversary, it can itself survive the ill-considered blow. If this view is correct, we should expect to find that these animals are aggressive and fearless, tough and hard to kill—features which have already been referred to the Porcupine, Ratel, Grison, and Badger. Of the last, Pocock states: 'When attacked, they are notoriously most savage and formidable antagonists, being gifted with exceptionally strong jaws, a thick, highly flexible and loose skin, and wonderful tenacity of life.' The same writer says of the Ratel: 'The skin is not only very thick, but also very loose, so that if seized by almost any part of it the animal can reach and bite its assailant.'

(7) There is another factor relating to these conspicuous forms which has

reference to their food, rather than to their enemies. It is a significant fact that their feeding habits are such as to exclude any advantage to be gained from aggressive resemblance. They do not depend for a living upon the capture by stealth of wary birds and mammals. The Porcupines are wholly herbivorous; the Skunks live on small terrestrial vertebrates and insects, and according to Merriam (in Pocock, 478) *Mephitis* is pre-eminently an insect eater; the diet of the Cape Polecat is said to be similar to that of Skunks; the Teledu feeds largely upon insects and worms; Ratels are omnivorous, with a predilection for honey; the Grison's diet is given by Pocock as 'mixed'; so is that of the Badger, who, however, subsists to a greater extent upon vegetable food. In short, the feeding habits and special protection of these animals is such that they have no need of concealment, either for offence or defence. This, it will be noted, is in striking contrast to such other Carnivora as Ocelots, Lynxes, Leopards, Tigers, and indeed members of the Cat-tribe generally, which depend upon prey that must be approached by stealth, and which are themselves cryptically coloured.

(8) Another point to be noted is the small size of the external ears in these animals, an attribute which supports the theory that they have little to fear from enemies: this feature is in marked contrast to such large-eared forms as the Fennec and Jerboa, in which hearing is an important factor in the capture of prey or avoidance of enemies.

It can only be concluded, then, that all these classes of facts lend support to the view that the warning attributes are *adaptive*: in other words, that they are of value to their possessors. The attributes we have discussed are precisely those which one would expect to find in species with a special means of protection against attack by predaceous enemies. With animals such as these *it pays to advertise*. For they possess a means of defence which, if known, will effectively prevent aggression. If only they are seen and recognized *in time*, they will, in general, be avoided.

IV. PROTECTIVE ADAPTATIONS IN HEDGEHOGS AND SHREWS

This view is supported by a parallel type of evidence from a third and quite unrelated group of mammals, namely, the Insectivora. Mr. R. I. Pocock (481) has drawn attention to the appearance and habits of Shrews and Hedgehogs in relation to the question of warning colours. Judging from the analogy supplied by the Porcupines, he inferred that Hedgehogs 'with their protective armature of banded spines' come into the category of self-advertising animals. Major Barrett-Hamilton has pointed out that many exotic species, such as the Egyptian *Erinaceus æthiopicus* and the South African *E. frontalis*—living as they do in areas where potential enemies are more numerous and varied than in Britain—are whiter than the British examples, the whiteness being particularly manifest over areas exposed to view when the animal is on the prowl, that is to say, over the forehead and sides of the head. This is a type of colour-scheme which makes for conspicuousness in a nocturnal animal. Further aposematic attributes include, at least in the British *E. europæus*, the ability to produce a violently offensive stench, and its noisy advertising behaviour when moving about at night.

Information supplied by Mr. Moffat to Barrett-Hamilton (21) describes how the Hedgehog advertises its presence by sounds, ' making a furious sniffing with its nostrils, and also rustling among the leaves and herbage in a way that no other small animal could do without great unwisdom. One can easily track hedgehogs—I think from a distance of 40 yards—by the perpetual noise they thus keep up, which tells us both *where* they are and *what* they are.' Barrett-Hamilton also says that according to Captain T. Hudson, the Indian *E. collaris* ' makes a grunting sound when irritated, and when touched suddenly, jerks up its back so as to throw its spines forward, making at the same time a noise like a puff from a pair of bellows '. This action at once brings it into the same category as a Porcupine.

The objection may be raised that Eagle-Owls, Badgers, Foxes, and Polecats are credited—at least occasionally—with the power of dispatching the Hedgehog: a well-trained dog can overcome the defensive armour ' at the expense of a bloody nose and sorely pricked paws '. But, as Pocock points out, if this is used as an argument against the theory of advertisement, it must logically be used also as evidence against the view that the animal's spine-armature is protective. And this view cannot be supported. For though the spines are ineffective against some enemies (probably only when pressed by hunger) there is no doubt that they normally baffle the efforts of Dogs and Rats and other animals, just as those of the Porcupine repel the attacks of the Lion and Leopard.

The Oriental *Gymnura rafflesii*, belonging to the same family as the Hedgehog, though without a spiny armour, probably comes into the same category of self-advertisers. Pocock has pointed out that here again the white and black coloration is so disposed as to make for conspicuousness after dark when the animal is about, and it possesses malodorous scent glands, the smell of which is described on page 229.

If we study the ecology of Shrews, we are led to the conclusion that they too probably belong to the category of self-advertisers. Although more evidence is needed on the subject, it appears certain that they are highly distasteful to many animals. It is true that Owls eat them. But Cats, though they frequently kill them, abhor the taste of these animals, owing presumably to their rank musty scent. This view is supported by the habits of the Shrews when alive, and by the frequent finding of their bodies when dead. In England, especially in autumn, dead Shrews are a common sight in the country. Loveridge (362), in his notes on East African mammals, states that the Swahili name for a Shrew is connected with a widespread belief common to almost all tribes, that if a Shrew attempts to cross a path or road it will immediately fall dead—a legend obviously invented to account for the corpses frequently seen in such situations. ' The true cause of death ', he says, ' is that they have been pounced upon by genets and mungoose, who, on discovering the pungent smell of their prey, abandon them.' It is significant that Voles and Field-mice are rarely thus seen.

Moreover, the habits of Shrews differ strikingly from those of small rodents, for instead of being silent, when moving about they 'frequently utter a series of shrill squeaking cries' (21).

In the case of the Indian Musk Shrew (*Crocidura cœrulea*) the strength of the odour, and the animal's habit of squeaking when wandering abroad after dusk, is well known. Swinhoe (606) describes a Chinese form, whose appropriate name of 'Chî-ch,oó' is a tribute to the peculiar chattering noise—like the jingling of money—which it makes when roaming abroad at night. Lieut.-Colonel D. D. Cunningham, F.R.S., in *Some Indian Friends and Acquaintances* (pp. 284–5), gives a remarkably interesting account of the habits of this familiar beast in India, quoted in part by Pocock (481). The following passages in this account are of especial interest in that, as Pocock points out, they 'supply all the facts necessary for the belief that the shrews in question are protected self-advertisers'. 'Every one in India is familiar with the great musk-shrews, or "musk-rats" . . . who are constantly invading houses and leaving unpleasant evidence of their visits in an overpowering and all-pervading musky odour. They are strange-looking creatures at any time, and particularly so whilst running about a garden in late dusk, *when their pallidly bluish-grey coats look as though they had been smeared with luminous paint and stand out conspicuous amid the surrounding gloom.* Soon after sundown they begin to come out and run busily about beneath the shrubs and among the long grass, *constantly uttering shrill, twittering cries* . . . they fearlessly enter rooms. . . . When they come in, they usually skirt along the angles where the walls and floor meet, coursing along, *scuffling and squealing as they go*. . . . If they be left unmolested, they are quite inoffensive . . . *but if they be in any way alarmed or disturbed during their progress, the air is forthwith filled by an intolerable smell of musk that adheres persistently to everything* that they may come in contact with. It seems to be as offensive to most dogs as to human beings and is doubtless a most effectively protective agent. *Many dogs, although eager to pursue musk-shrews, absolutely refuse to touch them*, and those who cannot resist doing so in the excitement of the chase show unequivocal signs of disgust and shame over the consequences.'

In the foregoing pages I have attempted to give a clear account of the type of combined equipment—both protective and advertising—characteristic of aposematic animals, as illustrated by the Mammalia, in order to introduce the conception upon which the theory of warning colours is based. We have seen that in three separate orders, namely, Rodentia, Carnivora, and Insectivora, certain members diverge in appearance, habits, and ecological relationships from other members of their respective orders, while they agree with one another, in possessing (1) protective adaptations (such as a combination of spiny armour, stinking secretions, fierce demeanour, toughness, or unpalatability) which render them dangerous or disagreeable as prey, and therefore relatively immune to attack *if recognized*, and (2) aposematic attributes (such as a combination of conspicuous coloration, advertising habits, odours, and sounds) which notify an enemy in no uncertain manner of their owner's unwholesome identity.

It is now necessary to deal a little more extensively with certain aspects of the subject which have already been referred to only in regard to mammals, and to introduce, in their proper place, further classes of evidence which illuminate wider issues upon which the theory of warning colours depends, and to discuss various points against which attacks have been made by critics.

5. THE PROTECTIVE ATTRIBUTES OF APOSEMATIC ANIMALS IN GENERAL

> He hath said in his heart, I shall not be moved: for I shall never be in adversity.
>
> PSALM X, 6

From what has already been said on the subject, it will be clear that the theory of warning coloration depends essentially upon three classes of evidence, namely:

(1) The presence of an advertising mechanism, which makes an animal conspicuous and easily recognizable in its natural surroundings. This mechanism may take any of several forms, such as brilliant coloration, bold pattern, free exposure, diurnal habits, gregariousness, displaying attitudes and movements, warning sounds and scents.

(2) The possession of some unpleasant or dangerous attribute, such as poison, effective powers of attack, repulsive odour, nauseous secretions, spinescence, hairy integument, or some other deterrent property which renders the animal relatively unattractive and distasteful to possible enemies.

(3) The assumption that different potential enemies learn to discriminate in the choice of prey; that when an animal is found by experience to possess dangerous qualities, it has only to be seen to be avoided; and that in leading to its immediate recognition, the conspicuous attribute is therefore of vital benefit to its possessor.

The first of these propositions has been dealt with in the foregoing section. We have now to consider the evidence relating to the second point. It will be necessary here to describe briefly the different classes of attributes which are believed to render various animals unpalatable; to inquire whether there exists in nature that relationship between coloration and edibility in insects and other animals which the theory demands; and to examine the evidence that these so-called protected species are in fact unattractive to, and avoided by, enemies.

The efficiency of defensive characteristics, such as poison or repulsive odour or taste, which many conspicuous creatures are assumed to possess as a means of protection, is still a subject about which there is a good deal of dispute; and it has been denied by McAtee (377) and others that the forms concerned are in fact either rendered 'inedible' or exempt from attack in the way the theory of warning coloration demands.

When A. R. Wallace, the pioneer naturalist and explorer, originally put forward his well-known theory to explain the conspicuous colours of caterpillars, his suggestion was based on the belief—at the time almost unsupported by actual evidence—that such caterpillars were protected by unpalatable qualities, and that birds would be found to refuse them as food. Subsequent criticisms that Wallace's explanation rested upon insufficient evidence, although at one time justified, did not invalidate the theory itself: on the other hand, such criticism had a stimulating effect.

Experiments were carried out by Jenner Weir (657), Butler (73), Weismann (658), and Poulton (494), the general results of which were to confirm Wallace's prediction. Subsequently the subject attracted a great deal of attention, and extensive experiments and observations were made—notably by Poulton (496, 505) and Pocock (482) in this country; by Marshall (395) in Africa; by Frank Finn (171) in India; and by Judd (297) and Pritchett (529) in America. The great accumulation of evidence brought to light by the work of these investigators established the theory of warning coloration upon a firm foundation of fact, and extended its application to a wide range of animals.

During the last twenty years an immense number of observations in the field and experiments on captive animals have been carried out in order further to test the theory in reference to different types of predator and prey. Among these investigations may be mentioned the work of Hale Carpenter (79), Carrick (88), Cott (111, 112, 116), Morton Jones (290, 291, 292), Kluijver (313), Myers (433), Phillips (469), Poulton (516), and Swynnerton (609). It has now been established beyond question that many aposematic insects and other animals are highly distasteful, while other, and especially cryptic forms, are greatly relished by different predators. The evidence is extensive, and in the following pages I can only attempt to give some account of the facts as they relate to particular groups of animals.

We must refer briefly here to the meaning of the terms 'unpalatable' and 'inedible' as applied to aposematic animals. It is necessary to emphasise the fact that inedibility is only relative. The acceptability or distastefulness of an insect is never absolute. It depends upon the interplay of several factors, such as the species of insectivorous enemy concerned; its past experience or 'education' in relation to food-animals; its powers of memory and discrimination; its present state of hunger or repletion; upon the relative abundance or accessibility of other kinds of food; and upon the actual food available at a particular instant. All these causes tend to operate independently of an animal's preferences, and constantly modify its diet according to circumstances. For this reason, it may well be doubted if *any* species, however well defended, is at all times and under all circumstances free from attack.

There are many instances in which protective devices and associated warning colours are known to be ineffectual against *certain enemies*. But this does not necessarily imply that they are not on the whole beneficial to the species attacked. For instance, in the case of stinging Hymenoptera, where at any rate the power of defence cannot be disputed, bumble-bees, honey-bees and wasps are known to be eaten by Flycatchers, Bee-eaters and other birds. At Pernambuco I have watched a lizard (*Ameiva*) seize, and after careful manipulation devour, a large and very formidable black fossorial wasp (Pompilidæ). Similarly, as we have already mentioned, ants have numerous specialized enemies. *Urocentron azureum*, a rare and handsome green and black Iguanid lizard from Marajó Island, at the mouth of the Amazon, feeds freely upon a species of tree-ant. So do various East African tree-frogs. Or again, different caterpillars which are protected by a covering of sharp prickles or irritating hairs form an important element in the diet of certain specialized feeders such as Cuckoos.

It is also, of course, quite obvious that different groups of animals differ widely in their taste and preferences. Thus particular types of prey are subject to different enemies. In the case of mammals and birds, for instance, Pocock (482) has shown that carabid beetles such as *Carabus violaceus*, *Pterostichus niger*, and *P. madidus* are readily accepted by birds (Harmonious Shrike-Thrush, Dial Bird, Spotted Bower-bird, Black Tanager, and Silver Pheasant), but rejected with every sign of disgust by mammals (Meercat, Banded Mongoose, White-tailed Mongoose). Conversely, different conspicuous moths such as *Hipocrita jacobææ* appear to be less unpalatable to mammals than to birds. Differences of taste are found between other groups of insect-eaters, such as lizards, frogs, and predatory insects, and between various orders within these groups. Thus the typically protected *Acræa* butterflies, which undoubtedly enjoy general immunity from attack, being avoided even by such indiscriminate feeders as mantids, are yet eaten by the predaceous Asilidæ (395).

Again, as Swynnerton (609) has shown, the acceptability varies for a single type of predator. Much depends upon the enemy's state of hunger. 'An *Amauris* or *Acræa* is unacceptable at most times to insect-enemies generally, but it is by no means 'inedible'. Given the appropriate degree of gastric activity it may even be acceptable to any of them.'

It thus follows that the relative abundance or scarcity of edible insects will modify the *apparent* food preferences of insectivorous animals. An animal is compelled by hunger to eat *unpalatable* food. If the preferred article is not present, the next best must be taken. It was in this connexion that more than fifty years ago Poulton directed attention to the antagonistic principle which sets a limit to the use of distastefulness as a protective device. This mode of defence, he says, 'depends for its apparently complete success upon the existence of relatively abundant palatable forms: in other words, its employment must be strictly limited' (494). In times of stress we have ample illustration of this principle in human affairs. Thus, during the siege of Paris, rats were eaten; during the Great War, the Germans made 'coffee' from acorns; under prohibition the Americans resorted to a mixture called 'near-beer'; and according to a correspondent of *The Times*, during the recent offensive round Madrid, civilian enterprise made use of anything and everything edible 'from dandelion to donkey'. Yet one would hesitate to argue—on the lines adopted by some critics of the theory of warning colours—that these substances, being accepted as food, are therefore not relatively unpalatable.

I have referred to the above points, since they supply an answer to a certain type of criticism which attempts to discredit the theory by citing examples of enemies which either habitually or occasionally attack aposematic animals, without taking into account the relative freedom from attack by enemies in general which such forms evidently enjoy.

In our earlier treatment of the subject we have dealt with aposematic animals essentially from the aspect of coloration and *appearance*. We shall now refer to the objective *attributes* by means of which such forms are protected, more or less, from predators. For the sake of clearness, I have distinguished between, and dealt separately with, the various visual, auditory, and olfactory warnings of real or assumed unpleasant qualities, and with these qualities themselves. From the ecological standpoint, we have here two different classes of phenomena. The former are psychological warnings intended to avert attack; the latter are physical weapons adapted to defeat attack: in the former we are dealing with questions of advertisement and passive self-revelation; in the latter with questions of armament and practical self-defence: the function of the one is to defy the enemy; that of the others to defeat him: in the one case we see projected towards the foe the outward expression of danger; in the other we see employed against him the practical machinery of protection: the one promises punishment; the other executes it.

What are these powers, these punishments, these weapons, and what not whose possession enables an animal—like the Pharisee of old—to go about in finery, that he may be seen of rivals and enemies?

I. POISON IN DEFENCE

Perhaps the most specialized and effective of all methods of defence is the use of poison. Toxic properties have been developed in a wide range of animal life, and are frequently associated with warning coloration. Many fishes possess poisonous properties which are highly effective as a means of defence against enemies. In some cases, such as the Sting Ray (*Trygon*), Spotted Eagle-Ray (*Aëtobatis*), Poison Toad-fishes (*Thalassophryne*), and Weevers (*Trachinus*), definite poison glands are associated with specially modified spines or fin-rays which function as weapons capable of inflicting painful injuries, and at the same time of inoculating their victims with the poison. In other cases, such as the Puffer (*Tetrodon*), the flesh is permeated with toxic substances. Various species belonging to both types are dressed in warning attire.

I have already referred to the little poisonous Cat-fishes of the genus *Plotosus*. The virulence of the venom of *Plotosus arab*, whose young are purple brown and bright yellow, 'something like a hornet striped fore-and-aft instead of crosswise', is evident from Alcock's account of a wound inflicted on his forefinger by a small individual not three inches long, which made his arm numb and useless for several days (2). The little venomous Weever (*Trachinus vipera*) is well known as bearing a conspicuous intensely black badge of warning on the dorsal fin, which is the only part of the fish visible when it rests submerged in sand. The 'sting' of this species causes such acute pain that fishermen 'have been known to attempt to throw themselves overboard in their distress' (446). It is interesting to note

Garstang's observation that while small fishes such as the Dragonet (*Callionymus lyra*) are habitually eaten by Gurnards, the Weever is never found in their stomachs—a fact which supports the view that the black dorsal fin assists recognition and acts as a danger sign.

Among certain Nudibranch Gastropods such as the orange-coloured *Cavolina farrani*, the conspicuous defensive papillæ, armed with batteries of stinging nematocysts, provide an analogous means of defence against natural enemies (496). So effective are these batteries as a deterrent, that fishes have been known to eat shelled molluscs such as *Margaritifera* which had been long pickled in formalin, in preference to fresh specimens of the Nudibranch *Chromodoris* (121).

The disagreeable properties of sea anemones have been referred to on another page, and it is only necessary here to mention Reighard's observation that tentacles of the anemone *Cassiopea*, when sewn into the mouth of the food-fish, invariably acted as a deterrent to the appetite of the Gray Snapper, even though the same food-fish were accepted after preservation in formalin, or after treatment with quinine or red-pepper (538).

The poisonous stings of hornets, wasps, bees, bumble-bees, and many ants are too well known to need mention here. Although these insects have many specialized enemies, who eat them in spite of their stings, there is no doubt that we have here a defensive weapon which any intending predator must take into account, and one which is, in general, extremely effective as a deterrent. Folsom states that some birds, such as young ducks, are fatally affected by eating honey-bees (178). The Common Toad (*Bufo b. bufo*), which relishes spicy fare such as ants and carabid beetles, will have nothing to do with hive-bees once it has learned its lesson (116).

The animals we have been considering possess poison-glands with apparatus in the form of spines or stings for wounding and inoculating enemies. In a somewhat different category are creatures, often no less venomous, whose flesh or integument is charged with poison. Many of the Puffers (Tetrodontidæ) are conspicuously coloured, and are known to possess poisonous flesh which no doubt renders them more or less inedible.

The same applies to many Amphibia, and especially to aposematic species like *Salamandra maculosa*, *Bombinator igneus*, *Phrynomantis bifasciata*, *Dendrobates tinctorius*, and others whose skin secretions are so effective a means of defence (113). With such forms the poison can take practical effect only if the animal is mouthed or eaten—an event which is frequently more fatal to the predator than to the prey. For instance, it is highly improbable that a dog could ever succeed in eating the formidable toad *Bufo marinus*: on the other hand, many dogs that have been rash enough to make the attempt have paid the forfeit with their lives. A fox-terrier belonging to Mr. Miles Moss met its end in this way at Pará some years ago; and Noble (445) remarks that the poison, one of the most virulent among the Amphibia, frequently kills dogs which have not learned to leave the toad alone.

II. DEFENSIVE SECRETIONS

Irritating or repellent secretions provide many animals belonging to widely unrelated groups with a more or less potent means of defence. Among insects, Coccinellid beetles emit, from pores round the tibio-femoral articulations, a pungent amber-coloured oily fluid, which renders these 'Lady-birds' highly distasteful to enemies. Similar properties are possessed by certain species of Chrysomelidæ. Carabid beetles, especially the larger members of the family, are likewise more or less distasteful, many species secreting a disagreeable acrid fluid from the tip of the abdomen. In the so-called 'Bombardier-beetles' (*Brachinus*) the repulsive discharge has caustic properties, producing on the skin an effect resembling that of nitric acid. Even more potent are the blistering properties of the Cantharid 'Spanish Fly' (*Cantharis vesicatoria*), which, in the product cantharidin, give these insects a commercial value.

A remarkable instance of this method of active defence has recently been given by Burtt (71), and refers to one of the giant black millipedes—a species of *Spirobolus* from the forests of Tanganyika Territory. Having found an unusually large specimen for which he had no box, Burtt buttoned it up in his hip-pocket, where it remained for about an hour. 'I felt the millipede', he says, 'moving about in my pocket and noticed that I was becoming sore in that neighbourhood, but paid little attention to it. However, whilst bathing shortly afterwards I was surprised to find that my skin had become completely blackened over an area of about nine square inches, with further red inflammation spreading rapidly down my thigh. Four days later all this blackened skin sloughed away, leaving a raw wound. This happened in June 1937; at the end of August 1938 the site of the injury is still visible.' The same writer subsequently examined the corrosive liquid which exudes, when the animal is molested, from pores at the sides of each segment. He states that it stains the fingers like iodine, has a pungent odour recalling that of nitrogen peroxide, and that its fumes cause marked watering of the eyes. It is interesting to notice in passing that we have here something closely analogous to a more recently evolved and more deadly method of attack, namely by the use of mustard gas!

Different bugs, notably members of the Pentatomidæ, exude evil-smelling fluids when handled. Among Hymenoptera, certain little stingless bees of the sub-family Meliponinæ emit caustic fluids which burn the human epidermis (662), and which must render them peppery fare for any predator. The irritant secretions discharged from special glands by Hymenopterous larvæ, such as *Crœsus septentrionalis*, and by Lepidopterous larvæ, such as *Dasychira pudibunda*, are well known. Other caterpillars such as *Vanessa io*, *V. urticæ*, *Deilephila euphorbiæ* and *Cucullia verbasci* eject disagreeable fluids from the mouth when roughly handled. Aposematic butterflies such as *Danais*, *Euplœa*, and *Acræa* discharge nauseous secretions when handled from wing-veins, leg-joints, and antennæ.

I have referred elsewhere to several cases of the kind among Orthoptera. Dr. W. A. Lamborn (328) has recorded striking evidence of the effectiveness of distasteful qualities in an immature aposematic grasshopper (*Zonocerus elegans*), whose colour-scheme is bright-yellow, slaty-blue, and red. He writes: 'My kitten seized one in its mouth, but dropped it instantly, and commenced to salivate. Strings of thick mucus an inch long appeared at the corner of its mouth with much frothy saliva, and the animal retched but did not actually vomit. It kept on rubbing its mouth against a tree in an endeavour to get rid of the cause, and was not its usual self for two or three hours. The Acridian had hopped off, apparently little the worse for its experience.'

I must draw attention here to observations given later under the heading of discrimination (p. 291), as affording further convincing evidence of the effectiveness (as a defence against insectivorous mammals) of the repulsive frothy secretions which are exuded by this and other aposematic grasshoppers, namely, *Z. elegans* and *Dictyophorus productus*, which with other lurid species were absolutely refused by Carpenter's monkey (79), and *Aularches miliaris*, similarly rejected by Alcock's Himalayan Bear (1), and an unnamed species in Burma which was avoided by Mackenzie's Slow Loris (387).

It will be seen that this method of defence does not rest merely upon a passive unpalatable attribute, but upon an active emission of the unpalatable substance which, since it occurs when the animal is seized or threatened by an enemy, enforces its effectiveness. In its highest development we find different forms whose specialized habits and modified structure enables them to *project* secretion at the enemy, and thus to discourage attack. When irritated, the Puss Moth larva (*Cerura vinula*) forcibly ejects in a spray its acid secretion directly towards its tormenter. Poulton has shown that the fluid—which causes great pain if it enters the eye—is a mixture of formic acid and water which may reach a concentration of 40 per cent. (492).

This mechanism reminds one of the spray of venom which the Ringhals Cobra (*Sepedon hæmachates*) directs in a fine jet at any intruder. In delivering its deadly discharge, the effective range is considerable—at least six feet (146); the aim accurate—and directed full at the face of the foe; and the consequences serious and often decisive—for if it reaches the eye this virulent fluid causes acute agony and temporary blindness.

Analogous among mammals is the horrible fluid-squirting habit of Skunks—with its awful result. Here, then, we have a similar type of defensive machinery evolved independently in three widely dissimilar forms—a caterpillar, a snake, and a mammal. In each case the discharge is preceded or accompanied by a display reaction; in each the defensive fluid is aimed directly at the adversary; in each a direct hit from the noxious artillery is likely to incapacitate the attacker and prevent further interference.

III. NAUSEOUS TASTE

Many other animals are protected by the nauseous taste or evil odour of their body juices or flesh—a device that has been elaborated in forms so diverse as butterflies and molluscs. Among aquatic animals, for instance, an excellent example is provided by the marine Tectibranchiate mollusc *Oscanius membranaceus*, which secretes from its general body surface a fluid containing sulphuric acid (201). It has been shown experimentally by Bateson (26) that palatable food that has been soaked in dilute acids is generally refused by fishes, and doubtless this species is thus afforded protection from attack, for, according to Garstang, it is not, in fact, eaten by fishes.

Different Lepidoptera are known to be highly distasteful, both as larvæ and pupæ, and in the adult state. When in his famous memoir of 1862 Bates founded the theory of mimetic resemblance—which he based on the belief that certain insects possess advantages over others in being relatively free from attack —he pointed out that 'recently killed specimens of the Danaoid *Heliconidæ*, when set out to dry, were always less subject than other insects to being devoured by vermin. They all have a peculiar smell. I never saw the flocks of slow-flying *Heliconidæ* in the woods persecuted by birds or dragonflies, to which they would have been an easy prey, nor when at rest on leaves did they appear to be molested by lizards or the predaceous flies of the family *Asilidæ*, which were very often seen pouncing on butterflies of other families.'

A high degree of distastefulness has been developed in Lepidopterous larvæ such as *Halia wavaria*, *Cucullia verbasci*, *Zygæna filipendulæ*, and *Hipocrita jacobææ*. The effectiveness of this method of defence against widely different types of predators is well illustrated by the conspicuous caterpillar of the Magpie Moth (*Abraxas grossulariata*), which has provided a subject for numerous experiments. The earliest were those conducted in 1863 by Butler (73), who offered them to the lizard *Lacerta viridis*. He states that notwithstanding their eagerness for all kinds of food 'from a lemon-cheese-cake to a spider', they would seize these insects only to drop them again in disgust. Later experiments with frogs yielded similar results. He says: 'When they first became aware of the introduction of the caterpillars, they seemed greatly excited, sprang forwards, and licked them eagerly into their mouths; no sooner, however, had they done so, than they seemed to become aware of the mistake that they had made, and sat with gaping mouths, rolling their tongues about, until they had got quit of the nauseous morsels, which seemed perfectly uninjured, and walked off as briskly as ever. After this, it was useless to attempt to persuade the frogs to touch one of these caterpillars' (72). The caterpillars were also rejected by spiders: 'I repeatedly put them into the webs both of the geometrical and hunting spiders (*Epeira diadema* and *Lycosa* sp.); but in the former case, they were cut out, and allowed to drop; in the latter, after disappearing in the jaws of their captor down his dark silken tunnel, they invariably reappeared either from below, or else taking long strides up the funnel again' (73).

Similar results were obtained by Jenner Weir when he offered these caterpillars to insectivorous birds belonging to the following species: Robin, Yellow Bunting, Reed Bunting, Bullfinch, Chaffinch, Crossbill, Song-Thrush, and Tree-Pipit. 'My first experiment', he says, 'was with the larvæ of *Abraxas grossulariata*; and in order that the birds might be fairly attracted towards them, I placed them on a shelf in the aviary amongst other eatable species. I watched the birds carefully; they soon ate up all the well-relished and dull-coloured species, but left *Abraxas grossulariata* untouched. I quitted the aviary for some hours, but on my return, they were still crawling about unmolested' (657).

Further observations were made by Weir in 1886 on the food-preferences of the lizards *Lacerta viridis*, *L. agilis*, and *L. vivipara*. His earlier conclusions on the distastefulness of the Magpie Moth were confirmed: one caterpillar was eaten by *L. agilis*; otherwise both larvæ and adults were invariably refused after being tasted. The following notes from his diary, which are incorporated in Poulton's work on the protective value of colour and markings in insects (494), are given here for comparison with observations on the behaviour of other widely unrelated predators under similar circumstances. Having seized one of the caterpillars, the Green Lizard 'immediately dropped it, afterwards licking his jaws as if to remove the unpleasant taste. . . .' Fifteen days later the same lizard again bit an *Abraxas* larva, 'but refused to eat it, and afterwards rubbed his nose and mouth against the moss as if endeavouring to remove a disagreeable taste'.

Pocock (482) tried fowls with the Magpie Moth, which 'was inspected by several, but only pecked by one, which at once dropped it, and made no further attempt'. It is interesting to compare with this the behaviour of a Pipistrelle Bat (*Pipistrellus pipistrellus*) when offered the same species by Whitaker (663). 'It took a good bite at this, and then spat it out, and backed away to the far side of its cage, coughing and spluttering in the most ludicrous manner; and, moreover, it was some little time before it would trust me sufficiently to take a mealworm from my fingers. . . .'

Well protected as this unpalatable insect undoubtedly is from the majority of predators, it must not be imagined that it is *immune* from attack. White (664) has recorded two Magpie Moths from the stomach of a Meadow Pipit (*Anthus pratensis*) shot in North Uist. The Cuckoo (*Cuculus canorus canorus*), which is well known to specialize on food (such as hairy caterpillars) largely avoided by other birds, has been seen devouring *grossulariata* larvæ on gooseberry bushes in a garden at Newburn on Tyne: 'As many as six cuckoos at once came to do so, and continued until larvæ and pupæ had disappeared. Cuckoos did not visit other neighbouring gardens, which were without gooseberry bushes, and none of the other birds in the gardens attacked the *grossulariata*' (664).

It is evident from the above-mentioned experiments that in spite of the different predilections shown by different groups of predators, distastefulness as a deterrent to attack may operate over a very wide field. That this is the case has been conclusively demonstrated by Morton Jones as a side issue of his important experiments on the relative acceptability of insects to birds. He found that when extracts of various gaudily coloured insects (including beetles, moths, and a bug), which had been proved to be highly inacceptable to birds, were mixed with cream, and offered along with control portions of plain cream to ants, the mixtures refused by the ants were amongst those most consistently refused by the birds (290, 291, 292).

IV. PROTECTIVE INTEGUMENT

In other cases protection is provided by a tough, bony, or chitinous exoskeleton which renders the animal difficult, unpalatable, or indigestible fare. Certain aposematic fishes, such as the tropical Trigger-fishes (Balistidæ), Trunk-fishes (Ostraciontidæ), and Puffers (Tetrodontidæ); and many Coleoptera, Hymenoptera, Orthoptera, and insects of other groups, are protected in this way.

For many other aposematic animals belonging to various groups, hairs, or spines, provide a relatively effective means of defence. Sometimes the hairs possess irritating properties, as for instance those of lepidopterous larvæ like the Oak Eggar (*Lasiocampa quercus*) and the Drinker (*Cosmotriche potatoria*), which produce a rash when handled. Sometimes they are grouped together to form more or less specialized defensive weapons, as in the tail-quills of Porcupines, and the dense flat-topped tufts or ' tussocks ' of Lymantriid caterpillars such as the Pale Tussock (*Dasychira pudibunda*), which carries conspicuously on its back a series of bristling batteries resembling miniature shaving-brushes (Plate 26).

Often the defensive bristles are more generally distributed over the body: they may be simple, barbed, or branching; scanty or numerous; long or short; slender or stout; easily detached or firmly fixed; but in general they are themselves conspicuous or are associated with conspicuous colours, and are more or less effective as a means of protection from general enemies.

V. TENACITY OF LIFE

Finally, an important attribute shared by numerous aposematic forms and intimately associated with the possession of a warning apparatus, is the possession of a tough physique. Typically we find that such animals are exceptionally hardy of constitution, relatively resistant of injury, and wonderfully tenacious of life. The vital significance to aposematic animals of powers of resistance and of surviving injury depends upon the fact that conspicuous appearance does, in a sense, actually invite attack by those enemies who have not learned, or are unable to learn, by experience to recognize and avoid them at sight. This applies particularly to the attacks of young vertebrates during the period of experimental tasting; of insect-eating Carnivora and other forms which hunt mainly by scent; and to those of invertebrate enemies such as spiders and mantids, where recognition is determined by taste or scent, rather than by sight.

Accordingly ' toughness ', when associated with special means of defence, will greatly increase the chances of escape or survival of experimental attack. Various instances of this have already been mentioned. Trimen (630) first drew attention to the property in connexion with certain aposematic African Lepidoptera. Referring to the remarkable elasticity of structure in Danaine and Acræine butterflies, he says: ' No pressure of the thorax, short of absolute crushing of the tissues, suffices to kill or even paralyse these butterflies: and the collector who treats them as he would species of other families, soon finds his collecting box alive with the struggling occupants.' Even after being bent double the wings will resume their natural position with nervures unfractured. 'It is not difficult to perceive how important, as a reserve means of defence, this unusual elasticity of structure may prove. That birds and other eaters of insects may occasionally capture a butterfly of these malodorous tribes before discovering its distasteful character is not an unreasonable supposition, especially in seasons when an exceptional scarcity of food may prevail. In such a case it may be safely stated that the chances are very greatly in favour of a *Danais* or an *Acræa* escaping, if not wholly unhurt, yet without serious injury, after rough treatment that would have proved fatal to a harder but less elastic animal.'

Trimen found the same elasticity of structure in certain Agaristid and Zygænid moths, as, for instance, *Pais decora*, *Eusemia euphemia*, and *Glaucopis formosa*—all typically aposematic species defended by a powerful odour. The difficulty experienced by birds such as Bulbuls and Babblers in holding and killing butterflies of the genus *Charaxes* has been clearly demonstrated by Swynnerton (610). In one experiment, for instance, a *Charaxes candiope* broke away after being captured 'scarcely less than thirty times' in succession by a Layard's Bulbul (*Pycnonotus layardi*), before it was finally mastered and swallowed.

Similar 'tough' qualities are found in aposematic Orthoptera (86), Crustacea (108), and in other groups; and Carpenter aptly remarks: 'This resistance is part and parcel of the process whereby an aposematic insect teaches an enemy that it is harmful or unpalatable' (80).

6. THE RELATION BETWEEN WARNING COLOURS AND DISTASTEFUL ATTRIBUTES

> We must take species separately, and study the nature of each.
>
> ARISTOTLE

I. METHODS OF INVESTIGATION

The nature of the relationship between coloration and palatability in insects and other animals, and the effectiveness of other protective adaptations in relation to predatory enemies, may be investigated in a variety of ways: namely—by a comparative study of the ecology and adaptations of the animals themselves; by direct observations in the field on the food and feeding-habits of predators; by properly conducted feeding-experiments with animals either in captivity or under natural conditions; or by the examination of the pellets, fæces, and stomach-contents of wild animals.

(1) **Comparative Studies of Natural Groups**—Of these methods, the first affords valuable evidence of an indirect nature. I have repeatedly stressed in this work the need for an ecological outlook when attempting to explain the biological significance of coloration. In assessing the status of an animal in reference to conspicuousness or concealment, to take account of size and form and pigment and pattern is not enough. These must be correlated with the animal's environment, with its general habits, and with its special behaviour in the presence of an enemy. To divorce the animal from its natural conditions of life is to deprive its appearance of much significance which it may possess. Size must be taken into account, because a large advertisement is more efficient than a small one, and because, conversely, a small object is more easily concealed than a large one: coloration must be taken into account, because certain pigments and patterns tend to catch the eye and help the memory more than others. But we have to remember that there is no such thing as conspicuousness or concealment *per se.*

The normal environment—more especially the background—is an all-important factor; for conspicuousness depends essentially upon differentiation, i.e. upon the degree of contrast in colour and tone between an object and its surroundings. A red Coccinellid beetle resting on a geranium flower would appear as procryptic as a green weevil on a nettle leaf; but the former, seen in its natural surroundings, stands out from them as conspicuously as a pillar-box does. Conversely, the most gaudily coloured fish, that in the hand appears glaringly conspicuous, may actually be difficult to detect in its highly coloured coral-reef haunts and dressed primarily for concealment. Again, the animal's general habits must be considered, because an advertisement or a cryptic colour-scheme is rendered effective by its method of display. Under this head we have to include resting attitudes in relation to colour and pattern, habits of exposure or retreat, habits gregarious or solitary, diurnal or nocturnal activity, movement or immobility. Finally, special reactions and adaptive behaviour in the presence of a predator must be taken into account, such as, on the one hand, nonchalant exposure, intimidating postures, special displays of colour, warning sounds, advertising movements, discharges of noxious secretions, and the use of weapons; and on the other hand, escape reactions such as flight, hiding, dropping, death-feigning.

(2) **Field Observations on Feeding Habits**—The second method, that of direct field observations on the food and feeding behaviour of wild animals, is one of prime importance. Evidence from this source, together with that based upon feeding experiments, is especially valuable because it furnishes data relating to an animal's reactions in the presence of unpalatable prey, and to its power of association and discrimination, and memory, which cannot be directly determined by the examination of stomach or pellet contents alone. Unfortunately considerable difficulties attend accurate observation and identification under field conditions, and few serious attempts have been made to approach the problem from this direction. Speaking generally, such information is as hard to obtain as it is valuable. Most predators are active creatures: it is often impossible to approach them closely: their movements can rarely be predicted, and seldom followed for long. There are, however, certain circumstances—quite apart from casual or chance observations—under which this method can be adopted by an experienced observer with a certainty of success.

To this end, the habits of insectivorous birds when rearing young in the nest present exceptional opportunities—for the observer has a known and restricted area or territory defined for him; he knows the exact spot to which the bird must return with its prey; he knows also that active and persistent hunting for prey will be continuous throughout many hours of the day and on many consecutive days; and finally (taking suitable precautions such as the erection of a hide), he can book, as it were, a front seat in the stalls, from which, unobserved, he can watch the unrehearsed performance on this little stage, and record, with pencil and camera, the details of the drama as acted in a state of nature. Smaller actors, such as predatory arthropods, like orb-weaving spiders and praying mantids, which await their victims in ambush, or like many predatory diptera, which haunt a particular habitat, or like hunting wasps, with whom the hunt can be followed on foot—these offer similar opportunities for intimate observation.

(3) **Feeding Experiments**—The experimental method, whether with captive or wild animals, has much to recommend it, and has in the past been widely adopted by workers in preference to any other as a source of evidence regarding relative palatability. It is, however, sometimes open to the criticism that experimental conditions, especially in the case of vertebrates in captivity, distort the

feeding reactions so as to render the experimental data untrustworthy. This view, for instance, has been put forward in a very vigorous attack on the experimental method by McAtee (376). The difficulties suggested by this writer have been answered in detail by Swynnerton (609) and Poulton (524). But the careful and detailed experimental studies of Marshall and Poulton (395), Hale Carpenter (79), Swynnerton (609), Morton Jones (290, 291), Kluijver (313), and others supply in themselves the best reply to his objections. No one would deny that the experimental method of investigating the food-preferences of predatory animals is one beset with difficulties, but these are not absent in any experimental work on animal behaviour: they are certainly not insuperable; and this method has yielded, and can yield, a vast amount of invaluable data relating to the theories of warning coloration and mimicry.

The fact that frogs and birds depend essentially upon vision, as opposed to the olfactory sense, when hunting for and selecting prey, renders them peculiarly good subjects for the study of the relation between coloration and edibility: for to these predators, *appearance is everything*: external show—revealed in form and size, pattern and colour, display and movements—is their only guide in the choice of food. It is therefore specially to the feeding habits of tailless Anura and insectivorous birds that we should look for the most reliable evidence under this head. Conversely, as has been pointed out by Dr. J. G. Myers (433), mammals such as the Coati, which hunt by scent, are not very suitable subjects. But it must be borne in mind that the ultimate choice of rejection of prey by such animals affords equally reliable evidence so far as edibility is concerned, even though the significance of colour and pattern in determining the selection in this case is less clear.

(4) **Analysis of Stomach Contents**—Finally, there is the method of analysing material that has been eaten. Many authorities are agreed that our knowledge of the subject must come in the main from the evidence of post-mortem examination. This method, when carried out on a sufficient basis, provides a reliable statement of the numbers and kinds of animals actually eaten under natural conditions, and thus furnishes statistical data of value and accuracy. Curiously enough, this method of approaching the subject has been little explored—except from the point of view of economic ornithology. Its possibilities are indicated in an analysis by the writer (111, 112) of animal-remains derived from the stomachs of tree-frogs taken in East Africa and the Canary Islands, and referred to on a later page. In view of the criticism that has been directed against the conclusions drawn from experimental feeding—and against the theories which these conclusions support—the incontrovertible supporting evidence of stomach contents is especially valuable. In the stomach contents of wild animals we have a type of evidence beyond the reach of critics: this is, and must be, the final court of appeal. Its chief limitation is that it can tell us little of actual feeding behaviour—of the predator's psychology, of its rejections and refusals.

In investigations of this kind it is sometimes possible to take advantage of a predator's special methods of discarding indigestible or unpalatable parts of a meal, which, consequently, may be looked for near roosting- or nesting-places. Thus bats of various species, such as the Long-eared Bat (*Plecotus auritus*) and the Greater Horseshoe Bat (*Rhinolophus ferrum-equinum*), habitually seek special resting-places where the food is devoured, and from which the wings of moths and other insect remains are dropped to the ground, (332, 389, 516). In other cases the excrement is shed beneath the roosting-place, or, as in the case of owls, pellets are ejected and may be searched for near the nesting-site.

II. WARNING COLORATION IN THE AMPHIBIA

We have already considered certain evidence—especially in reference to the Mammalia—that warning colours are typically associated with effective means of protection against the attacks of predaceous enemies. It is now necessary to study this relation between self-advertisement and self-defence in various other groups.

When investigating the distribution of warning colours in a particular group of animals, it must be remembered that conspicuous coloration has not necessarily a warning significance; for the advertisements of nature have other or additional functions, being directed against rivals of the same sex or towards members of the opposite sex or other individuals of the same species. Generally speaking, this is especially true in certain highly organized groups where there is a more or less elaborate courtship, as among lizards, birds, and mammals. With birds, where brilliant colours reach their highest development, it is not at all clear that they have an aposematic function against general enemies, though Marshall points out that the flesh of different highly conspicuous South African species—including the Ground-Hornbill, Wood-Hoopoe, Drongos, and Egrets—has a bad smell, and was refused as food by a captive Mongoose (395). The distastefulness of two black species of Drongo (*Dicrurus afer* and *D. lugwigi*), at any rate to certain meat-eaters such as the cat, has been remarked upon by Swynnerton (608). The same is true in South America of the black and red vulture *Catharistes aura pernigra*, a horrible brute whose conspicuousness is only exceeded by its unpleasant habits and disgusting odour—as I know from personal experience with the species on Marajó Island. However, it is doubtful in such a case whether biological significance should be attributed to the association here of conspicuousness and distastefulness—until more is known of the creature's relationships to other animals in the field.

It will accordingly be convenient to begin our inquiry here in a group of animals where the complication of secondary or alternative functions of conspicuousness does not arise. Such a group is provided by the Anura, where conspicuous coloration is known to have little, if any, sexual significance.

The Anura, or tailless Amphibia, a group comprising the frogs, tree-frogs, and toads, exhibit a wide range of coloration. The great majority of these creatures wear procryptic, variously patterned uniforms, in which greens, greys, and browns predominate. But with a few it is far otherwise. There are certain species, arrayed in boldly patterned costumes of conspicuous, saturated hues, which almost vie in brilliance with those of the most gorgeous tropical insects and birds. Now unlike many of the latter, frogs are poorly equipped for escape—they cannot fly, and at best their powers of locomotion are relatively feeble. Moreover, their principal enemies—snakes and birds—are known to depend largely upon vision in hunting prey. If, then, there is any truth in the theory of warning colours, or at any rate, if the theory is applicable to the Anura (and there is no reason why this particular group should be an exception), we should expect to find that these gaudy members of an otherwise generally procryptic group possess a specially effective means of defence against predators. And the available evidence indicates that this is certainly the case.

One of the earliest, and most pertinent, observations on this point is contained in the following account of certain Nicaraguan frogs by the naturalist and explorer, Thomas Belt (45): ‘ In the woods around Santo Domingo there are many frogs. Some are green or brown, and imitate green or dead leaves, and live amongst foliage. Others are dirty earth-coloured, and hide in holes or under logs. All these come out only at night to feed, and they are all preyed upon by snakes and birds. In contrast with these obscurely coloured species, another little frog hops about in the day-time dressed in a bright livery of red and blue. He cannot be mistaken for any other, and his flaming vest and blue stockings show that he does not court concealment. He is very abundant in the damp woods, and I was convinced he was uneatable so soon as I made his acquaintance and saw the happy sense of security with which he hopped about. I took a few specimens home with me, and tried my fowls and ducks with them ; but none would touch them. At last, by throwing down pieces of meat, for which there was a great competition amongst them, I managed to entice a young duck into snatching up one of the little frogs. Instead of swallowing it, however, it instantly threw it out of its mouth, and went about jerking its head as if trying to throw off some unpleasant taste.’

As one of the most poisonous frogs in the world, the case of *Dendrobates tinctorius*, whose varied colour-schemes include vigorous patterns in which white, yellow, red, or electric blue form an important element contrasted against a dull ground of maroon or black, is almost too well known to need mention here. According to Gadow (195), the strongly poisonous secretion of this species is said to be employed by the Indians of Columbia for poisoning their arrow-heads, the poison, which acts on the central nervous system, being used especially for shooting monkeys.

Another South American species, *Atelopus stelzneri*, likewise as poisonous as it is conspicuous, was observed by Darwin when visiting Bahia Blanca in 1833, and its singular coloration he has vividly described in *A Naturalist's Voyage*. ‘ If we imagine, first, that it had been steeped in the blackest ink, and then, when dry, allowed to crawl over a board, freshly painted with the brightest vermilion, so as to colour the soles of its feet and parts of its stomach, a good idea of its appearance will be gained. If it had been an unnamed species, surely it ought to have been called *Diabolicus*, for it is a fit toad to preach in the ear of

Eve. Instead of being nocturnal in its habits, as other toads are, and living in damp obscure recesses, it crawls during the heat of the day about the dry sandhillocks and arid plains . . .' (135). Now in regard to the effectiveness of its poisonous properties, I have referred on pages 292 and 296 to evidence given by Budgett (67) and by Professor Graham Kerr, who proved in the Paraguayan Chaco that *A. stelzneri* is unacceptable as food and that it enjoys a high degree of immunity from predatory enemies. Budgett found similar attributes in *Phyllomedusa hypochondrialis*, another conspicuously coloured species from the same locality. In this case, the animal is green or blue above, with scarlet and black flanks.

Among African species, *Phrynomantis bifasciata* stands out as perhaps the most highly conspicuous. Grey or jet black in ground colour, this frog normally wears two vivid stripes of pink or full vermilion extending from the nose along each side of the body to the flanks, and a splash of the same pigment over the back posteriorly, the legs being black with vermilion spots. In its habits the animal is sluggish and it freely exposes itself. To my own knowledge, it is diurnal. When alarmed or roughly handled, great quantities of a sticky, poisonous, milky secretion are produced, sometimes causing inflammation in the hands of its captor. The deterrent effect of this noxious fluid may be appreciated from the following account by Loveridge (366): 'I have previously drawn attention to the poisonous nature of the secretions of this frog, a further example came to my notice at Mwaya. One of my boys brought me a bag containing a mixed catch of frogs from bananas—*Hyperolius*, *Megalixalus*, *Leptopelis*, and half-a-dozen *Phrynomerus* [*Phrynomantis*]. I chloroformed the whole lot in the bag. An hour later I tipped the catch out on to a table and began picking out the various species. The *Phrynomerus* had exuded a considerable amount of intensely sticky dermal secretion which had gummed the smaller *Megalixalus* together. After separating these and dropping them into water I could not get the gummy mucus off my fingers by washing and so rubbed them in the dust—as a monkey would do—then by rubbing them together shed the mucus like so much gutta-percha. Shortly afterwards irritation set in on my finger-tips, entirely comparable to the irritation produced by stinging nettles, and it actually appeared to spread within my arm up to the elbow. . . .'

In the United States, the Pickerel Frog (*Rana palustris*) is remarkable for its poisonous properties. Surface (604) gives 'Poison Bully' as one of its popular names in Pennsylvania. The frothy skin-secretion is stated by Wright frequently to kill other species of frogs brought home with it in the same jar (678). According to Ditmars, it is rejected as food by the frog-eating Black Snake (*Zamensis*) (144). The value of the poison in defence has recently been discussed by Dunn (157), whose experiments prove that it confers what amounts to absolute immunity from its greatest potential enemy, the Garter Snake (*Thamnophis sirtalis*). Captive Garter Snakes which 'were sufficiently at ease to be almost continually about the business of sex' and whose voracious appetite caused them to seize immediately any frog, were offered the most readily obtainable local species *Bufo americanus*, *Rana clamata* and *R. palustris*. Of these, the first two were eaten with avidity. '*Rana palustris* was always seized with the same eagerness, but the results were very different. The attacking snake *always* released the frog, uninjured and in short order. The snake then proceeded to gape and yawn, and go through the motions of ejecting a mouthful (although nothing was actually in the mouth), then to move about and continually wipe or rub the side of the mouth against the floor or walls of the cage.' These experimental results are in complete agreement with field observations—for Surface, who has reported on the stomach contents of snakes from Pennsylvania, records not a single Pickerel Frog from any snake, although other common frogs of the area were all eaten (603). Now in view of these facts, it is very interesting to note that a peculiarity of the species, by which it differs from the closely related and relatively palatable *R. pipiens*, is the coloration of the posterior ventral parts and hind limbs, which are bright orange or yellow—the hues so generally associated with, and a sign of, dangerously poisonous properties in Anura.

A better-known example is the European Fire-bellied Toad (*Bombinator igneus*). This case is especially interesting in that the warning colours of the legs and belly are so situated that a peculiar exhibition-pose must be adopted by the toad for their display. When irritated or alarmed, the animal reacts by hollowing its back, lifting the chin off the ground, and turning the limbs upwards and outwards so as to show their brightly coloured under surfaces; or alternatively, he may turn right over, so as to show the red and white marks on his grey-black belly. Once again, the question arises: Is this animal really protected by a degree of virulence which other, inconspicuous, species lack? This question is best answered in the words of Gadow (195): 'The secretion of the skin is very poisonous, and the fire-toads are thereby well protected. I know of no creature which will eat or even harm them. I have kept numbers in a large vivarium, together with various snakes, water-tortoises, and crocodiles, but for years the little fire-bellies remained unmolested, although they shared a pond in which no other frog or newt could live without being eaten. Hungry water-tortoises stalk them under water, touch the intended prey with the nose in order to get the right scent, and then withdraw from the Bombinator, which has remained motionless, well knowing that quick movements, or a show of escape, would most likely induce the tortoise to a hasty snap, with consequences to be regretted by both.'

Somewhat similar habits occur in an American toad *Bufo americanus*. This animal is cryptically coloured above; but when disturbed it rolls over on its back, and exposes the light skin of the belly, which is conspicuously marked with black blotches. A somewhat different display of conspicuous colour has been recorded by Annandale (7) in the case of a Siamese toad *Callula pulchra*, which inflates the body with air when interfered with, so as to unfold and expose on the back a pair of broad yellow stripes which are normally hidden in folds of the loose skin.

We have seen, then, that certain of the most poisonous and most surely protected species of frogs and toads either wear the conspicuous liveries of white, yellow, red, or blue upon a dark ground, which in many groups of unrelated animals are regarded as a warning sign to potential enemies, or else make special displays of such colours when their lives are endangered. It might, however, be misleading were I not to point out here that the converse is by no means true, for many other species of Anura are known to be highly distasteful and well protected by poison although in coloration they are relatively inconspicuous or even highly procryptic. Such is *Hyla venulosa*, the ‘ flying frog ’ of the Amazons, from whose skin on being handled there exudes a copious discharge of a sticky acrid secretion which cannot fail to act as a deterrent to potential predators : such is the bark-like *Hyla vasta* of Santo Domingo, whose skin poison is said by Barbour (19) to be so strong as to burn one’s hands painfully when the frog is handled : such is the huge-mouthed rapacious *Ceratophrys cornuta*, which likewise combines poisonous properties with cryptic coloration and habits : such also is the South American *Bufo marinus*—that giant among toads—whose highly developed paratoid glands secrete an extremely virulent poison. This frequently kills dogs that inadvertently molest the animal, and doubtless renders the toad potentially immune from all natural enemies.

But the point to be noted here is that although cryptic coloration may, or may not, be associated with effectively noxious properties, *where very conspicuous colours occur in the group they are characteristically associated with an effective means of defence.* I do not know of any typically aposematic species which has been shown to be unprotected and relatively palatable to enemies.

Among the Urodela, or tailed Amphibia, there are indications that a similar relation between conspicuousness and distastefulness may be traced. *Salamandra maculosa*, the so-called Fire Salamander of Europe, affords a striking example of virulent poison advertised by warning colours. Coal-black in colour, with bold irregular chrome-yellow patches on the back and limbs, the animal is as conspicuous as an Automobile Association road sign, and like the latter, the sign displayed is a sign of danger. For the Salamander is notoriously poisonous, a few drops of the milky skin discharge causing death in a small animal. Its potency is described by Gadow (195), who once shut two Bull Frogs into the same enclosure with a number of these Amphibians. ‘ Next morning ’, he says, ‘ the huge frogs were found dead, each having swallowed a salamander, which they were not acquainted with and had taken without suspicion.’

Similar poisonous properties occur in other members of the group. For instance, the American *Diemyctylus torosus* is well defended in this way. Hubbard offered this black and orange species to a Garter Snake (*Thamnophis elegans*) : out of eleven trials, only once was the animal attacked—this after a fast of eleven days. Of this encounter, we read : ‘ As soon as the *Diemyctylus* was introduced the *Thamnophis* made only a hurried examination, then seized the newt by the middle, and, working its jaws from side to side moved up nearly to the head. Then, instead of swallowing its captive, the snake slowly relinquished its hold and finally dropped its intended victim. That this foretaste of its anticipated meal was enough to satisfy the *Thamnophis* seemed clear, for it went about for an hour afterwards, opening its jaws at frequent intervals, as if trying to get rid of a bad taste; and the lesson was learned so thoroughly that in the three remaining trials it took no notice of the newt' (274).

III. WARNING COLORATION IN OTHER GROUPS OF ANIMALS

The larvæ of Lepidoptera furnish a natural group of creatures peculiarly apt in an investigation of the relation between colour and edibility; for here, of course, there is absolutely no question of conspicuousness having any sexual or intraspecific significance. Since, however, caterpillars have frequently been studied in this connexion, and besides numerous scattered observations have been the main subject of an important memoir by Poulton (494), I do not propose to consider them here, beyond mentioning that our knowledge of these creatures, whether relating to members of widely different families, or to forms living in widely separated regions, strongly support Wallace's theory.

The subject has also been well explored in certain other groups and stages in the life history, notably among Lepidoptera, Coleoptera, Orthoptera and Hymenoptera. I can only refer here briefly to the relationship under consideration in a few other groups less thoroughly investigated. The subject is obviously one presenting a wide field of inquiry—especially in regard to various tropical and to marine forms about whose natural history little is known at present.

Mottram's observations on the feeding habits of fishes and birds in nature led him to conclusions with regard to mayflies which indicate the parallel application of this principle in that group of insects. He showed that the several British species of Ephemeridæ can be arranged in an order of palatability, both for birds and for fishes, headed by *Ephemera danica*, as probably the most palatable, and with *Heptagenia sulphuria* as the least. Distastefulness of the latter is indicated by Mottram's observation that it was never seen to be taken by Trout, even on occasions when considerable hatches of the insect were observed (427). Now it is significant that *H. sulphuria*, the Yellow May Dun, is a vivid yellow colour which presumably makes it a conspicuous object on the water: 'It is certainly more easily seen than any other of the smaller British Ephemeridæ.'

To take an example from a very different group of animals, the Diplopoda or millipedes, I may refer here to the following pertinent observation. A long-eared dog, *Otocyon virgatus*, kept by Loveridge in East Africa, used to spend a good deal of its time turning over stones in search of millipedes, which were gobbled up greedily. However, on being offered a black and yellow Polydesmid, the animal pawed it over for some three minutes, eventually refusing to eat it (362). Millipedes are usually regarded as more or less unpalatable fare, protected as they are by the peculiarly offensive secretions of the stink-glands or so-called 'glandulæ odoriferæ'. It is therefore very interesting to note that the dog, which had acquired a considerable taste for these unwholesome animals, yet recognized the aposematic species as unfit for food—thus providing evidence that this warningly coloured form is an especially distasteful member of its group.

In the lower forms of littoral and marine life the meaning of bright coloration is less clear, though the association of conspicuousness with special powers of defence may probably be regarded as pointing to an aposematic function in distantly related groups. What appears to be an excellent example of warning coloration among Crustacea is afforded by the Land Crab *Sesarma meinerti*, whose habits have been studied by the present writer in Beira (108). Its imposing colour-scheme of dark purple, orange, and vermilion; its defiant and aggressive demeanour when surprised in the open; its menacing attitudes and warning display; its pugnacity, show of temper, and effective powers of defence when interfered with; its relative freedom from attack; and its tenacity of life, and remarkable powers of resistance and of regeneration, all point to this conclusion.

An instance among British Tectibranch molluscs is recorded by Garstang (202). Certain species in the suborder, such as *Scaphander lignarius*, *Haminea hydatis*, and *Philine aperta*, are largely preyed upon by fishes and are inconspicuously coloured. On the other hand, the related *Oscanius membranaceus*, a form rendered highly distasteful by defensive acid secretions, 'is not eaten by fishes, and is handsomely coloured with red-brown and yellowish markings'. I have referred elsewhere to another interesting case among Gastropoda of the Nudibranchiates *Cavolina farrani* and *Chromodoris reticulata*; and among Polychæta to the Terebellid *Polycirrus aurantiacus*, where experimental evidence of effective protection lends support to this interpretation of their conspicuous coloration (496).

Brilliant hues in certain Echinodermata may perhaps also be explained in the same way. Semon is inclined to regard the bright coloration of the Echinoid *Asthenosoma* as having warning significance, to teach enemies to keep clear of its poison spines (563); and Mortensen believes that the conspicuous black coloration of some Holothurians—which are all the more conspicuous when living on a white sandy bottom—may have a like function. 'Those forms', he says, 'which have Cuvierian organs possess a very effective means of protection; those peculiar sticky, white threads, which dart through the water like arrows . . . entangling anything they meet, must be very dangerous weapons' (417).

7. THE EFFECTIVENESS OF PROTECTIVE ATTRIBUTES ASSOCIATED WITH WARNING COLOURS

> And ye have respect to him that weareth the gay clothing.
>
> JAMES II, 3

We have considered above the correlation between warning colours and dangerous or distasteful qualities as it occurs in different systematic groups of animals. A complementary type of evidence regarding the relationship between coloration and edibility, and the effectiveness of distasteful attributes for protection, may be derived from a study of the food selected by predatory animals from such natural or artificial assemblages of prey as are available under field or experimental conditions.

The problem has been studied from this point of view by several investigators ; and in the hands of such observers as Swynnerton, Hale Carpenter, Poulton, and Morton Jones the present method of approach has furnished much conclusive evidence in support of the theory of warning coloration. I can only refer here to the main results of such observations ; and for further details the reader is referred to the original memoirs.

I. EVIDENCE FROM EXPERIMENTS WITH CAPTIVE ANIMALS

(1) **Insect Coloration, and Relative Edibility, in reference to Monkeys**—In 1921 Carpenter published the results of an extensive series of experiments carried out in East Africa with two *Cercopithecus* monkeys (79). A large and varied assortment of insects—offered to or found by the monkeys—were classified according to conspicuousness (as indicated by their appearance and habits) and according to edibility (as indicated by the monkeys' reactions). Analysis of 615 observations with the first individual on 244 different species of insects gave the following results : of 143 aposematic species, 120 (83·9 per cent.) were classified as distasteful, and 23 (16·1 per cent.) as edible ; and of 101 cryptic species, 83 (82·2 per cent.) were classified as edible, and 18 (17·8 per cent.) as distasteful. These results, which were supported (though less strikingly) by experiments with the second monkey, are in complete accord with the view that warning colours are in general a sign of distasteful qualities.

(2) **Insect Coloration, and the Food-preferences of a Lemur**—Closely similar results were obtained by W. W. A. Phillips in experiments carried out in Ceylon on a Lemur (*Loris tardigradus*), which was offered a variety of butterflies and moths (469, 523). Taking the results as a whole, it was found that insects

with procryptic colours and behaviour were accepted, while those with aposematic colours were rejected.

II. EVIDENCE FROM EXPERIMENTS WITH WILD ANIMALS

(1) **Insect Coloration, and the Relative Acceptability of Insects to Birds**—Among the most extensive and valuable experiments yet undertaken on the relation between coloration and edibility are those carried out in America by Dr. F. Morton Jones, whose work has been published in two important papers in the Transactions of the Royal Entomological Society of London (290, 291). His investigations began with the establishment of a feeding-tray at the edge of an extensive natural woodland on the island of Martha's Vineyard, Massachusetts. This tray was provisioned daily with water, and with a supply of seeds, suet, and other food which served to attract wild birds frequenting the area. For the purpose of each experiment, a variety of freshly killed insects were placed on the tray in addition to, or instead of, other food. Direct observation of the bird visitors through binoculars, and retabulation of the insects left on the tray at frequent intervals in the course of each experiment, enabled Morton Jones to classify the insects used according to their acceptability. This was expressed numerically in the following way. During the several experiments all those insects taken by the birds in the first period before retabulation were given an acceptability-rating of 100; all those left after the birds had ceased to visit the tray were given a rating of 0; and those eaten during each of the intermediate tabulations were given their appropriate rating between 100 and 0—by a method of calculation described in Appendix B, page 380, of his paper (290). From the data thus obtained for each species in the several experiments, a numerical expression of the average acceptability rating was arrived at. Finally, the list of species, when arranged according to the order of preference, was divided for purposes of subsequent discussion into three sections: Section I containing species with ratings from 100 to 60; Section II, from 60 to 25; Section III, from 25 to 0.

This is not the place to attempt a detailed account of the results obtained by Morton Jones. I must, however, refer to certain of these which seem especially significant and relevant to the present subject. The first point to be noticed is the frequent occurrence of aposematic coloration among insects of lowest acceptability. Of the 31 species, belonging to 3 different orders, included in Section III, 19 were conspicuously marked with yellow, orange, or red, 4 more exhibited the same colours, but less conspicuously, one was brilliantly metallic and polished, while the remaining 7 exhibited other types of coloration. No fewer than 343 out of 423 insects in this section were highly conspicuous. Secondly, among the 2,409 insects—belonging to 90 species—of highest acceptability in Section I, not one conformed in its resting attitude either to the yellow, orange, or red type, or to the metallic type of coloration. On the other hand, with a few exceptions, procryptic species were in general highly acceptable.

This relation between coloration and acceptability was strongly confirmed by Morton Jones in a second series of experiments carried out on the same lines, but with different insects and different birds in southern Florida (291). As before, acceptability ratings were calculated for each species. To facilitate comparison, the insects were tabulated according to natural orders, and in certain of these groups that data are most significant. For instance, his classified list of moths comprises 180 specimens belonging to 23 species: of these, 135 moths belonging to 19 dull-coloured, nocturnal species were rated between 76·5 and 100, and earned an average acceptability of 90·8. The remaining 45 moths, belonging to 4 gaudily coloured diurnal species, were rated respectively as 12·2, 9·8, 3·5 and 0·0, with an average acceptability of 6·7. In the combined experiments only one (0·74 per cent.) of the cryptic moths was left on the tray uneaten, while of the aposematic species 39 (86·6 per cent.) were left upon the tray at the conclusion of the experiments. Somewhat similar were the results obtained with Orthoptera. Out of 30 cryptic examples of this order, belonging to 6 species, only 4 (13·3 per cent.) were left uneaten at the end of the experiments; but of 28 examples of the aposematic grasshopper *Rhomalea microptera*, 25 (89·3 per cent.) were left upon the tray at the end of the same experiments.

(2) **Relative Acceptability of Insects to Nesting Birds**—Finally, mention must here be made of experiments carried out by Carrick (88) near Glasgow. Carrick tested the protective value of aposematic coloration by offering birds mixtures of aposematic and neutral-coloured insects on feeding-trays close to nests where fledglings were being fed. In a series of seven experiments at nests of the Wren, Willow-Warbler and Sedge-Warbler—during which the birds' movements were closely watched through binoculars—a total of 58 neutral specimens (mostly brown and grey Diptera and caterpillars) and 44 aposematic specimens (bees, wasps, and caterpillars) were attached alive to the feeding-tray. Of these, 50 (86 per cent.) of the former and only 4 (9 per cent.) of the latter were eaten.

These experiments are of particular value, since—like those of Morton Jones—they record the uninfluenced behaviour of wild birds, free to come and go, and to seek and select food—whether at the feeding-tray or elsewhere—at will.

III. EVIDENCE FROM THE EXAMINATION OF STOMACH CONTENTS

(1) **The Food of Bats, in Relation to Insect Coloration and Edibility**—Further data bearing upon the present problem is afforded by investigations on the food eaten by wild animals under natural conditions, as, for example, in the studies by Poulton, Kluijver, and the present writer on the food, respectively, of Bats, Starlings, and Tree-frogs. I shall refer to Kluijver's work on a later page in connexion with selective feeding by insectivorous birds; and we must now consider briefly what light the prey of Bats and Tree-frogs can shed upon the question of relative acceptability.

Sir Edward Poulton has brought together much important evidence relating to the association of aposematic coloration with distasteful qualities in his valuable work on the food preferences of Bats (516). A collection of moths' wings obtained in Uganda by Professor G. D. Hale Carpenter from a rest-house occupied by Bats yielded on examination 20 Hawk-moths (Sphingidæ) belonging to 7 species, and one Noctuid. Without exception all were procryptic in coloration.

Similar results in the case of British Bats—probably the Long-eared Bat (*Plecotus auritus*)—relate to the wings of moths collected from various shelters, porches, lofts, and similar situations in eight widely scattered localities (seven English and one Scottish): of the 1,328 specimens represented in the collection, there was a striking preponderance of Noctuid moths, and all but 16 belonged to species with procryptic colouring and instincts. All the common moths known to be highly distasteful were entirely absent from the list. 'The great interest in this list of species is the conclusive evidence of preference which it provides. Important as are the experiments on captive insect-eaters, necessarily deprived of their accustomed variety of food and freedom of choice, these results, presented to us on so large a scale by the bats themselves, are far more significant and trustworthy, and they confirm the strong support, already yielded by observation and experiment on other insect-eaters, to Wallace's theory of the meaning and development of Protective (Procryptic) Resemblance and the contrasted Warning (Aposematic) Colours of insects.'

(2) **The Prey of Tree-frogs, in Reference to Insect Coloration and Edibility**—The same general avoidance of highly conspicuous insects by an entirely different class of predators is clearly shown in investigations carried out by the present writer on the natural food of certain Tree-frogs in Portuguese East Africa (111) and in the Canary Islands (112). Among a total of 11,585 food-animals recovered from 995 frogs belonging to 8 species, only 20 (0·17 per cent.) specimens belonged to the typically aposematic group 'AA'. The relevant figures are given in Table VI, which summarizes the data according to the various orders of prey eaten.

TABLE VI

Number of Food-animals recovered	Orthoptera	Hemiptera	Coleoptera	Diptera	Hymenoptera	Araneæ	Total
Total prey identified	63	705	273	193	10,300	51	11,585
Aposematic 'AA' prey	0	4	4	5	7	0	20
Percentage 'AA' prey	0·00	0·58	1·48	2.63	0·68	0·00	0·17

WARNING COLORATION IN REFERENCE TO PREDATORY ENEMIES

8. EXPERIMENTAL EVIDENCE THAT VERTEBRATE ENEMIES LEARN BY EXPERIENCE

> Feed me with the food that is needful for me.
>
> PROVERBS XXX, 8

IN the preceding section we have considered the purpose and effectiveness of warning coloration from the point of view of the aposematic animal—the possible victim of aggression. We saw, firstly, that there is an association between aposematic coloration and dangerous or distasteful attributes; and secondly, that these attributes are, in general, effective as a means of defence against predators.

We must now regard the subject from the other side—from the point of view of the aggressor. Here, again, we are led into two lines of inquiry: firstly, into certain psychological studies of predatory animals; and secondly, into the actual evidence for discrimination and selective feeding.

I. AVOIDANCE OF APOSEMATIC PREY IS NOT INSTINCTIVE, BUT ACQUIRED

If warning coloration is of any value in leading to the recognition of unpalatable or dangerous qualities in its possessor, such value can only relate to enemies which either instinctively avoid aposematic prey, or else are able to learn by experience to do so. Now, regarding instinctive avoidance, in different classes of vertebrate enemies the evidence here is conclusive.

In the case of birds—one of the first groups to be studied in this connexion—Lloyd Morgan clearly demonstrated that *the young do not instinctively avoid dangerous or unpalatable prey*. At first they will strike with perfect indiscretion at anything of suitable size. Soldier-beetles and Lady-birds, aposematic caterpillars, such as the Cinnabar, 'worms' made of red worsted—these were invariably tested and *only avoided as the result of experience* (414).

With young or inexperienced mammals, lizards, and fishes the same appears to be true. Similarly in the case of frogs and toads (where movement of the prey is the essential trigger which releases the feeding reaction), anything and everything of suitable size is at first tasted.

What we therefore have to consider is this: to what extent are predatory animals capable of profiting by the experience of experimental feeding, of associating appearance with taste, and of remembering to avoid what is not good to eat ?

These questions raise an important issue, for upon the answer must depend any attempt to explain the significance and origin of warning colours and mimicry. If animals are indiscriminate feeders (as, for instance, is implied by McAtee in his criticism of warning coloration), then aposematic appearances can have no more biological meaning than the marks on the moon.

Many experiments, like those carried out by Poulton (494, 496), Beddard (33), Finn (171), Judd (297), Marshall (395), Pritchett (529), Reighard (538), Pocock (482), Swynnerton (609), Carpenter (79), Morton Jones (290, 291), and Carrick (88)—designed to test the efficiency of cryptic and warning coloration—throw light upon this question. The subjects used in these experiments were mainly mammals and birds, and as I shall have occasion to discuss feeding reactions in these two groups under the heading of selective feeding, I need only add here one or two relevant observations.

II. EVIDENCE OF LEARNING BY EXPERIENCE IN MAMMALIA

Alcock has given us a very vivid description of the feeding behaviour of a young Himalayan Bear when offered unpalatable prey. This animal had been brought in straight from its mother's lair, and was allowed to live an almost free and natural life in a large garden. Alcock's account is peculiarly pertinent to the subject under discussion, and I give it in his own words : 'Now there is a grasshopper of this country whose colours at once proclaim with emphasis that, like Socrates among men, it is not like its fellows. Instead of being green or brown as most grasshoppers are, so as to avoid being seen, it is black, with lurid red cross-bands on its body and glaring yellow blotches on its fore-wings, so that it is about as conspicuous an object as a harlequin would be at a funeral. When you touch it, it begins to dribble out a pungent evil-smelling froth, and then you begin to suspect that its colours are meant to advertise this unpleasant fact to all whom it may concern. At any rate, I resolved to see if my little bear's interpretation of the matter accorded with my own, so one evening I offered him one of these " blazer " grasshoppers, whose name I may mention is *Aularches miliaris*. One smell was enough to make him turn his upper lip inside out in the most comical way. In a short time I again offered him the insect, and then he stood up on his hind legs and smacked it out of my hand with his paw in exactly the same way as he used to treat the offer of a lighted cigar. I several times afterwards brought him an *Aularches miliaris*, and the mere sight of the insect was enough to make him try to shuffle off : but if I insisted on his facing it, he would knock it out of my hand with a hearty cuff, and if I had forced it into his mouth I have no doubt he would have bitten me' (2).

Another instance among Mammalia of rapid learning by experience is that of a Slow Loris (*Nycticebus coucang*) belonging to Mr. J. M. D. Mackenzie. This animal would eat almost any insect, but there was at Maymyo, in Burma, one type of grasshopper which, having once been tasted—with unpleasant consequences to the Loris—was thereafter left untouched (387).

Experiments conducted by Phillips (469) in Ceylon on a Slender Loris (*Loris tardigradus*) provide additional evidence of discrimination, and point to the distastefulness of aposematic insects offered. This animal ate most Lepidoptera, but some moths and butterflies—notably Tiger Moths, White Ghost Moths, and Red-bodied Swallow-tail Butterflies—he would not look at, or when seized in error, they were *released immediately without being killed.*

III. EXPERIMENTAL TASTING AND HABIT FORMATION IN BIRDS

Evidence of learning and discrimination in the case of birds is given in the following section. I need only refer here to the work of Lloyd Morgan, whose classical experiments with young birds proved clearly that the choice of food depends, not upon inherited instinct, but upon individual experience. Chicks do not instinctively avoid dangerous or unpalatable objects, but strike at first with perfect indiscretion at anything of suitable size. Everything has to be examined and tested in the light of individual experience. But they have retentive memories. ' There does not seem to be any congenital discrimination ', he says, ' between nutritious and innutritious objects, or between those which are nice and those which are nasty. This is a matter of individual acquisition. They soon learn, however, what is good for eating, and what is unpleasant, and rapidly associate the appearance with the taste.' Cinnabar caterpillars, Soldier-beetles, and Lady-birds were invariably first tasted, and avoided only as a result of experience. The ability to learn rapidly, after only one or two trial encounters, was clearly shown by his domestic chicks, ducklings, and Moorhen chicks. After tasting and being stung by bees, they quickly learned to avoid these insects, and in certain cases would not subsequently touch either bees or the drone-flies (*Eristalis*) which superficially resemble them. On the other hand, if a bee had at first been swallowed with no ill-effects, a second would be eaten, and the drone-flies were not then avoided.

Dr. Julian Huxley informs me that Lloyd Morgan once told him he had experimented with young chicks, giving them grains of different sorts steeped in something nauseous, until finally he realized that he had no food available to which they were not negatively conditioned, and they were thus in grave danger of starvation in the midst of plenty.

While individual experience based upon experimental tasting plays such an important part in habit formation, the fact must not be overlooked that in certain cases the young tend to learn feeding habits by imitation of the parents. For instance, this appears to be the case with young Pied Wagtails, which are closely attended by their parents while learning to forage for themselves. During this apprenticeship, which may be seen on almost any roadside or lawn in the summer, the young notice what insects are brought to them, how they were captured, and soon acquire the necessary technique.

Crows enjoy a considerable reputation for intelligence, and in the present connexion the following observations by Lieut.-Colonel Neville Manders in Ceylon are especially relevant. He writes (390): 'I saw an old crow and two young ones on the Rifle Green this morning; one of the youngsters had hold of a bone with a piece of gristle attached to it. It was so firmly adherent that the bird could not detach it as the bone constantly moved with the bird's efforts, and eventually it gave up. Then the old bird, which had been standing by all the time, went to the bone, put its foot on it, thereby gaining a purchase, and tore off the gristle without difficulty; the young bird after two or three attempts did the same.

'An old crow had a piece of hard-boiled potato off which it was picking pieces and giving them to a full-fledged young one close by. A goodly number of detached pieces lay on the ground and attracted the attention of some other crows, which flew down and began picking them up; seeing this the youngster did likewise, though it made no attempt to do so before their arrival.'

IV. FORMATION OF THE AVOIDING HABIT BY LIZARDS

One of the earliest experiments on the rapidity of habit formation in lizards is due to Sir Edward Poulton (496), who describes the case of a Chameleon, which after attempting to eat, and being stung by one Hive-bee, would thereafter have nothing more to do with the insects, although it was a healthy specimen, feeding freely upon other (procryptic) insect-food. 'For many months after this I put bees into the cage at irregular intervals; but the chameleon's education in this direction was complete, the single experience was sufficient, and no other bee was touched.'

Describing the behaviour of a Wall Lizard (*Lacerta muralis*) when offered a Hornet Clear-wing Moth (*Trochilium crabroniformis*), Poulton has also shown how rapidly these animals may profit by experience. On the first occasion the lizard appeared highly suspicious: it examined the insect very keenly from a distance, approached it cautiously, and eventually seized it with the greatest care, 'behaving exactly as it would have done with a wasp or bee' (496). On discovering the deception, the moth was eaten without further ceremony. After a few days another moth of the same kind was offered to the same lizard; 'but the lesson had been learnt, and the insect was seized without special examination or caution, and devoured directly it was seen'.

In her experiments with lizards, Pritchett found that the black and yellowish-brown Blister-beetles (*Cantharis fulvipennis*), at first seized by *Sceloporus floridanus* and *Gerrhonotus infernalis*, were quickly dropped, and that when introduced on the following day most of the lizards had learned their lesson (529). These experiments show how acceptance or refusal of a particular insect depends upon the results of previously acquired experience—a conclusion which is supported by experiments and observations on group after group of vertebrate animals.

V. INTELLIGENCE AND DISCRIMINATION IN THE ANURA

Less experimental work bearing on the problem of adaptive coloration has been carried out with the more lowly frogs and toads, and I therefore propose to deal here with the Anura in somewhat greater detail, in an attempt to show how the mental equipment and feeding behaviour of these animals is related to the theory of warning coloration.

As a group, the Anura provide apt material for such a study, both on account of their relatively simple feeding reactions, and on account of the fact that they hunt for, and select, their food entirely by sight. The feeding reaction of a frog or toad is relatively a simple matter, being fundamentally an automatic response—a ready-made neuromuscular mechanism, whose machinery is set in motion by an appropriate stimulus provided by the sight of moving prey. Now what we must attempt to decide is this : Are these animals bound by an inflexible feeding instinct—condemned throughout their lives to snap up any object, whether it be palatable or not, which happens to stimulate the feeding reflex ? Or, alternatively, is there evidence that intelligence plays a part in the feeding habits, and that individual experience, associations, and memory step in to modify behaviour that is based upon an instinctive routine ? In short, is their feeding indiscriminate, or is it selective ?

(1) **The Mistaken View that Frogs and Toads are Indiscriminate Feeders**—The earliest experiments bearing on selective feeding in the Anura are those conducted by Butler (73) and by Poulton (494). When testing the edibility of various insects, Butler found that Frogs, after tasting and rejecting with signs of disgust the conspicuous larvæ of *Abraxas grossulariata* and *Halia wavaria*, subsequently would have no more to do with them. Poulton pointed out that tree-frogs prefer houseflies to butterflies. But the evidence for discrimination by frogs in these early tests is inconclusive. For instance, *Hyla arborea* used by Poulton refused wasps and Coccinellid beetles, but ate bees (*Apis* and *Andrena*). Other observations by Kirkland (312), Garman (200), Hargitt (228), McAtee (376), and others, to the effect that Toads are known to eat aposematic insects such as Wasps (*Polistes*, *Vespa*), Squash Bugs (*Anasa tristis*), Potato-beetles (*Leptinotarsa decemlineata*), as well as Ants and many other specially protected forms, have been cited as evidence that these creatures are more or less indifferent both to warning colours and to the unpalatable qualities which they advertise. For instance, a ' partially domesticated ' toad accepted a large number of stinging insects offered by McAtee ' although at times he showed considerable but ludicrous signs of discomfort. Not less than 30, and perhaps as many as 40 Hymenoptera were taken by this animal in about an hour. He finally left the spot, apparently to get away from a locality characterized by such extremely spicy food, which nevertheless he was apparently unable to refuse ' (376).

Hargitt, who tested Tree-frogs (*Hyla*) with various insects, came to a similar conclusion. ' The insects most commonly supplied were flies, small beetles, grasshoppers, spiders, etc. On one occasion a wasp was released in the cage and at once began to buzz about or run up the sides of the cage actively. It was but a few moments ere a specimen leaped eagerly and captured the prey. Then a most interesting performance took place. No sooner was the wasp seized than it was whipped into the mouth, and in turn stung the frog; the frog in turn showed a lively appreciation of that fact, and made an apparent effort to eject the creature; but the process of ingestion had gone too far, and deglutition was completed without further ado, nor did the frog show the least further sign of distress. On another day the operation was repeated and very much after the fashion of the preceding.' From this the author concludes: 'It may be doubted whether Amphibia show any particular discrimination based on that type of experience' (228).

Now, detailed experiments carried out in 1911 by Schaeffer (557), and in 1934 on a larger scale by the present writer, point to a very different conclusion, and prove the important influence of individual experience in leading to selective feeding. I have cited the above experiments by McAtee and Hargitt in order to show how easily false conceptions may be arrived at by insufficient data. In my own experiments with Toads, described below, during the first two days 31 out of 34 individuals (91 per cent.) together ate 86 Hive-bees. If the trials had been discontinued at this stage, what conclusion would be drawn from the experiments? Surely that bees cannot be regarded as distasteful to, or well defended against, these amphibians. Yet it is abundantly clear from continued trials that the very opposite is the case.

(2) **Avoidance Reaction in Frogs**—The investigation by Schaeffer (557) to test the facility with which Frogs learned to avoid disagreeable food (hairy caterpillars and chemically treated or electrically stimulated earthworms) throw considerable light on the feeding reactions and intelligence of these animals, in proving beyond question (1) that Frogs do not instinctively avoid unpalatable prey; (2) that they learn after a few trials to discriminate between palatable and distasteful prey; and (3) that the lesson is remembered for *at least* ten days. Referring to the rapidity of learning, Schaeffer states: '*Rana clamata* avoided hairy caterpillars after at most four trials; *Rana sylvatica* formed the habit in seven trials; *Rana virescens* formed the same habit in four trials, three on one day and one on the following day. . . .' It is interesting to note that the hairy caterpillars were refused 'while more than twenty different kinds of insects, etc., were eaten', an observation which testifies to the Frogs' powers of discrimination.

VI. FEEDING REACTIONS, HABIT FORMATION, AND MEMORY IN THE TOAD

During the summer and autumn of 1933 I carried out a detailed series of experiments on the feeding reactions, habit formation, and memory of the Common Toad (*Bufo bufo*) (116). These experiments represent an attempt to furnish reliable experimental proof of the effectiveness of the protective adaptations of Hive-bees as a means of defence against Toads: in other words, to determine whether hive-bees are acceptable or distasteful to these animals, and to discover

—if they proved distasteful—how quickly the toads learned to recognize and to avoid the insects, and whether the lesson of avoidance, once learned, is remembered.

The toads undergoing test were placed, one at a time, upon the landing-board of an active beehive. Left close beside the entrance, and facing it, the animals were allowed the opportunity to feed freely and without interference upon the outgoing and incoming workers, until each voluntarily terminated the test by jumping down, sooner or later, from the platform. Every toad was tested in this way twice daily for seven consecutive days.

In order to obtain decisive results and to avoid so far as possible errors due to chance, to climatic effect and to the variable condition of the hives, various precautions were taken: (1) the experiments were attempted on a large scale, involving 33 toads (excluding 1 which died) in a total of 714 trials, which together extended over more than forty hours; (2) the toads were divided for experimental purposes into five groups, with each of which the experiments were started on a different date and carried through independently; (3) by selecting a particular hive, out of seven available, and by choosing the time of day for the trial, according to prevailing weather conditions, it was possible to maintain tolerably constant experimental conditions as regards the activity and numbers of bees available; (4) each toad was kept for a week without food before the first trial, and was allowed no food other than the bees it ate during the week of experimentation; and (5) each was given a test feed of mealworms during the twenty-four hours following its last visit to the hives—that is to say, at the end of Experiment I.

(1) **Observations on the Feeding Behaviour of Individual Toads**—In the first set of trials, referred to as Experiment I, 34 toads were tested individually in the way described above twice daily for a week—their behaviour while undergoing test being carefully noted. I give below, by way of example, the records for a single individual, No. 18 in the series, a female 74 mm. in length.

5th September—Placed upon the platform of hive (i): the toad regarded emerging and homing bees with apparent interest: hungry, and showing no signs of fear of the insects, she flicked at and missed three bees in succession as they crawled out of the hive. At the fourth attempt she was successful, snapping up and swallowing a bee with no apparent ill-effects. Three more bees were then snapped up and swallowed in quick succession. Evidently stung by the last of these, she showed signs of discomfort—eye closure and gulping movements. Taking no further notice of the bees, she crawled to the end of the platform, frequently closing her eyes, and jumping clear at 7 minutes. Replaced on hive (i): she watched bees at the entrance closely for a few moments, and then deliberately turned round, walked away to the end of the platform, and jumped off.

6th September—On hive (i): snapped up and swallowed a bee: she was stung inside the mouth: gulping, with eyes closed, she walked backwards away from the entrance. At 3·5 minutes a second bee was eaten. At 7·5 minutes, snapping up and swallowing a third bee, she was stung again. After uneasy gulping and blinking movements, which lasted 1½ minutes, she began walking to and fro along the platform like a sentry, jumping off at 10 minutes. Replaced: she turned away and jumped at 12·5 minutes.

7th September—On hive (vii): a bee was eaten. She then backed away on being approached by another crawling bee. At 2 minutes a second bee was eaten, followed by convulsive movements of the throat and general appearance of discomfort—the toad probably being stung. Having eaten a third bee shortly 4 after this, she now appeared to be afraid of the bees as they crawled around her, three times retreating backwards when approached by the insects. At 14·5 minutes a fourth bee was flicked up and swallowed, the toad being stung on the tongue. She now again retreated before advancing bees, jumping off the platform at 16·5 minutes. Replaced: she walked to the end of the platform, and jumped clear at 18 minutes.

8th September—On hive (vii): she turned to watch two or three bees crawling about the platform, and then walked away from them without attempting to feed, jumping off the hive at 2 minutes. Replaced: bees within easy striking distance were ignored. She turned and walked away; presently, however, returning to watch the movements of the insects, but after considerable crawling about and inspection she jumped off at 4·5 minutes.

9th September—On hive (vii): she flinched at the sight of approaching bees, dropping the head, and then turned so as to face away from the bees passing through the entrance: jumped down at 2 minutes. Replaced: the toad walked away immediately, and jumped clear at 2·5 minutes.

10th September—On hive (i): she turned away at once, walking to the end of the platform, and jumping off at 10·5 minutes. Replaced: she watched several bees closely; then turned away, jumping at 12·5 minutes.

11th September—On hive (vii): several bees came within easy reach but were left untouched. She turned to watch the insects, following their movements, but hesitated to approach, walking slowly away at 3·5 minutes and jumping at 4·5 minutes, after deliberately turning away from, and crawling past, bees within close reach. Replaced, she jumped almost immediately from the hive.

After this—in a test feed given to show that the refusal of bees was due to unpalatability of the prey rather than to some other cause, such as sickness, repletion, or loss of appetite—she filled up on 36 mealworms!

(2) **Modification of Feeding Behaviour in Relation to Acquired Individual Experience**—Taking a broad view of Experiment I, perhaps the most striking point brought out is the very marked change in the behaviour of the toads undergoing test as the trials proceeded and as the creatures gained experience—a change all the more remarkable in that it became more or less apparent in every toad tested. ‘An association is formed between the appearance of the hive-bee and the stimulus of a sting or an unpleasant taste, and the modification of the feeding instinct and general behaviour is so rapid and definite that not even a casual observer could fail to notice it.

‘On the one hand we have the inexperienced, untrained toad: it sits watch-fully, as if taking in the surroundings ; catching sight of a bee, it turns to face the insect, and approaches with quick alert movements, or else advances with stealthy strides like a cat stalking a bird, pausing frequently, all the while regarding its prey with fixed attention ; the body is carried high, with the belly well raised from the ground ; every movement of the quarry is watched and followed, the head being bent from side to side, or the body turned, so as always to keep the objective in full view. When within striking range the toad pauses in its stride and points like a well-trained spaniel at the sight of game—the head well raised, the back arched, and the body braced in readiness. Then with a rapid forward lunge and an almost invisible flick of the tongue the bee is whipped into the mouth.

'Compare with this the toad that has learned its lesson : at the sight of a bee it turns its back towards the enemy, then crouches in a corner, with the body depressed and flattened, the head bowed, the eyes closed and withdrawn into the head, and the legs sprawling sideways : remaining thus inert, it shows no further sign of interest in the insects. If approached by a bee it displays great uneasiness, flinching, shrinking or jumping away as if in dread of it, now and then winking or wiping the mouth with the fore limb as if to remove an unpleasant taste ; or again, the toad may show signs of extreme fear, going into contortions, jumping about in an excited manner, wiping imaginary insects off its back with vigorous sweeping movements of the feet, and retreating from the enemy at top speed.

'Finally, the well-trained toad is offered mealworms at the termination of the experimental tests. There is an immediate return to normal feeding behaviour. Almost at once the toad manifests renewed interest in the moving insect-food, and fear and hesitation are replaced by the usual eager hunting movements, the intent watching, the rapid advance, and disposal of prey.'

(3) **Rapidity of Habit Formation**—Let us now turn, for a moment, to the actual data. Out of the 34 toads tested, 31 (91 per cent.) accepted 125 bees during the week. But it is the daily distribution of this numerical record that is so significant : these are the figures : 5 7

1. Number of toads [1] which ate bees : 25, 16, 10, 6, 5, 3, 0
2. Number of bees eaten : 45, 41, 18, 10, 8, 3, 0

The drop from 41 bees eaten on the second day to 18 on the third is striking.

Examining the records for *individual* toads—a summary of which is given in Table IX—we find considerable variation in the rate of learning, whether this is estimated by time, by the number of bees eaten, or by the number of internal stings received before the habit of avoidance was established. It is noteworthy that *even the slowest toads had learned their lesson by the seventh day*, on which not one of the 33 individuals which completed the tests would touch a bee. Another very interesting fact is that '*out of 33 toads used for the experiment no fewer than 10 individuals learned to avoid the bees entirely after a single trial acceptance* ; in 9 of these cases a single bee was eaten at the toad's first visit to

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[1] Omitting No. 29.

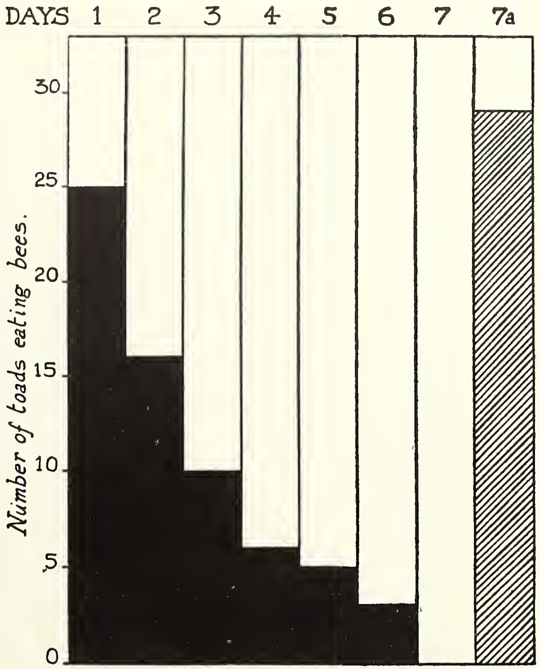

FIG. 57.—Showing the number of toads which accepted bees (black) on seven consecutive days, and the number which accepted mealworms (shaded) at the conclusion of the experiment

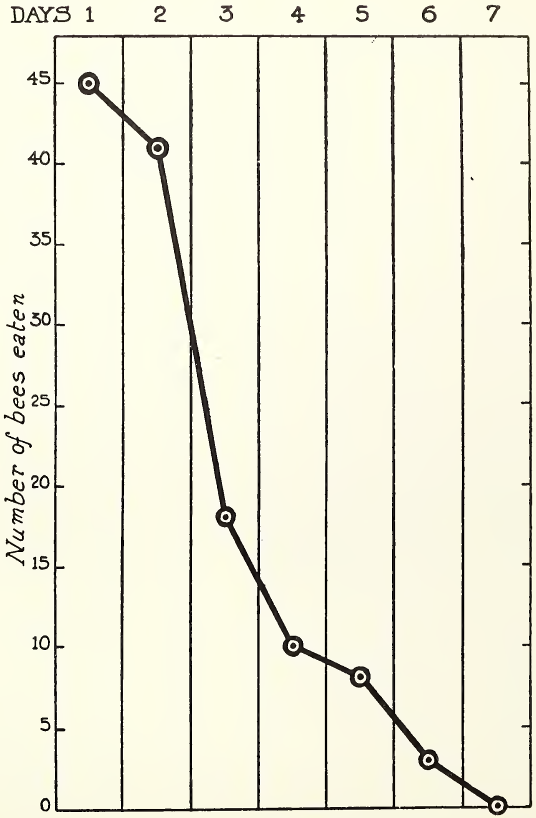

FIG. 58.—Showing the number of bees eaten by the thirty-four toads on seven consecutive days

the hive, and each on subsequent visits throughout the week would have nothing more to do with the insects'. These results appear all the more remarkable when we remember that the toads were hungry (having had no food other than bees for at least a fortnight), a condition shown by the test-feed of mealworms offered as a check after the experiment, when 29 of the toads ate a total of 444 mealworms (see text figure 57).

(4) **Permanency of the Association**—With the object of testing the memory of toads which had previously learned to avoid bees, a second series of trials (referred to as Experiment II) was carried out with 18 toads which had completed Experiment I a fortnight earlier, and which in the interval had been kept without food. As before, a test-feed of mealworms was given at the termination of the experiment. The results of these and of the previous trials are condensed in Tables VII, VIII and X on pages 287 to 289.

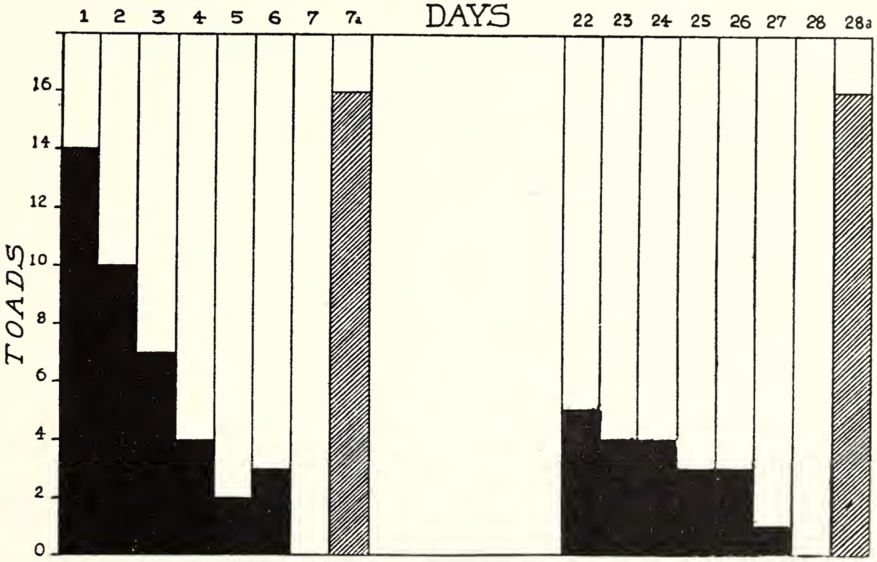

FIG. 59.—Showing the daily number of toads (groups C–E) which accepted bees (black) throughout Experiments I and II, and the number which accepted mealworms (shaded) at the conclusion of each experiment

If we examine these data, comparing the figures for the two weekly experimental periods, a number of interesting points will be noted. In the first place, the total number of toads which accepted bees is reduced from 16 to 9, and the total number of bees eaten from 87 to 36. These differences, as shown by the successive daily records, is clearly brought out in text Figures 59 and 60.

Secondly, if we compare the rate of learning by *individual* toads in the two experiments, it will be seen (1) that in no single instance were more bees eaten by a particular toad in the second experiment; (2) that, on the other hand, with the exceptions of No. 25 which ate one bee during each set of trials, and of Nos. 17

and 19, which refused the insects throughout, every individual toad showed an improvement by a diminished number of trial tastings necessary to re-establish complete avoidance; (3) that in several cases the improvement is very marked (as in Nos. 22, 23, 26, and 27); and (4) that the number of toads altogether refusing bees throughout the respective experiments rises from 2 in Experiment I to 9 in Experiment II.

These experimental results appear the more striking when we remember that with the exception of a test-feed of mealworms offered immediately on the termination of Experiment I, no food other than bees had been available for a month before the second set of trials was begun, and that nothing at all had been eaten for fourteen days, so that the toad's appetite was considerably keener than at the commencement of Experiment I, which was undertaken after a fast of only one week.

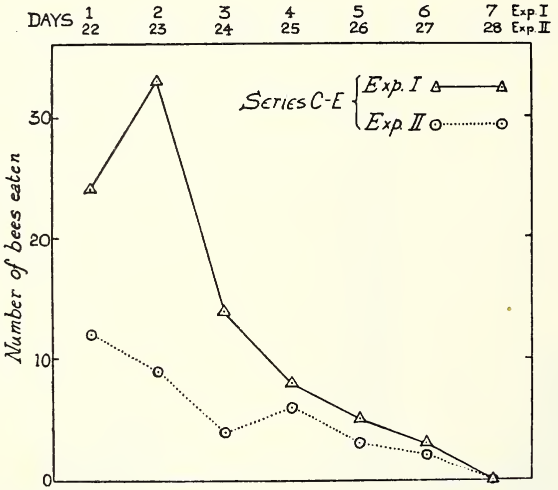

FIG. 60.—Showing the daily number of bees eaten by toads undergoing memory test in the course of Experiments I and II

In short, we are led to the following conclusions: (1) that acceptance or refusal of hive-bees depends largely upon the previously acquired individual experience of the toads; (2) that there is no instinctive avoidance of unpalatable prey—inexperienced toads readily accepting bees as food; (3) that individual toads appear to differ widely in intelligence and rate of learning; (4) that even under starvation conditions, and in spite of progressive hunger, these animals learn in a few trials (in ten cases only a single experience was necessary) to refuse and to avoid bees entirely, though other insects (mealworms) are readily accepted; (5) that the lesson of avoidance, once learned, may be remembered for at least a fortnight; (6) that toads recognize a difference in palatability, and are able to discriminate between hive-bees and mealworms; and (7) that hive-bees are highly distasteful to, and in general well defended against, predatory attack by toads.

TABLE VII

SHOWING THE NUMBER OF BEES EATEN BY INDIVIDUAL TOADS OF GROUPS C, D AND E ON EACH OF SEVEN CONSECUTIVE DAYS DURING EXPERIMENTS I AND II RESPECTIVELY

	EXPERIMENT I									EXPERIMENT II								
Days :	1	2	3	4	5	6	7		7–8	22	23	24	25	26	27	28		28–29
Toad No.	Bees eaten							Total	Meal-worms eaten	Bees eaten							Total	Meal-worms eaten
16	0	4	0	0	0	0	0	4	21	0	0	0	1	0	0	0	1	8
17	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	6
18	4	3	4	0	0	0	0	11	36	3	2	1	2	0	0	0	8	38
19	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	3
20	1	0	0	0	0	0	0	1	12	0	0	0	0	0	0	0	0	12
21	2	6	1	0	0	1	0	10	24	4	4	0	0	0	0	0	8	19
22	1	4	1	0	0	0	0	6	0	0	0	1	0	0	0	0	1	11
23	2	3	2	0	0	0	0	7	19	0	0	0	0	1	0	0	1	16
24	0	1	0	1	0	0	0	2	29	0	0	0	0	0	0	0	0	23
25	1	0	0	0	0	0	0	1	18	0	0	1	0	0	0	0	1	10
26	4	5	3	1	3	1	0	17	4	1	2	0	3	0	0	0	6	0
27	1	3	1	4	2	1	0	12	11	3	1	0	0	1	0	0	5	16
28	2	3	2	2	0	0	0	9	0	1	0	1	0	1	2	0	5	0
30	1	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	10
31	2	0	0	0	0	0	0	2	7	0	0	0	0	0	0	0	0	5
32	1	0	0	0	0	0	0	1	12	0	0	0	0	0	0	0	0	11
33	1	1	0	0	0	0	0	2	6	0	0	0	0	0	0	0	0	13
34	1	0	0	0	0	0	0	1	9	0	0	0	0	0	0	0	0	12

TABLE VIII

SHOWING (i) THE DAILY TOTAL NUMBER OF TOADS WHICH ACCEPTED BEES, AND (ii) THE DAILY TOTAL NUMBER OF BEES EATEN, BY GROUPS C, D AND E DURING THE SEVEN CONSECUTIVE DAYS OF EXPERIMENTS I AND II RESPECTIVELY

Days :	1	2	3	4	5	6	7	7–8
(i)	(i) Number of toads eating (a) bees							(b) mealworms
Experiment I . . .	14	10	7	4	2	3	0	16
Experiment II . . .	5	4	4	3	3	1	0	16
(ii)	(ii) Number of (a) bees eaten							(b) mealworms eaten
Experiment I . . .	24	33	14	8	5	3	0	219
Experiment II . . .	12	9	4	6	3	2	0	213

TABLE IX

EXPERIMENT I. SUMMARY OF DAILY EXPERIMENTAL DATA RELATING TO GROUPS A, B, C, D AND E

Toad No.	1	2	3	4	5	6	7
1	1,† 1*	..	..	1	..	..	..
2	1, 1, 1, 1*	1, 1†	1*	1*	1	..	..
3	1††	1°	1*	°	..	..	..
4	††	1*°	..	..	1*	..	..
5	1, 1	1, 1*	..	..	..	..	..
6	1, †††°	..	..	†°	..	..	..
7	..	1*	..	..	..	..	..
8	1, 1,° 1††°	..	..	..	†°	..	..
9	1	..	..	..	1*	..	..
10	1*††°	..	..	†	..	..	..
11	1, 1*	..	..	..	..	..	..
12	..	..	..	..	..	..	..
13	†1*°	..	..	..	††°	..	..
14	°	1	1	..	..	..	..
15	1	..	††°	..	..	..	..
16	..	1, 1, 1, 1	..	..	..	..	..
17	..	..	..	..	..	..	††(11 +)
18	1, 1, 1, 1*	1*, 1, 1*	1, 1*, 1, 1*	..	..	..	..
19	††	..	..	..	..	..	..
20	1*	..	..	°	..	..	..
21	1, 1*†	1, 1*, 1, 1, 1, 1	1*	°°	..	1*†°	°
22	1	1, 1, 1, 1	1	°	..	†	††
23	1, 1	1, 1, 1*	1, 1	..	..	°	..
24	††	1	..	1,°	..	..	..
25	1,†	..	..	..	..	°	..
26	1, 1, 1, 1	1*, 1, 1*, 1, 1	1, 1, 1	1*	1, 1, 1	1	..
27	1†	1, 1, 1	1	1, 1* 1, 1	1, 1*	1†	..
28	1*, 1	1*, 1, 1*	1, 1	1, 1*	..	..	..
(29	1, 1	..	1	—	—	—	—)
30	1	..	..	..	..	..	..
31	1, 1	..	..	..	..	††	..
32	1*	°	..	..	..	..	..
33	1*	1*	..	..	..	..	..
34	1*†°	††	..	..	..	..	..

'1' indicates that a bee was snapped up and swallowed.
* indicates that the toad was apparently stung internally after swallowing a bee.
† indicates that the toad received an external sting.
° indicates that the toad was mobbed and hustled off the hive.

TABLE X

SHOWING THE RATE OF LEARNING BY INDIVIDUAL TOADS IN EXPERIMENTS I (PART) AND II RESPECTIVELY, AS INDICATED BY THE NUMBER OF EXPERIENCES NECESSARY TO ESTABLISH THE HABIT OF AVOIDANCE

Toad No.	Bees eaten		Toad No.	Bees eaten	
	Exp. I	Exp. II		Exp. I	Exp. II
16 . .	4	1	25 . .	1	1
17 . .	0	0	26 . .	17	6
18 . .	11	8	27 . .	12	5
19 . .	0	0	28 . .	9	5
20 . .	1	0	30 . .	1	0
21 . .	10	8	31 . .	2	0
22 . .	6	1	32 . .	1	0
23 . .	7	1	33 . .	2	0
24 . .	2	0	34 . .	1	0

9. EVIDENCE OF SELECTIVE FEEDING BY VERTEBRATE ENEMIES IN A STATE OF NATURE

> Is not the earth
> With various living creatures, and the air,
> Replenish'd ; and all these at thy command,
> To come and play before thee ? Know'st thou not
> Their language and their ways ? They also know,
> And reason not contemptibly. With these
> Find pastime.
>
> MILTON

Various attempts have been made by critics of the theories of warning coloration, mimicry, and protective resemblance to belittle the psychological factors controlling the selection of prey, and to magnify the importance of ' availability ' in determining the diet of different animals. We have already seen that the theories of adaptive coloration depend essentially upon two classes of evidence, namely, that a certain relationship exists between coloration and palatability in the animals liable to be preyed upon ; and that different insectivorous or carnivorous enemies discriminate in the choice of their prey. Palatability or distastefulness of the prey, and differential preferences of the predator, lie at the root of the matter. Evidence regarding recognition, and active selection or rejection of prey by different classes of wild predators, is therefore of importance to our subject, and it is this evidence that I now propose to consider.

I. FOOD PREFERENCES EXHIBITED BY MAMMALS

Recent studies like those of Katz (301) and Morton Jones (291) indicate more and more clearly the considerable part played by psychological factors in controlling feeding behaviour. For example, Katz found that monkeys belonging to the genera *Cercopithecus* and *Cebus* showed definite predilections for particular food-stuffs. When presented with seven kinds of food simultaneously, the same monkey would nearly always eat them in the same order ; and only slight differences in the rating were found between individuals of the same, or even of the two species. The general order of preference was as follows : (1) grape ; (2) banana ; (3) apple ; (4) carrot ; (5) lettuce or cabbage ; (6) nuts ; (7) bread.

Further experiments showed that the rating of particular foods is modified by the nature of the previous meal. For instance, if first allowed to eat a large quantity of grapes, this item might be shifted from the first to the last place on the menu when the monkey was offered the usual mixture of seven food-stuffs. Whatever was first offered in quantity was subsequently rated lower or altogether rejected.

Such behaviour shows how little availability has to do with the result. On the contrary, Katz's experiments yielded evidence proving the close similarity of the monkeys' food preferences to those of a young child; and the author states: 'Their feeding behaviour reminds us of our own table manners. . . . Generally speaking, all the rules controlling the feeding behaviour of monkeys have their parallels in human beings.'

The extensive and detailed experiments carried out in Tanganyika by Professor G. D. Hale Carpenter on the relative edibility of insects—as indicated by the feeding behaviour of a monkey—furnish valuable evidence on the psychology of feeding. Of his numerous observations, recorded in an important paper published in 1921 (79), it will here be possible to mention only one or two which prove in a most conclusive manner that his monkey—a species of *Cercopithecus*—recognized a difference in palatability between various insects which it encountered when out hunting with its master, and that different species were eagerly pounced upon, or neglected, according to its experience of their properties as food. Various procryptic grasshoppers, namely, *Cyrtacanthacris ruficornis*, *C. cyanea*, *Catantops decoratus*, and *C. melanostictus*, formed the staple diet of this animal; however, there were several aposematic species which it would not eat on any account, and towards which its behaviour was illuminating. One of these was the Acridiid *Dictyophorus productus*, a heavy, bloated, sluggish insect, which freely exposes itself to view—in colour grey with bright red on the abdomen. Once when the monkey saw from a distance that a grasshopper was being brought to him, he became very excited: however, on getting a nearer view of the *Dictyophorus* his excitement subsided. He took it up from the ground, smelt it, and put it down again. To encourage him, Carpenter pretended to taste it. The monkey then licked it, only to get a taste of the yellow froth which it exuded. He then shook his head as if trying to get rid of a disagreeable taste and would have no more to do with this grasshopper. Shortly after this he seized with great eagerness and ate a huge procryptic grasshopper (*Cyrtacanthacris cyanea*) measuring some four inches in length. Four days later, before he had eaten anything, he was offered another *D. productus*: this was examined and licked, then dropped uninjured. When out hunting ten days after this, the monkey caught and ate another huge *A. cyanea*, absolutely ignoring a *Dictyophorus* which was on the ground just in front of him.

Similar refusal is recorded in the case of *Zonocerus elegans*, a large Acridian, conspicuous, clumsy and living freely exposed, bright yellowish-green in colour with undeveloped reddish forewings and with antennæ ringed alternately black and orange. When offered one of these showy morsels, the monkey just looked at it, and appeared to take no more notice. He was then shown another large Acridian, procryptic in colour: leaping up at once, he seized it, and ate it with extreme haste. Afterwards he went back to the *Zonocerus*, which he smelt and touched, but would not taste. Lamborn's more recent observation, quoted on page 256, will be recalled as referring to an immature example of this species which proved too spicy a mouthful for his kitten.

I have already mentioned the evidence of Alcock, whose Himalayan Bear having once sampled an evil-smelling grasshopper (*Aularches miliaris*) would never afterwards have anything to do with the insect.

Much further evidence of discriminative feeding, in the case of insectivorous bats, will be found in the important paper by Sir Edward Poulton, to which I have referred above (p. 273).

II. DISCRIMINATION AND SELECTIVE FEEDING BY BIRDS

I have already alluded (p. 265) to Belt's observation that his fowls and ducks refused to touch a vividly coloured red and blue frog when it was offered them. As a further example of deliberate avoidance of highly conspicuous frogs by birds, I may mention a very interesting case for the particulars of which I am indebted to Professor Graham Kerr. This refers to the South American Seriema or 'Crested Screamer' (*Cariama cristata*)—a large, stately creature, in outward appearance and in habits not unlike the African Secretary Bird, to which, however, it is quite unrelated. It is chiefly diurnal, feeding in open *campos* on a mixed diet of snakes, lizards, small mammals, insects, and berries. One of these birds was kept as a pet in the Paraguayan Chaco by Professor Graham Kerr. Though perfectly tame, the bird enjoyed complete liberty in the field, and being very fond of frogs, it was accustomed to go for walks with its owner, in anticipation of the amphibian titbits which were to be discovered beneath the logs and stones which were overturned for its inspection. Its preferences were thus observed under practically natural conditions. The various procryptic frogs unearthed were eagerly eaten. But the Seriema was under no misapprehension as to the unpalatability of the black and yellow and scarlet *Atelopus stelzneri*. One look was sufficient! It could never be induced to have anything to do with this highly coloured and highly flavoured morsel.

Further direct field evidence of preferential feeding and discrimination in birds is given by Mottram (427). He points out, for instance, that Swallows exhibit a great liking for the sub-imago of the Ephemeridæ, 'either taking the insects whilst resting on the water or after they have risen into the air. It is rare to see a hatch of these insects without these birds hunting them, so much so that by watching these birds the angler knows when to begin fishing.' In marked contrast Swallows have only on a very few occasions been observed to take the Black Gnat (*Bibio johannis*). 'A difference in the ease with which they may be captured cannot account for the selection, because the birds take other insects whose flight is quite as erratic . . . and also the "Black Gnat" is often over the water in such dense swarms that the birds would have but to fly through them in order to obtain a mouthful, a method of feeding which they often employ for the capture of many small insects which swarm in the air.' Similar observations were made on the choice of food by the Reed Bunting, which is an adept at picking the Ephemerid sub-imago off the water, but which 'has never been seen taking *B. johannis* (Black Gnat)'.

Some interesting observations by Mrs. H. H. Brindley (142) clearly show

how different birds recognize and deliberately avoid unsafe prey. She says: 'I attempted last summer to feed Coots with wasps, insects which are commonly held to be distasteful to most birds, and recognized as such by their coloration. Living wasps, floating on the water, were not touched except twice when the birds were excited with fighting for other food. Then in one case a Coot, and in the other a Mallard, picked up a wasp but immediately rejected it, shaking and wiping their bills. Bread with a living wasp attached to it was invariably passed over; and that this was not simply due to distrust of unknown food was shown by the fact that when a split raisin was put on the bread instead of the wasp, the whole crust was taken at once, fruit and all.'

A remarkable series of observations by Kluijver (313) on the biology of the Starling (*Sturnus v. vulgaris*) in Holland provide important indirect evidence of discrimination against unpalatable insects by these birds in a state of nature. Working over a period of three years, Kluijver obtained no fewer than 17,933 food animals, including 16,484 insects, from the gullets of nestlings which had been prevented by means of a neck-collar (worn for short periods) from swallowing the food brought them by their parents. In the material thus obtained, the 3,307 Lepidoptera included only one Burnet Moth (*Zygæna filipendulæ*) and two Cinnabars (*Hipocrita jacobææ*); the 4,490 Coleoptera included only two Lady-birds (*Coccinella bipunctata* and *C. conglobata*); and the 799 Hymenoptera only one fossorial wasp (*Crabro cribrarius*) and not a single bee or Vespid. Such omissions in the pabulum are significant, especially when it is realized that the records extended over three seasons, that the feeding territory of the main colony reached 100 acres, and that the types of insect referred to are both abundant and conspicuous in nature.

Much further evidence of discrimination by birds will be found in Morton Jones' investigations already referred to. In particular, we may mention here the preferences shown by Cardinals, Redwings, Grackles, and other birds for different types of seed and grain. In two experiments eight kinds of seed—including sunflower, maize, hemp, kafir, wheat, yellow millet, buckwheat, and rapeseed—were exposed first separately in measured quantities, and then thoroughly mixed together, to the visits of birds. The items were subsequently tabulated in the order of quantities consumed. In his discussion of the results, Morton Jones writes: 'The plain implication of these two experiments is that bird-preference decides acceptance, whether the food-items are separate or mixed; that choice for acceptance must be based upon promptly recognized visible differences in food-items of the same general character; and that under the conditions of experiment, *food preferences* rather than either *quantity* or *availability* decided the order of acceptance' (291).

No useful purpose would be served by here recording further examples of avian discrimination. Valuable evidence on the subject will be found by consulting the work of Lloyd Morgan (414), Beal (28, 32), Swynnerton (609), Pocock (482), and other authorities. But before passing on to the next group, I must in conclusion refer to a very remarkable case of discrimination, namely, the deliberate selection of the harmless drones of the Honey-bee by different birds. For indisputable evidence on this point we are indebted to the veteran economic ornithologist Beal. In his investigation of the food of the Cliff or Eaves Swallow (*Petrochelidon lunifrons*) this authority records (28) 34 Honey-bees from 11 out of 123 stomachs: all were drones, without a trace of a worker. Records in a later paper (32) increase the number of stomachs examined to 375. Here Beal states that ‘ the remains of 35 honey-bees (*Apis mellifera*) were identified in 13 stomachs. More were probably present but unidentifiable. All were males or drones. To what extent birds select their food has long been a matter of conjecture. When it is considered that the worker bees in the hive far outnumber the drones, it is evident that the foraging birds must meet many workers where they encounter a single drone. Evidently the drones are deliberately selected by the Eaves Swallow, for not a trace of a worker bee was found in any stomach.’ A similar selection by the Purple Martin (*Progne subis*) was noted. Five stomachs, out of 205 examined, contained the remains of Honey-bees, of which there were 11—drones all of them. Figures given elsewhere by Beal (29) indicate that the King-Bird (*Tyrannus tyrannus*) also picks out the drones in preference to the workers.

Finally, apart from individual discrimination of the type we have been considering, it must be remembered that different *species* differ markedly in their food preferences. I do not here refer to differences of feeding habits dependent upon structural adaptations; but rather to those *differential food preferences in related species* which are so familiar and so widespread a feature in the habits of wild birds from almost any type of habitat.

For instance, the Song-Thrush and the Blackbird constantly seek for prey in similar surroundings of garden and pasture, but the prey which they seek is not similar. The former habitually takes snails (*Helix nemoralis* and *H. aspersa*) as a regular part of its diet; the latter rarely touches them: the former prefers earthworms to fruit; the latter fruit to earthworms. Or again, Cuckoos feed on insects in an environment which supports Meadow-Pipits, Skylarks, Wheatears, and many other insectivorous birds, yet the latter rarely eat spiny caterpillars, while the Cuckoo is well known regularly to do so. Such differences are found everywhere—among birds of the hedgerow in Wren and Hedge-Sparrow; among birds of the tree-top in Carrion Crow and Rook; among birds of woodland and moorland, mountain and meadow, marsh and river—and they furnish an additional class of conclusive evidence. In these several types of environment, the prey *available* is the same while the prey *eaten* is different—a difference clearly due, not to ‘ proportional predation ’, but to active choice.

III. DISCRIMINATION BY LIZARDS

Turning now to another important group of predators, the Lacertilia, I have already referred to Poulton's observations on discrimination by a Chameleon and Wall Lizard, and to Pritchett's experiments on the food preferences of *Sceloporus* and *Gerrhonotus*.

A record of selective feeding by house geckos—which is all the more convincing in that it relates to the behaviour of wild animals—is given in the following note by Mr. W. A. Lamborn (327): ' I was much interested to watch last night the attitude of some Geckos on the ceiling of my dining-room to some moths, the selection exercised being so very definite. The moth No. 28 (*Hypsa* (*Asota*) *alciphron*) sat for a very long time at one place, where three separate Geckos came up and inspected it, but passed by on the other side, not molesting it. Neither did the moth move at all. The Geckos made frantic rushes at other sitting moths, occasionally securing one, but many were too alert for them.'

In Tanganyika Carpenter also notes (87) that a Gecko frequenting the walls of a house, where it was observed preying upon nocturnal insect visitors, would pay no attention to a conspicuous Carabid—dark in colour, with orange patches—which among many other beetles were attracted to the lights. Further evidence of a similar nature has recently been given by Sevastopulo in the case of Geckos (*Hemidactylus*) in Calcutta (565).

Darlington's experiments (134) on mimicry in Cuba, to which I have referred on page 413, must also be mentioned here, as affording striking evidence of discrimination by lizards (*Anolis sagrei*) in the choice of palatable and rejection of unpalatable beetles from a mixed assemblage of aposematic, mimetic, and non-mimetic species. These observations support the conclusion that lizards are selective, rather than indiscriminate, in their feeding habits, that they associate appearance with taste.

IV. DISCRIMINATION BY SNAKES

It is, of course, well known that (as with birds and other groups) different species of snakes exhibit preferences for different kinds of food, and that some are very specialized in their feeding habits. For instance, the habit of frog-eating is one that has arisen independently in many unrelated genera, and is of wide occurrence, especially in the tropical and sub-tropical regions of both Old and New Worlds.

Thus, in Africa the arboreal Leaf Snakes, such as *Chlorophis neglectus*, the semi-arboreal Water Snakes, such as *Albabophis rufulus*, and Grass Snakes, such as *Natrix olivacea*, are known to be confirmed frog-eaters (20, 111, 444). In India *Dipsadomorphus* has adopted similar habits, apparently preferring small frogs to all other food (144). In Australia *Dendrophis*, a strictly arboreal genus, feeds exclusively upon lizards and ' such batrachians as can be found among the branches, i.e. small species of Hyla ' (144). In the Neotropical region the arboreal genera *Leptophis* and *Herpetodryas* likewise subsist mainly upon a batrachian pabulum.

Similarly other genera have developed a tendency to specialize in other types of diet, such as other snakes, or lizards and birds, or birds' eggs, or insects. Apart, however, from a knowledge of general food preferences such as these, little is yet known of *individual* preference and power of discrimination in snakes. What we have to consider is this: Do these frog-eating species (for instance) exhibit particular preferences? Can they discriminate between the more and the less palatable prey?

Unfortunately this is a subject which has received little attention; and on this account the observations quoted below are of particular interest. In his Notes on the Batrachians of the Paraguayan Chaco, Budgett describes the food preferences of a grass snake, which was able to discriminate between palatable and unpalatable batrachians. Referring to an agile olive-green frog named *Paludicola signifera*, he writes: 'I put this species into a cage in which were many brightly coloured frogs, including *Phryniscus nigricans* [*Atelopus stelzneri*] and also *Phyllomedusa hypochondrialis*. In this cage was also a small grass snake. Hitherto it had taken no interest at all in the gaudy frogs in its cage; but as soon as the little *Paludicola* made its first spring, it was caught in mid-air by the snake.' It is only necessary to add here that the coloration of *Atelopus stelzneri* and *Phyllomedusa hypochondrialis* is in each case typically aposematic; that of the former—a brilliant toad-like species—being black above irregularly spotted with yellow, and black beneath with scarlet blotches, the palms of the hands and soles of the feet being scarlet; while in the latter—a conspicuous grass-frog—the back is brilliant green, grey or blue, the belly white, and the flank scarlet with transverse bars of black.

I have referred above (p. 267) to an observation of Gadow's which strongly supports the view that snakes and other reptiles discriminate in the choice of available prey. Various snakes, water tortoises, and crocodiles which he kept in a large vivarium never molested his Fire-bellied Toads (*Bombinator igneus*), although no other frog or newt in the pond could escape being eaten.

Another striking piece of evidence is afforded by Dr. R. L. Ditmars, who carried out in New York Zoological Park a valuable experiment to test the powers of discrimination in the King Cobra (*Naia bungarus*). 'To test the assertion that *N. bungarus* feeds but seldom upon the Viperine snakes, possibly possessing an instinctive dread of the deep wounds liable to be inflicted by the fangs of such reptiles, the following experiment was conducted.

'A large, thick-bodied, harmless water snake (*Tropidonotus taxispilotus*), and a poisonous water moccasin (*Agkistrodon piscivorus*), of much the same proportions, were selected for the experiment during a period when the big cobra was voraciously awaiting its weekly meal of a living snake. The door of the cage was rolled back, and the poisonous snake thrown inside. The cobra made the customary rush for the food, but upon reaching the snake paused abruptly.

'This was the first time in the feeding of this king cobra in our Reptile House that he failed immediately to seize his victim and begin to swallow it. The moccasin was permitted to remain in the cage for about five minutes, during which time the cobra reared slightly from the door, and regarded it intently. To ascertain whether the cobra was hungry, a common striped snake was placed in the cage. It was grasped and swallowed without hesitation.

'The moccasin was again introduced. There was the same rush, and the same careful examination of the newcomer. This time, annoyed by the unceremonious treatment that it had received, the pit-viper showed fight. Upon this display of hostility the cobra backed off hurriedly, nervously dilating its hood, and rearing upward. The moccasin was finally removed unharmed, and the large, harmless water snake was quietly placed in the cage. To the human observer it matched the moccasin closely, and made a show of temper considerably more emphatic than the former, but the cobra attacked it without an instant's hesitation and soon swallowed it. This experiment was repeated, and always with the same result. The cobra appeared to distinguish instantly the dangerous character of the poisonous snake ' (146).

V. FOOD PREFERENCES AND DISCRIMINATION IN ANURA

So long ago as 1887 Poulton referred to the food preferences exhibited by tree-frogs. When specimens of *Hyla arborea* were presented with flies and butterflies (which latter are ' dusty unsatisfactory things to eat ') they manifested a distinct preference for the former. ' There is a most extraordinary difference in the behaviour of such a Frog in the presence of a Housefly and of a Butterfly respectively, and in fact the latter is often disregarded ' (494). Other experimental evidence bearing on discrimination in frogs and toads has already been referred to under an earlier heading.

We must now pass on to consider a further very important class of evidence, namely, that furnished by the stomach and intestinal contents. This method, when carried out on a sufficiently large scale, gives us an easily obtained and reliable record of the kinds of prey actually eaten by a species in nature.

(1) **Evidence Based upon the Comparative Examination of Stomach Contents**—In this connexion, perhaps the most satisfactory method of approaching the problem of discrimination is by the comparative examination of the stomach contents of predatory forms living in the same habitat, where the same food is available for different species. If predaceous animals are indiscriminate feeders, and if availability be such an all-powerful factor as Dr. McAtee supposes, we should, in such circumstances, expect to find close agreement in the kinds of prey captured. Actually, striking differences are observed.

For example, in the case of Anura, in different genera taken under uniform conditions and in the same habitat, the food is found to differ markedly. For example, a comparison of the prey recovered from 17 frogs (*Rana temporaria*) and 45 toads (*Bufo bufo bufo*) collected at the same times and from the same area of heath land association at Land's End in the summer of 1932 showed the following striking dissimilarity in the main food items :

TABLE XI

Food	*Rana temporaria* (17)	*Bufo bufo bufo* (45)
Mollusca	25·4 per cent.	0·6 per cent.
Lepidoptera	13·2 ,,	2·4 ,,
Diptera	9·2 ,,	0·9 ,,
Formicidæ	0·4 ,,	41·6 ,,

The differences are shown graphically in text figure 61.

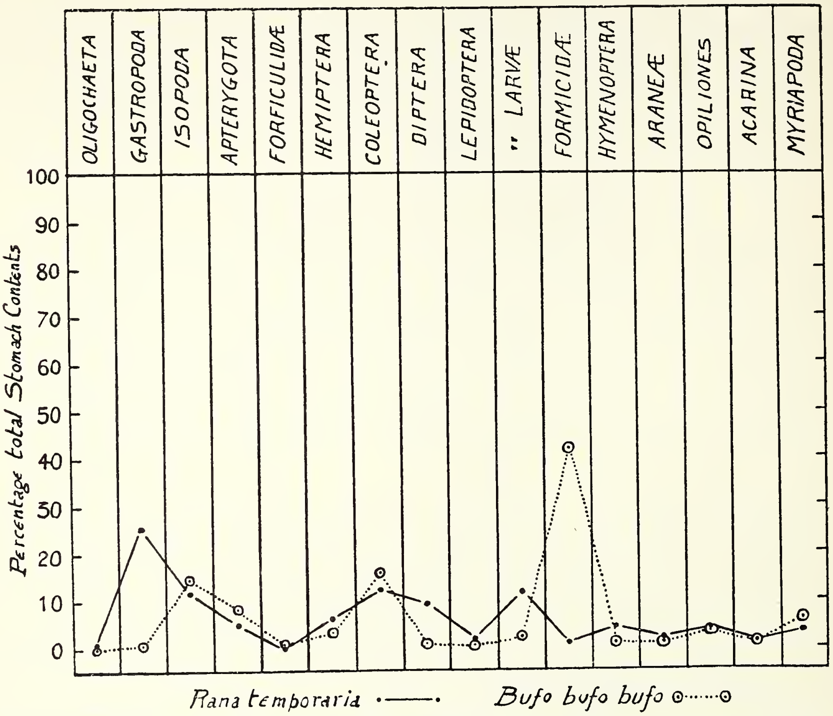

FIG. 61.—Food preferences of *Rana temporaria* and *Bufo b. bufo*, as shown by percentage analysis of stomach-contents

The differences exhibited by these species in their relations to ants are especially striking. The toad is a keen ant-catcher: the frog will hardly touch one, except incidentally. Such, at any rate, are the conclusions at which I have arrived after examining the alimentary tracts of some 634 frogs and toads, collected over a period of several years, taken at almost every hour of the day and night, from different localities and from different types of habitat. The actual figures are as follows:

TABLE XII

Species	Predators			Prey		
	Number of Stomachs examined	Number of Stomachs containing Ants	Per cent.	Total Number of Food-animals	Number of Ants	Per cent.
Bufo bufo bufo	352	145	41·2	8694	4239	48·7
Rana temporaria	282	8	2·8	1120	9	0·8

Many of these frogs were taken in situations where ants abounded; and a considerable number were captured feeding in close company with toads whose stomachs were crammed with the insects. Yet only in a single frog's stomach were two ants found, and one in each of seven others (out of 282 examined). What a contrast is presented by the toad, who relishes this spicy pabulum—as will appear from the following records of ants recovered from nine toads which contained 112, 112, 117, 138, 172, 210, 251, 341, 363 specimens respectively.

In another food item, namely Mollusca, the differences are almost as remarkable. Slugs and snails form an important element in the frog's diet: the toad touches them only occasionally:

TABLE XIII

Species	Predators			Prey		
	Number of Stomachs examined	Number of Stomachs containing Mollusca	Per cent.	Total Number of Food-animals	Number of Mollusca	Per cent.
Bufo bufo bufo	352	26	7·4	8694	32	0·4
Rana temporaria	282	84	29·8	1120	226	20·2

The highest figure for individual toads is two in a stomach, while frogs commonly contained from four to seven specimens, and I have one record of eighteen snails (*Trichia subvirescens*) from a single stomach.

Figures such as the above show very clearly how a comparative study of predatory habits points to selective discrimination in the choice of food.

Passing on to consider, for a moment, the food habits of tree-frogs in Portuguese East Africa, we find once again marked dissimilarity in the prey of two species—*Hyperolius bayoni* and *Megalixalus fornasinii*—living side by side in a common environment and captured under generally like conditions. Both species are approximately of the same size; both were frequently taken together in similar situations and on the same type of vegetation; both were collected and examined in large numbers from the same locality. Yet the main food items were distributed in the following unequal manner among the 110 and 360 stomachs examined:

TABLE XIV

Food	*Hyperolius bayoni* (110)	*Megalixalus fornasinii* (360)
Hymenoptera	96·2 per cent.	11·6 per cent.
Hemiptera	1·6 ,,	46·3 ,,
Coleoptera	1·3 ,,	7·1 ,,
Diptera	·4 ,,	26·3 ,,
Lepidoptera	·2 ,,	4·8 ,,

It appears from these observations that *Hyperolius bayoni* is a specialized ant-eater—in fact the 110 specimens which I examined had eaten little else: on the other hand, the relations of *Megalixalus fornasinii* to ants are very different:

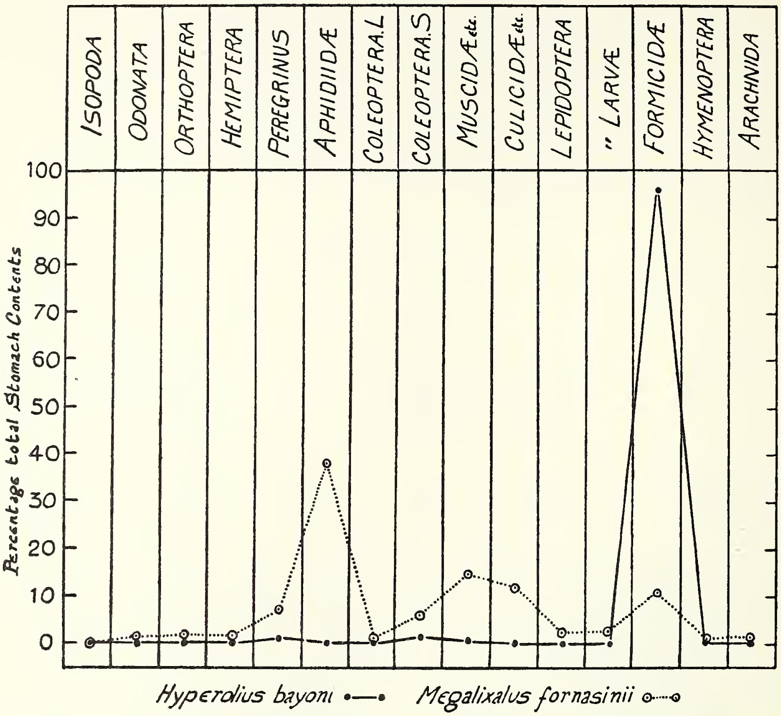

FIG. 62.—Food preferences of *Hyperolius bayoni* and *Megalixalus fornasinii*, as shown by percentage analysis of stomach-contents

TABLE XV

Species	Predators			Prey		
	Number of Stomachs examined	Number of Stomachs containing Ants	Per cent.	Total Number of Food-animals	Number of Ants	Per cent.
Hyperolius bayoni .	110	104	94·5	3688	3547	96·2
Megalixalus fornasinii	360	67	18·6	1119	121	10·9

Or again, as regards Diptera, we find that *fornasinii* is essentially a fly-catcher—these insects being found in greater bulk, and in a greater number of stomachs than any other order of insects: but the group is almost entirely neglected by *H. bayoni*. (See Table XVI.)

TABLE XVI

Species	Predators			Prey		
	Number of Stomachs examined	Number of Stomachs containing Diptera	Per cent.	Total Number of Food-animals	Number of Diptera	Per cent.
Hyperolius bayoni .	110	14	12·7	3688	16	·4
Megalixalus fornasinii	360	133	36·9	1119	294	26·3

Such differences in the selection of food cannot be explained as due to the effect of environmental conditions, i.e. to differences in the insect food available. For, as we have seen, there is considerable overlap, if not entire agreement, in the habitat occupied by the frogs, and, *so far as food-animals are concerned*, there can be little difference in the conditions of life—certainly not enough to account for the marked divergence in the food eaten by these species.

Further evidence will be found in my account of the ecology of tree-frogs in the Lower Zambesi Valley (111). But statistics of this kind make dry reading; and having shown, as I hope, the convincing nature of the evidence for discrimination by these animals, I can now bring the section to a close by indicating the bearing of this evidence upon the problem of warning coloration.

(2) **Avoidance of Aposematic Prey by Tree-frogs**—I have referred on page 274 to the striking deficiency of food-animals belonging to the typically aposematic group 'AA'. There, in a discussion of the significance of colour and pattern in relation to edibility, I tabulated (in Table VI) the percentage distribution of aposematic prey belonging to various orders. In Table XVII the data relating to the 'AA' group are presented in relation to the various species of tree-frogs whose food habits I have studied:

TABLE XVII

Species	Stomachs examined	Total Prey	Aposematic Prey	Per cent.
Hyperolius marmoratus . . .	40	2,648	0	0·00
Hyperolius bayoni	110	3,641	1	0·03
Hyperolius argus	254	3,249	4	0·12
Megalixalus fornasinii . . .	360	829	9	1·09
Megalixalus brachycnemis . .	11	31	0	0·00
Leptopelis johnstoni	8	6	0	0·00
Phrynobatrachus acridoides . .	15	564	0	0·00
Hyla arborea var. *meridionalis* .	195	617	6	0·97
Total . . .	993	11,585	20	0·17

We have, therefore, to account for the fact that of 11,585 food-animals which were classified according to colour-status, and which were obtained from the stomachs of no fewer than 993 tree-frogs, only 20, or 0·17 per cent., belong to the typically aposematic group 'AA'.

It might, of course, be objected that frogs—feeding at random—disgorge the unpalatable insects after they have been captured and their disagreeable nature discovered. On this view, the scarcity of aposematic remains in the material analysed would supply but slender evidence that the frogs, associating appearance with taste, discriminate in the first place between what is good to eat and what is not. The issue here lies between ejection and refusal: Do the deficient figures represent aposematic prey voided or avoided? Are they to be explained as rejections due to unpalatable flavour in the mouth, or to unpleasant associations in the brain?

No doubt frogs do, on occasion, disgorge unsuitable prey which has inadvertently been snapped at: thus Sir Edward Poulton has recorded of *Hyla arborea*: 'Three Frogs in succession caught a queen Wasp and then rejected it, after which it was untouched.' But in my experience it is only with (relatively) unpalatable or unwieldy prey which cannot be swallowed easily and at once that ejection occurs: (a queen wasp is a very considerable mouthful for *Hyla arborea*). In most cases—certainly with relatively small insects which are snapped up with the tongue and instantly swallowed at a gulp—'the process of deglutition is complete before the error is discovered, and the frog, whether he will or no, has to put up with the consequences'.

This view, which I put forward elsewhere (111), was based upon experiments showing that frogs (*Rana temporaria*) and toads (*Bufo bufo bufo*), when experimentally tasting wasps, swallowed and retained their baneful ration, and this in spite of gulping movements, depression of the eyes, restlessness and other signs of discomfort. Strong confirmation of this has been afforded by subsequent experiments with toads, described above. In the course of these experiments, during which a total of 161 hive-bees was eaten, not a single bee was ejected once it had been fairly flicked into the mouth.

(3) **Bees and Wasps rarely Eaten by Frogs**—In the light of what has been said, the figures relating to Hymenopterous prey are interesting. I have discussed elsewhere (111) the important place which ants occupy in the diet of different Anura in general, and of certain tree-frogs in particular. The point to which I would draw attention here is the marked deficiency of Hymenoptera *other than ants*, and especially of bees and wasps, in the prey recovered from these tree-frogs—a deficiency which appears to be most significant when we consider the great abundance of such insects in nature, and which furnishes additional evidence—if such be needed—that these animals select their food by discrimination, rather than at random. The relevant figures are given in Table XVIII, which summarizes the data for seven species from the Zambesi and one from the Canary Islands.

TABLE XVIII

Species	Tree-frogs			Food-animals		
	Number of Stomachs with recognizable Contents	Number of Stomachs containing Hymenoptera (other than Ants)	Per cent.	Total Number of Food-animals	Number of Hymenoptera (other than Ants)	Per cent.
Hyperolius marmoratus	38	3	7·9	2,675	3	·11
Hyperolius bayoni	107	1	0·9	3,688	1	·03
Hyperolius argus	?	?	?	3,300	4	·12
Megalixalus fornasinii	245	8	3·3	1,119	9	·80
Megalixalus brachycnemis	9	0	0·0	31	0	·00
Leptopelis johnstoni	6	0	0·0	13	0	·00
Phrynobatrachus acridoides	15	2	13·0	602	3	·50
Hyla arborea v. *meridionalis*	184	7	3·8	1,210	9	·74

Of the above, stinging Hymenoptera were represented by eight insects only, namely, six Andrenid bees (*Nomia* sp. and *Halictus* sp.), one Pompilid wasp, and one Sphegid (*Notogonidia* sp.).

Further evidence on this point is provided by the complete analysis by Liu and Chen (335) of the stomach contents of 170 *Rana limnocharis* and 50 *R. nigromaculata.* Hymenoptera were represented in this material by 181 and 18 specimens respectively, and it is significant that bees and wasps (*Sphecoidea*, *Vespoidea.* and *Apoidea*) were entirely absent.

Noble's important work on the Amphibia collected by the American Museum Congo Expedition (444) includes data relating to identifications of 6,387 food-animals recovered from the stomachs of 595 frogs and toads belonging to 43 different species. Of these, bees and wasps are represented by no more than 11 specimens. Moreover, 14 species of frogs and toads from Nicaragua whose stomach contents were examined by the same authority contained none of these insects (442). Similarly in his investigation of the food of the Carolina Tree-frog (*Hyla cinerea*), Haber (221) recovered but a single wasp (Scoliidæ) from 100 stomachs examined. All this evidence strongly points to the conclusion that in nature bees and wasps are in general avoided as food by these batrachians.

VI. FOOD PREFERENCES AND DISCRIMINATION IN FISHES

J. C. Mottram brought forward extremely interesting and valuable evidence—based upon observations in the field—that Brook Trout (*Salmo fario*) appreciate and recognize a difference in palatability between different kinds of insects. For example, he showed by observations made on many days and on different waters, that when the fish have a choice of both insects, the sub-imago of the Olive Dun (*Baëtis vernus*) is taken more frequently than the Black Gnat (*Bibio johannis*). Similar observations indicate that the sub-imago of the Iron Blue Dun (*Baëtis *pumilus*) is preferred to the Pale Watery Dun (*B. binoculatus*), and that the smaller Ephemeridæ are more palatable than the Reed Smut (*Simulium*). Since relative abundance of the different insects, and the ease with which they may be seen and captured, doubtless play a part in the selection, the following evidence, which takes into account these factors, provides an even more convincing argument against indiscriminate predation. Two species of May-flies known as the Yellow May Dun (*Heptagenia sulfuria*) and the Turkey Brown Dun (*Leptophlebia marginata*) are, according to Mottram, hardly ever taken by Trout. He states of the former that it ' has never been seen to be taken by a trout, though a great number have been observed floating down where fish were feeding. On two occasions considerable hatches of this insect were seen, but the fish left them alone ' (427).

In his paper on Warning Coloration in a Nudibranch Mollusc (121), Crossland describes the conspicuous appearance of certain Chromodorids and their distastefulness to natural enemies. Fishes which were accustomed to take food thrown from the window of his houseboat, and which would accept ' almost anything ' offered, even including shelled specimens of *Margaritifera vulgaris* which had been kept in formalin for three weeks, would have nothing to do with *Chromodoris reticulata* or *C. diardii.* The value of their warning coloration as a signal of distastefulness is nicely illustrated by the following observation on the behaviour of the fish *Pimelepturus cinerescens* : ' If a specimen of *C. reticulata*, which is white underneath (but for a few purple spots under the edge of the mantle), fell on the sand wrong side up, the fish would at once attempt to take it. If, however, the slug fell right side up, so displaying its gorgeous mantle, *Pimelepturus*, swimming over it a few inches away, took no more notice of it than of a stone.'

Valuable evidence of the same kind has been obtained by Reighard (538). Gray Snappers (*Lutianus griseus*), living freely in a large shoal under natural conditions, and fed with their natural food-fish *Atherina laticeps*, were taught to avoid specimens which had been dyed red, and at the same time rendered unpalatable by sewing tentacles of the anemone *Cassiopea* into their mouths. Among 150 Snappers, 178 experiences of swallowing tentacled-fish sufficed to establish the association between red and unpalatability—that is, an average of rather more than one experience for each Snapper—and subsequently both ' tentacled ' and ' untentacled reds ' were refused. Twenty days after the close of the association experiment, red fish remained entirely untouched and appeared to excite no interest in the Snappers, while uncoloured fish was taken at once.

VII. THE EFFECTIVENESS OF DISPLAYS IN PREVENTING ATTACK

Before concluding the present section, it will be convenient to consider what is the effect of warning *displays* on predatory animals. Hitherto we have been concerned mainly with warning *coloration.* But it has been shown on an earlier page that instinctive intimidating reactions—which reveal the intended victim by the transmission of visual, auditory, or olfactory stimuli intended to discourage attack *from a distance*—form part and parcel of the aposematic make-up. Such displays are also resorted to by other animals having no means of protection to justify them—that is, they are intended to *bluff*, rather than to *warn*, enemies.

Now there arises the important question : Are these intimidating reactions really of selective value in the struggle for existence ? Do the sudden changes in appearance, the exhibitions of colour, the warning sounds and smells and movements, really protect their authors from attack in the way which, on the theory of warning coloration, is supposed ? There is at present a great need for further experiment and observation on the effectiveness of displays, which offer a wide field for future research having both ecological and psychological aspects of great interest.

However, in many cases the evidence at present available points conclusively to the protective value of these exhibitions—even when the performer is in fact quite unprotected and relying upon the success of pure bluff. By way of example, I give below a few instances which are of interest because they show how the stratagem may succeed, both when the warning is a genuine danger signal, and also when the display represents a false-warning on the part of a palatable and defenceless animal.

(1) **Bluff by a Chameleon**—Chameleons are somewhat helpless creatures. They are unprotected physically by armour or by poison. They cannot escape by burrowing or by flight. They are so specialized that they are confined throughout their lives to a definite arboreal habitat. They are palatable, and have many avian and reptilian enemies which eagerly devour them when they can be found. Now it is certain that their main line of defence is concealment. Whatever their appearance when seen under artificial conditions, no one who has any practical experience of species like the East African *Chamæleon dilepis* in the field can fail to remark how wonderfully their cryptic scaly suits serve to conceal them in their natural leafy surroundings. This result is due in part to the power of colour-adjustment. There is, however, a second use to which this power is put—it can be used for purposes of display, as well as for concealment. When alarmed or angered, they can with startling suddenness undergo transfiguration : the green dress becomes a black one ; the animal swells to twice its natural size ; it exhibits the bright interior of its mouth ; it hisses like a snake. Self-effacement has been replaced as a policy by self-advertisement and threat—this is the second line of defence. That this bluff may be highly successful appears from the following incident recorded by Crossland. ‘ While staying in Zanzibar my host’s fox terrier showed hostile interest in a chameleon some one had brought into the house. The chameleon invariably tried to run away when attacked, but those who know the species can imagine the ludicrous ineffectiveness of a chameleon’s flight. In a few seconds the impossibility of escape seemed to reach the animal’s brain, when it at once turned round, opened its great pink mouth in the face of the advancing foe, at the same time rapidly changing colour, becoming almost black. This ruse succeeded every time, the dog turning off at once ’ (121).

(2) **Increase in Size as a Fear Stimulus**—In support of the view that the coloured ruff of the Australian Frilled Lizard functions as an effective ‘ scare-

organ ', Saville-Kent mentions instances of dogs (which will readily rush upon and destroy larger and more formidable lizards such as Monitors) refusing to tackle a displaying *Chlamydosaurus* (555).

This frill-expanding habit opens up a problem of the greatest interest. The power of actual or apparent increase in size—so wonderfully elaborated in *Chlamydosaurus*—is a display device widely spread throughout the animal kingdom. As we have seen, the expansions may be horizontal, vertical, or transverse in relation to the body, or due to general inflation of the body cavities with air or water. In most cases, whether used in warning or bluffing (enemies), in threatening (rivals), or in courtship, they are correlated with appropriate habits of *orientation, so that their effect may assume its greatest magnitude from the observer's standpoint.*

Now what is the significance of sudden enlargement from the observer's point of view ? That it does appear to startle, if not terrify, different animals is certain. How and why does increasing size act as a fear-stimulus ? And what classes of animals are most affected ? These questions suggest many problems. which could be dealt with experimentally ; which offer considerable scope to any one willing to give time to them , and which, so far as I can ascertain, have never yet been investigated.

It will be borne in mind that the main element in the present display (Fig. 55) is the erection of a frill which nearly encircles the head. The mechanism is somewhat similar to that of an umbrella, and like it the frill can be opened or shut at the will of its owner. Now, umbrellas are not generally used for purposes of intimidation. But the interesting fact remains that when so used they are in certain circumstances most effective. As I have recently proved by frequent experiments, cats and dogs, horses and cattle, fowls and parrots, all tend to be greatly alarmed if a closed umbrella pointing in their direction is suddenly spread. If one may judge from the reaction of domestic cats, it may well be that larger forms like the Lion would show greater respect—when encountered in the open—for an umbrella than for a rifle. Perhaps some sportsman in the tropics will test the value of this type of fear-stimulus as a deterrent to attack by one of the larger Carnivora !

(3) **Intimidating Displays by Insects**—As an example of true warning by an aposematic animal, Carpenter's observations on the African Acridiid *Phymateus viridipes* are interesting. This is a large, hard-bodied grasshopper, green in colour, with spiny thorax edged with red : it is sluggish in its habits and lives freely exposed in the open. When attacked by a predator this insect deliberately erects its wings vertically, thus displaying their purplish-red and black colour. On two occasions when individuals were being examined by a *Cercopithecus* monkey, the display prevented further interference and terminated the interview : he would never eat this species. The same reaction was seen successfully to intimidate a fowl : ' The fowl ran up to the grasshopper, which remained apparently unconcerned until the fowl was close, when it raised the tegmina and wings vertically, spreading out the latter to show the brilliant tints. The fowl halted, gazed at the grasshopper, turned round and walked away (79).

Similar evidence is presented by Manders (390), who records the case of a Mynah being successfully deterred by the display of a grasshopper (*Acridium violascens*) ; by Ridley (266), who observed that a Gecko was intimidated by the light of a fire-beetle (*Lampyris*) ; by Weismann (496), who found that Sparrows, Chaffinches, and Fowls refused to attack the displaying snake-like larva of *Chærocampa elpenor* ; and by Pitman (473), whose Lemurs (*Perodicticus potto*) were terrified by the larva of *C. nerii*. 'The male Potto which has always been the more friendly of the pair, looked at it once and then disappeared with remarkable speed for so inactive a species. The female, crouched in her corner, let the larva crawl almost under her nose before taking any lively interest. After a little while she began to crawl slowly away.' It is interesting to notice that, according to Neave, natives are successfully imposed upon by the display of the related *C. osiris* larva. In these and many other Sphingid caterpillars the essential element in the display is the sudden appearance of the startling abdominal 'eyes', which are bulged out conspicuously on each side of a swollen 'head' by the retraction of the caterpillar's head and thoracic segments, and which, with the black gleaming 'pupil' and pale surrounding 'iris', suggest in a striking manner the eyes of some vertebrate, such as a snake.

In conclusion, Marshall's observations on two Baboons which were offered a full-grown larva of the last-named species not only provide striking evidence of the effectiveness of the display—proving that the transfiguration does intimidate, and indeed terrify enemies—but also throws light on the reactions and psychology of the aggressor. His account is so illuminating and relevant that I quote his own words: 'The female baboon ran forward expecting a tit-bit, but when she saw what I had brought she flicked it out of my hand on to the ground, at the same time jumping back suspiciously ; she then approached it very cautiously, and after peering carefully at it from the distance of about a foot, she withdrew in alarm, being clearly much impressed by the large blue eye-like markings. The male baboon, which has a much more nervous temperament, had meanwhile remained at a distance surveying the proceedings, so I picked up the caterpillar and brought it towards them, but they would not let me approach, and kept running away round and round their pole, so I threw the insect at them. Their fright was ludicrous to see ; with loud cries they jumped aside and clambered up the pole as fast as they could go, into their box, where they sat peering over the edge watching the uncanny object below. . . . On concealing the larva I managed to coax them down again, and then seizing the rope to which the male was tied, I drew him slowly towards me holding up the larva in the other hand ; he simply screamed in abject terror, so I let him go, and they retired to their box' (395).

PART III

DISGUISE

INTRODUCTORY

There are things whose strong reality
Outshines our fairyland ; in shape and hues
More beautiful than our fantastic sky,
And the strange constellations which the Muse
O'er her wild universe is skilful to diffuse.

BYRON

EVERY one is more or less familiar with the fact that many insects and other animals are so profoundly modified in colour, structure, and instincts as to resemble closely some specific object of their environment—a stipule or grass stem ; a leaf or a liana ; a twig or a thorn ; a naked stone or a mat of moss ; a flake of bark or a fragment of lichen ; a frond of sea-weed or a piece of coral ; a flower, the dropping of a bird, or another animal.

Such deceptive resemblances to particular objects intergrade with the more generalized cryptic appearances which have formed the theme for the first part of this book. But in their extreme manifestation they involve principles which are distinctive. For these resemblances are no longer abstract ; they are actual. They are not arbitrary ; but elaborate and specific. And their value rests not upon the principles of visual concealment : but upon those of disguise. Such animals are impostors, rather than self-effacers : and we have here to consider the various disguises which are adopted, and the methods by which the deception is achieved, together with the functions which it serves.

Just as visual concealment has been put to a variety of uses by animals—enabling them to escape observation by their enemies, or to approach or ambush prey undetected : so disguise may be protective or aggressive—either serving to deceive a predator as to the nature, posture, or whereabouts of prey ; or allowing a predator to approach or to allure his quarry undetected. In the first case, the misleading appearance will deter or deflect attack by potential enemies ; in the second, it will facilitate the capture of prospective victims.

SPECIAL PROTECTIVE AND AGGRESSIVE RESEMBLANCE

> These seem to be wonders, but have had so many confirmations from men of learning and credit, that you need not doubt them ; nor are the numbers, nor the various shapes of fishes, more strange or more fit for contemplation, than their different natures, inclinations and actions ; concerning which I shall beg your patient ear a little longer.
>
> IZAAK WALTON

1. SPECIAL RESEMBLANCE TO PARTICULAR OBJECTS

DECEPTIVE resemblances fall into a number of fairly well-marked categories, depending upon the type of appearance produced, and upon the role reserved for it in the relations of animals to prey and to enemies. Many animals obtain security or subsistence by a passive likeness to some seemingly innocuous object of no interest to enemies or to prey respectively. It is both sound in principle and convenient in practice to follow Poulton in drawing a distinction between these likenesses, which are known as Special Protective and Aggressive Resemblance ; and cases of Batesian Mimicry and Alluring Coloration, where palatable prey appear in the guise of other animals positively distasteful or dangerous, or where potential predators simulate objects which are both innocent and attractive.

I. LEAF-RESEMBLANCE IN VERTEBRATES

There lives in the Lower Amazon Valley a little Nandid fish named *Monocirrhus polyacanthus*, which bears a remarkable resemblance to a dead leaf. In reply to a request for certain information on its appearance and habits in nature, my friend, the Rev. A. Miles Moss, of Pará, has been kind enough to supply me with notes and sketches based upon his personal observations.

The ' Peche de Folha '—for that is its appropriate popular name in Brazil—appears to be locally common and widespread. Its habitat is in the smaller streams and tributaries, always in the clear, dark, fresh water of *igapós* and floods, where there is abundant vegetation, with very little disturbance or flow in the water. According to Coates (99) the habits of the fish indicate that it is only at home in water which is always quiet and still. In such surroundings, hanging head downwards, it either lies at an angle just beneath the surface, and ' drifts about at the whim of every little current ' ; or, as Miles Moss says, it rests on the bottom, *lying motionless on its side* and lost to view among the water-logged foliage and weeds, or again it may appear to be suspended at an *angle* from water weeds, stalks, and stems. When taken up in a net, *the fish lies flat and motionless like a dead leaf.* ‘ So close is the resemblance between fish and leaf that when netting . . . numbers of waterlogged dead leaves have to be “ caught ” and very carefully scrutinized.’

Now it is interesting to consider how the resemblance to a leaf is brought about. In form, the fish is strongly compressed, the body being of extreme thinness, the head tapering to a narrow point in front, and the tail narrowing behind, so that it would pass well for its model when seen from any aspect. The illusion is heightened by the ‘ beard ’—a slender tab of flesh below the chin, which wonderfully simulates a leaf-stalk. Moreover, the fish frequently lies at rest with the dorsal and anal fins shut down against the body, and with the tail closed up like a fan, so that these parts do not interrupt the leaf-like contour.

Its coloration is such as to further the deceptive resemblance. Mr. Moss states : ‘ No two fish in a multitude are exactly alike, but they may be roughly grouped under three colours : (1) light grey with dark grey markings, much or little of irregular disposition, only a few dark lines or spots being constant ; (2) a golden-tan, with only a few mottlings of dark-brown ; (3) the dead-brown colour, with all darker markings consequently obscured. *But,* chameleon-like, they can all change colour in less than an hour, according to the light or darker conditions of environment.’

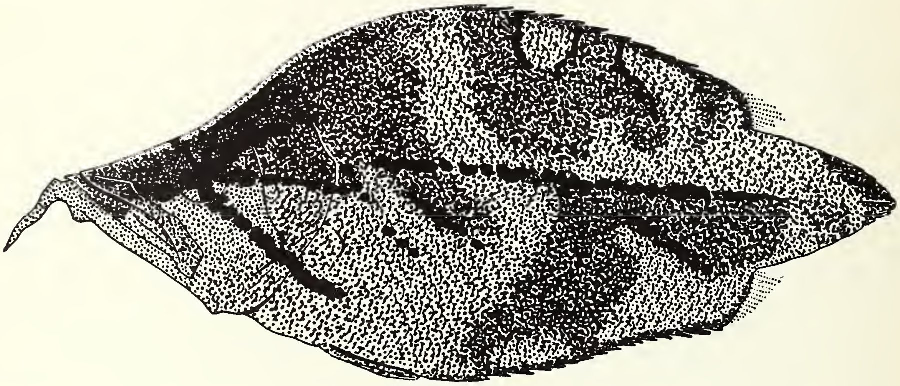

FIG. 63.—*Monocirrhus polyacanthus*

In addition to the irregular markings which pass well enough for patches of mildew on rotten foliage, many specimens have the eye rendered inconspicuous by a number of radiating dark bands which cross the iris and continue over the scales of the head and body, thus partially obliterating the round black pupil. Also, there is frequently the suggestion of a mid-rib painted in dark pigment along the side.

Even more remarkable, however, are the fish’s habits. I have recently had the pleasure of observing at first hand the movements and feeding behaviour of *Monocirrhus* in the Zoological Society’s aquarium at Regent’s Park. The fish has a wonderful capacity for floating motionless, or almost so, for long periods of time. Suspended sometimes on its side, or at an angle, or head downwards, or resting lightly on the bottom, no visible movement is made which belies the suggestion that this is, indeed, a water-logged leaf, drifting passively with the water. Close inspection shows that the fish has the most perfect control of its movements and position. Its method of swimming is strikingly different from that of most fishes, in that the body is held rigid—either straight or slightly curled—locomotion being effected not by lateral strokes of the body and tail, but by rapid undulations of the very minute dorsal and anal fins, which are themselves colourless and transparent, and so practically invisible.

The ' Peche de Folha ' is carnivorous, and it appears to subsist solely upon small living fishes. Coates tells us that these are apparently deceived by the motionless leaf-like form, allowing the fish to drift to within a few inches of its prey, ' when suddenly the end of the slowly moving leaf opens—a swift dart, and the little fish is interred within the larger one. In proportion to the size of the fish, the mouth is very large, and evidently can form a strong inflowing current, for the prey seems quite helpless to evade the yawning jaws, and in one gulp disappears entirely.'

One specimen which I observed feeding was very hungry after a fast of some days, when a number of ' Millions ' Fish were introduced into its tank. At once it turned round and gradually moved towards a selected victim. On this occasion, however, its approach had been slightly impetuous, for its prey became alarmed and darted out of reach. After this failure, another specimen was selected, and the Leaf Fish now advanced with an almost incredible precision, until it was close enough to make the fatal forward dart—a dart rendered highly effective by a mechanical device (similar to that in the John Dory) of the jaws which project forwards as they open, and so increase the fish's potential speed and reach.

We see, then, that the appearance in life, the general behaviour and instincts, and the precise predatory habits throw much light on the nature and function of the resemblance ; and I entirely agree with Mr. Miles Moss in regarding the fish, in its own sphere, as one of the finest possible examples of resemblance for aggressive purposes. I have referred in some length to the ' Peche de Folha ' because it well illustrates the value—so frequently stressed in these pages—of studying problems of adaptive coloration in nature, where form, colour, and pattern can be related to an animal's habitual attitudes and instincts, and to its physical and biological conditions of life.

Willey (668) has described a Chætodontid fish, *Platax vespertilio*, from Colombo, which like the last is leaf-shaped and leaf-coloured, and in addition has habits and instincts appropriate to its make-up. He states that, if pursued, the fish has the unique habit of toppling over, feigning death, and sinking inertly to the bottom—when it looks very much like a yellow waterlogged jak leaf. Its local name of ' Koskolaya ' (jak leaf) shows that the resemblance is also recognized by native fishermen.

A related species of *Platax*, probably *P. teira*, has been observed by Mortensen (417) at Little St. Cruz Island, in the Philippines. This investigator also testifies to the striking leaf-like appearance and behaviour. ‘ At one place of the island ’, he says, ‘ there is a very small Mangrove, with a fine, sandy flat outside. Here were seen swimming among the floating old leaves of the Mangrove trees some small fishes, which looked so exactly like the leaves, that it was by no means easy to see which was a leaf and which a fish. The colour of the fish varies from yellow to dark brown, to suit the different shades of the leaves. Further, the fish swims very gently, swimming now on the side, now erect, exactly like the leaves swaying with the gently moving water.’

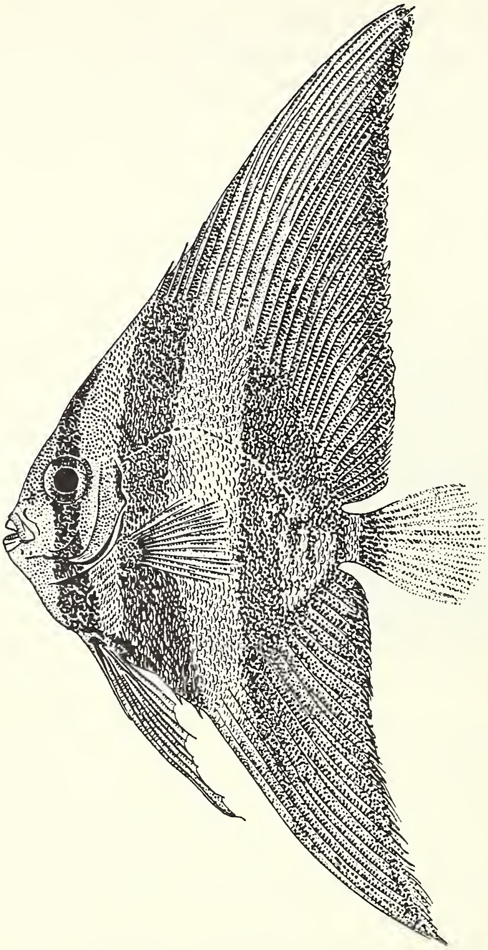

FIG. 64.—*Platax vespertilio*

It is of particular interest to compare how, in contrast to the last species, the leaf-like appearance has been attained in the present genus. Both fishes agree in having the body extremely compressed : but in every other respect the modification of form has proceeded along divergent lines. With *Platax* the body is greatly heightened, owing to the enormous development of the dorsal and anal fins—which, being opaque and pigmented like the body, produce the contour vertically to a point above and below. At the same time, the body is much shortened, both by modification and illusion—for not only is the head blunt in profile, but the caudal fin is unpigmented, transparent, and almost invisible in water. A further characteristic described by Willey (not well preserved in the spirit material which I have examined) is the strengthening of the remarkable elevated contour behind by a line of dark pigment which passes along the posterior border of the dorsal and anal fins, *and continues between them across the base of the transparent tail.* The general contour is, indeed, somewhat suggestive of the leaf butterfly *Kallima*, and like the butterfly, the fish bears on its surface lines of pigment and spots like those found in decaying leaves.

In these two genera, then, a similar appearance has been attained in a diametrically opposite manner, and the fishes provide a most striking example of morphological divergence and adaptive convergence. In *Platax*, as opposed to *Monocirrhus*, it is the greatly elongated and pointed dorsal and anal fins, rather than the protruding snout and tapering caudal, which draw out the contour to represent leaf stalk and tip ; it is the fore and hind profile of the fish, rather than the dorsal and ventral, which play the role of leaf margin ; it is the caudal, rather than the dorsal and anal fins, which break the simulated contour, but are prevented from spoiling the deception by their transparency and loss of pigment which renders them invisible in water ; and it is a transverse band running vertically from fin to fin, rather than a longitudinal stripe running horizontally from snout to tail, which now suggests leaf venation. In short, the entire likeness is laid down on vertical instead of horizontal lines—entirely *different* parts of the fishes doing duty for *corresponding* parts of the leaves which they resemble. The one essential adaptive feature where the genera agree is the reduction of the body by an astonishing degree of compression. Taken together, these phenomena are sufficiently remarkable, the more so when it is realized that the fishes, themselves belonging to different families, and hailing from different continents and different environments, yet agree in simulating a leaf not only in outward appearance, but also by instinctive behaviour.

I take my next example of leaf-resemblance among vertebrates from a quite unrelated group of animals. While out collecting, one October morning, in the rain forests beyond Souza, near Pará, I was called by one of the native boys who frequently accompanied me as assistants on these occasions, to see a ' Sapo ', or toad, which he had found. On reaching the spot, it was some little time before I could distinguish anything on the forest floor where we stood, except the usual carpet of fallen leaves and an occasional Lycopod. Then, suddenly, I recognized it—a small toad squatting motionless among the leaves, the creature itself bearing quite an extraordinary resemblance to a leaf. Till then I had never seen so perfect an example of sheer deception. The resemblance is brought about in the following way: the snout, being sharply pointed, represents the tip of the leaf; the back is flattened, and the general form of the animal so depressed as to give the appearance of extreme thinness. This effect is enhanced by a well-marked flange or fold of skin extending backwards from the eye along the side of the body and down the outer side of the thigh. This causes the ventral surface to be thrown into deep shade, the shaded area being sharply limited above by the projecting lateral fold. Thus the only conspicuous part of the animal is the flat upper surface of head, body, and hind limbs, the latter usually being placed with the feet resting against, and partly hidden beneath, the shins, and with the thigh drawn back so that the lateral fold of skin is stretched and bridges the gap between the side of the body and the knee. This device, clearly shown in Plate 35, and in Fig. 66, No. 10, goes far towards obliterating the legs. Thus we see that the visible form and contour of the toad is very similar to one of the leaves amongst which it lives. This resemblance is further increased by its size, its green colour, by the faint mid-dorsal line corresponding to a mid-rib, and by the presence on the back of two small jet-black spots which give the exact appearance of holes in a leaf.

I have referred elsewhere to the habits of this interesting little toad—*Bufo typhonius* (107). ' It remained quite motionless while I arranged my tripod within a few inches, focused the camera, and took several time-exposures; nor did it make any attempt to escape when it was picked up, but allowed itself to be handled without a struggle, evidently relying on the " crouching habit " to escape observation—just as a young Stone Curlew will do under similar circumstances.' Bringing it home, I kept the animal for six weeks in a box, the bottom of which was strewn with damp leaves: it was interesting to notice that it never made any attempt to hide beneath these, but instead always sat in full view on top of them. When feeding, its method was to wait in ambush until a moth or fly approached within the danger zone of the flexible sticky tongue.

We have already seen how, in *Platax* and *Monocirrhus* respectively, the leaf-form has been arrived at independently in an utterly different manner. But both these fish have in common a compressed form of body, that is, they are flattened laterally. Now we have in *Bufo typhonius* yet another method of attaining this end. In this toad, the form is depressed, that is, the flattening is from above downwards: the edges of the ' leaf ' are formed neither from the anterior posterior, nor from the dorsal-ventral margins, but from the animal's sides, and the ' mid-rib ' runs neither across the side, nor along it, but down the centre of the back—that is to say, in the only position in which it could fulfil its apparent function. When we consider the above facts, they appear very remarkable; and it is difficult to explain these modifications, so diverse in their nature and so consistent in their effect, on any view other than that they have been evolved for one end, namely, disguise.

II. DIFFERENT METHODS BY WHICH THE APPEARANCE OF THINNESS IS PRODUCED

The types of leaf used as models by different animals are very various. They may be long or broad in shape ; green or brown in colour ; they may be living or dead ; they may be fresh and flat, or withered and curled. But of all qualities presented by leaves, *thinness* is one of the most constant and typical. While these organs, upon which the process of photosynthesis essentially depends, vary vastly in size, contour, and complexity, they are, and for physiological reasons normally must be, thin. Now among animals in general extreme thinness is rare. It can be attained only at the cost of profound modification of the body and of the various internal organs. It becomes therefore a question of great interest to consider how, among different leaf-like animals, the appearance of thinness has been produced.

FIG. 65.—*Rhampholeon boulengeri*

(1) Actual Thinness Produced by Compression or Depression of the Body—Sometimes, of course, the quality is real, and is effected, as we have already seen, by extreme compression, as in the fishes *Monocirrhus* and *Platax*, or by extreme depression, as in the little toad *Bufo typhonius* and the Leaf-insect *Phyllium*. These forms have, as it were, gone in for a very specialized type of slimming. Among lizards a beautiful example of the kind is seen in a minute chameleon known as *Rhampholeon boulengeri*, from the Belgian Congo (Fig. 65).

(2) **Deceptive Appearance of Thinness Produced by the Wings of Insects**—More often, and typically among insects, a similar effect is brought about by the wing surfaces, whether held vertically, as in butterflies, such as *Kallima*, and in grasshoppers, such as *Tanusia* and *Systella*; or horizontally, as in moths such as *Timandra* and *Oxidia* and Mantids like *Chœradodis* and *Phyllocrania*, —in which the body is either relatively small, or else largely concealed in the position of rest.

Probably there is no more perfect example of leaf-resemblance among Lepidoptera, or indeed anywhere in the animal kingdom, than that seen in the Oriental genus *Kallima*, whose realistic outline and colour—with the false leaf-stalk, midrib and pointed apex, the suggested lateral veins and counterfeit mould marks, and the apparent borings of insects—complete the deception to the last detail. This, of course, is the classical example of protective resemblance and is too well known to need any description here; but it is by no means an isolated or exceptional one. For instance, similar cases are plentiful among the genera of South American forest-dwelling butterflies such as *Pierella*, *Catoblepia*, *Taygetis*, *Anæa*. Others again, like the beautiful, clear-winged species of *Haetera*, while not themselves resembling leaves, have yet achieved the same result in a different way, for when they alight on the leafy carpet of the forest, all trace of their hyaline wings is obliterated by the foliage pattern which shows through them as though they were made of glass—and so like the plankton of the sea, they too have almost attained a state of invisibility by becoming transparent.

Moths, like butterflies, are frequently protected by more or less detailed resemblances to foliage. Since these insects mostly settle with the four wings extended flat, the more specialized leaf-like forms have characteristic markings such as the false mid-rib extending right across the upper surface of the four wings, illustrating in a very beautiful way the principle of coincident disruptive coloration. This is well seen, for instance, in *Gorgonia augusta*, of British Guiana, and in *Timandra amata*, of Great Britain. Quite different is the arrangement found in moths like *Miniodes ornata* and *Phyllodes consobrina*. Here the hind wings are highly conspicuous, but are covered, in the resting insects, by the fore wings—each of which accurately reproduces the appearance of a leaf. In the former (see Plate 39) the resemblance is quite extraordinary—with imitation mid-ribs and lateral veins marked out in black on a brown ground and spurious holes depicted by patches of white scales.

(3) **Deceptive Appearance of Thinness Produced by Obliterative Shading**—But there are many cases in which the quality of thinness is less real than apparent; in which dissimulation takes the place of slimming. As examples of pure camouflage perhaps the most remarkable cases are those which mainly depend upon Thayer's principle of obliterative shading. There is no doubt that the great difficulty of recognizing relatively bulky animals like *Chamæleon dilepis*, the commonest Chameleon of the Lower Zambesi, is due to the fact that *the body which is actually so solid and rounded is apparently so slim and flat*: the eye, therefore, fails to distinguish it from the leaf forms among which it crouches.

The same principle applies to larger lizards, like the Brazilian *Iguana tuberculata*—for although there is here no detailed resemblance to a leaf, the combined effect of obliterative shading with a superimposed disruptive pattern, based on the hues and tones of foliage, render the reptiles very easily overlooked when seen among foliage. On a smaller scale, and in a very different group of animals, the delusion is much more perfectly seen in different Sphingid caterpillars, whose great fleshy bodies are transfigured, by the combined magic of green colour-harmony, obliterative shading, and a pattern of diagonal stripes, into the under-surfaces of the thinnest ' leaves ' imaginable. (See Plates 5 and 8 and Fig. 3.)

Now in such cases, not only is there firstly a general obliteration of the caterpillar's solidity and relief by counter-pigmentation, which produces the effect of a flat surface ; but secondly upon this apparently flat surface is superimposed in fake relief the appearance of the lateral veins and intervening concavities of a leaf. Such an optical illusion has been described by Hingston, who writes of the Sphingid larva of *Protambulix strigilis* (or some closely related species) in British Guiana as follows : ' The ground-colour of this caterpillar was greyish-green. Along the mid-dorsal line was a dark green longitudinal stripe. On its sides was a series of oblique stripes, triangular in shape and divided into light and dark areas. This large caterpillar fed on an Anonaceous shrub with large oval leaves. The general colour of the caterpillar resembled that of the leaf. Furthermore, its habit was to align itself along the mid-rib and grip the base of the leaf with its posterior suckers. As a result of this attitude the mid-dorsal longitudinal band on the caterpillar became continuous with the dark mid-rib on the leaf, and this, of course, added to the harmonization. Also its side stripes fitted in fairly exactly with the lateral leaf-ribs. These ribs were separated from one another by distinct concavities of the leaf surface, and . . . this succession of concavities with elevated ribs separating them resulted in the formation of oblique shadow marks on the surface of the leaf. Now, the oblique stripes on the sides of the caterpillar fitted in exactly with these shadow marks. They were the same distance apart, the same tapering shape, also they had about the same degree of obliqueness, and their division into two areas, dark above and light below, made them fit in with the shading of the leaf on which the raised ribs were naturally illuminated and the concave areas near them naturally in shadow. It was evident, when one studied the living caterpillar . . . that the lights and shadows on the leaf surface were represented on the caterpillar by patterns of colour ' (265).

One of the most perfect examples with which I am acquainted is that of the larva of *Smerinthus ocellatus*, the Eyed Hawk-moth, already referred to on page 43. Here we find a wonderful degree of optical flattening, effected by a correlation of inverted countershading with inverted attitude ; and upon this canvas is painted in lighter and darker tones the picture of leaf-venation. (Plates 5, 8).

It is particularly interesting to find that this same device—whereby a diagonal design on an opticially flattened surface roughly represents a leaf with its lateral veins—has been evolved independently by different lizards, such as the Brazilian twig-dwelling *Polychrus marmoratus*, whose green scaly coat is frequently adorned by darker and lighter diagonal bars (see Fig. 66). Such picture painting in natural pigments on an *apparently* flattened surface, of which we have here considered examples, pervades almost every department of animal life, and almost every environment, and it is, of course, beautifully illustrated in terms of *general*, rather than *special*, resemblance in the cryptic coats of many mammals, in the patterned plumage of countless birds, and in the disruptive dresses worn by snakes and lizards, frogs and fishes. While it is less commonly employed as a means of representing particular objects in the animal's environment, such cases are by no means rare, and other examples—like that of the pelagic prawn *Hippolyte acuminata*, whose appearance is described on a later page—will be found in this work.

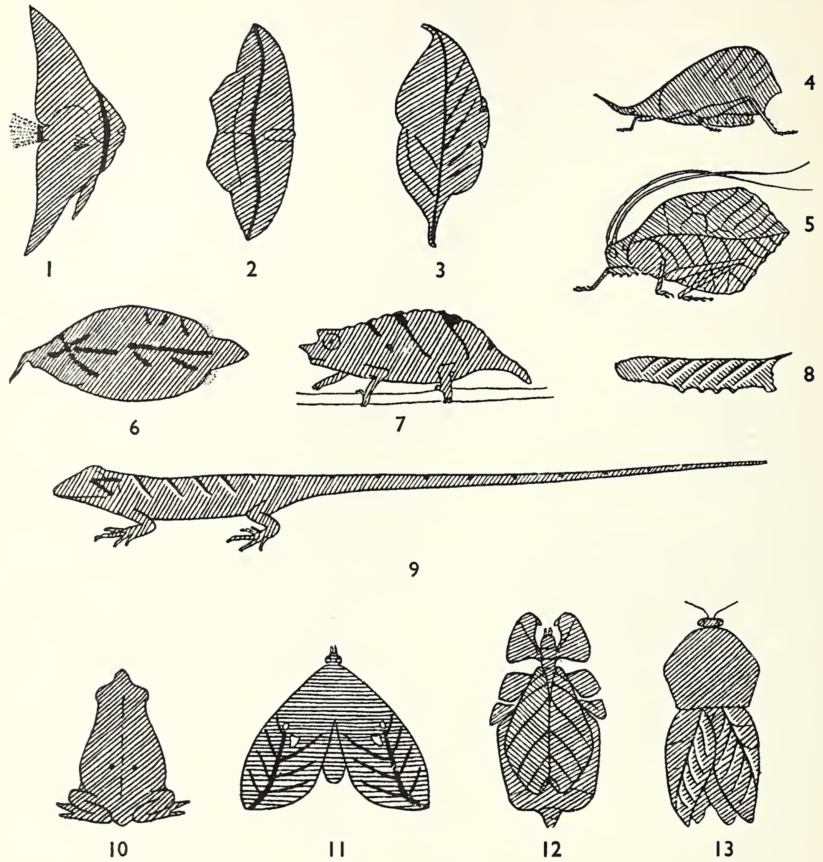

FIG. 66.—Special resemblance to leaves in a variety of animals: 1 *Platax vespertilio*; 2 *Timandra amata*; 3 *Kallima paralekta*; 4 *Systella rafflesii*; 5 *Cycloptera* sp.; 6 *Monocirrhus polyacanthus*; 7 *Rhampholeon boulengeri*; 8 *Smerinthus ocellatus* (larva); 9 *Polychrus marmoratus*; 10 *Bufo typhonius*; 11 *Miniodes ornata*; 12 *Phyllium crurifolium*; 13 *Chœradodis rhomboidea*

(4) **Deceptive Appearance of Thinness Produced by Structural Modifications**—A very different deceptive arrangement making for apparent flatness is that which depends upon structural modifications in the form of folds of skin or ridges of chitin, which produces a spurious likeness to the margin of a leaf. The thinly produced lateral folds of skin seen in *Bufo typhonius* have already been mentioned. A South African member of the same genus, known as *B. superciliaris* (Plate 37), also exhibits this feature—except, perhaps, after a very full meal, when all rough ways are made smooth ! But what makes this large and handsome toad so interesting in the present connection is its *coloration.* The dorsal surface of its head and body is flattened, but curiously concave between the prominent brow-like ridges above the eyes, which, in continuation with folds of skin on the flanks, more or less sharply separate the upper from the lower surfaces. The upper area is coloured brown, or grey, generally with darker blotches and other markings which make it wonderfully like the surface of a dead, withered and weather-stained leaf. Now, immediately beneath this dorsal region, there is an *abrupt and extensive change of tone* : from the superciliary ridge and skin-fold downwards the sides of the head and body are coloured a deep rich chestnut-brown. Being the complementary colour to the greens of the forest, and situated as it is on parts of the body already in shade, the colour serves to deepen and intensify that shade, thus producing the optical effect of a very dark clear-cut mass of shadow beneath the edge of a leaf. The colour-scheme is, in fact, a total inversion of that shown by obliteratively shaded animals. And its purpose is also the reverse—for *instead of serving to suppress lateral relief, it serves to exaggerate it* ; instead of making the side of the toad appear flat, it makes it appear to project outwards as a distinct, sharply defined shelf. The whole device is a most admirable and beautiful example of the art of applied camouflage. One almost despairs of describing these things in a convincing way. They have to be seen to be believed. In this toad we find an instance of what we have noticed over and over again in different animals—colour and contour, form and pattern combined to create a spurious impression on the sense of sight. We have here the structural effect of a real fold enforced by the optical effect of an unreal shadow : we have a large solid toad, whose form is so split by deceptive painting that the upper part of it looks like a thin and ancient leaf, the lower part like the deep and dark shade cast by the leaf. Added to all this we have to remember the habits of the toad himself, squatting motionless on the forest floor, partially covered by real leaves beneath which he hides—and the illusion is perfect.

Turning to an entirely different group of animals, ridges which serve to sharpen the edges of the body, and thereby render the appearance of slimness possible, occur in several insects. An interesting example of this type of deception has been described by Nicholson, and refers to an Australian grasshopper known as *Goniæa australasiæ*, which, he states, is commonly found on the ground amongst dead Eucalyptus leaves. Being itself brown in colour, but varying considerably in different individuals, its range of tones is approximately that of the dead fallen leaves. Now, as Nicholson points out, the robust form of the insect would nevertheless render it conspicuous among such thin, flat objects as leaves, were it not for a special structural modification, found both in the nymph and the adult insect, in the form of a prominent laterally compressed ridge extending along the mid-dorsal line of the large prothorax. In the nymph, this ridge is continuous with a similar mid-dorsal ridge extending along all the abdominal segments: in the adult, it is almost continuous with that formed over the back by the closed tegmina; and in both cases this thin edge, extending as it does along the full length of the back, produces ' a very deceptive appearance of thinness and flatness, except when viewed from immediately above ' (440).

(5) **Deceptive Appearance of Thinness Produced by Resemblances to Curled Leaves**—Finally, there are other leaf simulators which get round the slimming problem in another way—or rather, they evade the problem altogether by resembling a *curled or crumpled leaf*—their bodily substance comfortably stowed away inside what appears to be a hollow space. This favourite device is very beautifully illustrated by the pupæ of certain Brazilian butterflies of the genus *Ageronia.* Whilst collecting near Rio de Janeiro, I happened to come across a pupa of *A. amphinome*, hanging on the wall of an old shed, in a situation where it naturally attracted attention. Partly green in colour, with brown vein-like markings and reddish rusty spots, and partly dark-brown, the deceptive resemblance was rendered strangely convincing by the presence at its free end of two thin and somewhat twisted filaments suggesting the torn ends of a curled and shrivelled leaf. When such pupæ are suspended, as is normally the case, in the near-by forest foliage, they must be wonderfully concealed from the eyes of insectivorous foes.

Somewhat analogous is the case of the British Angle Shades moth (*Phlogophora meticulosa*), which rests, generally on herbage, with its fore wings folded round the body, and creased or wrinkled, so that the moth looks like a crumpled decaying leaf—buff in colour, with dark-brown, pinkish, and olive-green markings.

A similar appearance has been reproduced in certain caterpillars which wear a cryptic costume suggesting a rolled or curled leaf, as seen, for instance, in certain Sphingid larvæ which have been so beautifully figured from life in Pará by Miles Moss (420). The sketches, in Fig. 48, based on his figures, of *Enyo japix japix*, *Epistor cavifer*, and *Epistor lugubris*, will indicate better than a long description how the illusion has been effected in these wonderful examples of deceptive decoration.

III. SPECIAL RESEMBLANCE TO BARK

When we consider how great is the modification of form necessary to bring about the likeness of various animals to leaves; how high is the degree of perfection attained, often to the minutest detail; and how widespread are such cases, both in different groups of animals, and in different parts of the world—it is not surprising to find that cryptic resemblances to other objects such as bark or lichen (which generally involve less divergence from type) should be even more common and widespread, both zoologically and geographically.

Examples of bark-like moths, longicorn beetles, weevils, spiders, phalangids, and other invertebrates are too familiar to require more than the briefest notice here. Among moths, for instance, this cryptic contrivance has been evolved independently in group after group, among bark-haunting species of the Sphingidæ, Noctuidæ, Notodontidæ, Tortricidæ, Pyralidæ, and Geometridæ. These include what are undoubtedly some of the most effective instances of protective resemblance in the animal kingdom—the British *Hyloicus pinastri*, the East African *Xanthopan m. morgani* (Plate 30), and the Brazilian *Protoparce rustica* affording excellent examples from the first family; the Oak Beauty (*Pachys strataria*) (Plate 11) and Garden Carpet Moth (*Xanthorhoë fluctuata*) (Plates 10, 12), both British species, from the last.

It is significant that in those cryptic species—such as *Boarmia gemmaria* (Plate 33) and many other Geometrid moths, which habitually expand and expose all four wings when at rest, both the fore and hind wings are similarly, and inconspicuously coloured; frequently with the pattern repeated on, and coinciding right across the four wings (thus greatly increasing the disruptive effect): whereas in other species—such as *Catocala electa* and *Triphæna fimbria*, which rest with the fore wings folded back so as to cover and conceal the hind wings, the latter are often differently, and sometimes very conspicuously coloured, when they constitute the so-called 'flash colours' (see p. 374). Moreover, it is noteworthy that certain Brazilian butterflies of the genus *Ageronia*, which are in the habit of resting in a moth-like manner, with the four wings expanded flat against the bark of trees, have also developed a moth-like colour-scheme, in that the cryptic bark-like coloration is worn on the upper surface of all four wings, while these may be brightly coloured beneath. This is a complete reversal of the usual arrangement in butterflies whereby the under surfaces, exposed in the normal resting attitude, are cryptic, while the upper surfaces are generally more conspicuous, and often exceedingly brilliant in hue.

Broadly speaking, relatively little modification of form is needed to enable a beetle or a bug or a moth to masquerade more or less successfully as a flake of bark or as an excrescence on a tree-trunk or paling; although to that end, depressed form and a disruptive pattern, instinctive stillness and adaptive orientation are important factors in completing the disguise. Nevertheless, certain specialized insects—such as the wonderful flake-like, vegetable-feeding, Pentatomid bug *Phlœa subquadrata* of Brazil, or the remarkable flattened fungus-feeding Aradid bug *Dysodius lunatus*, also from Brazil (Fig. 41), show a degree of adaptation which must, as highly perfect examples of special protective resemblance, claim our wonder and admiration.

With arboreal vertebrates, parallel, and often very remarkable resemblances of the kind are found—notably among climbing frogs, lizards, and birds. The first group is well illustrated in East Africa by the grey Polypedatid tree-frog *Chiromantis xerampelina* (Plate 28); and in North America by certain Hylid tree-frogs, such as *Hyla squirella*, an excellent photograph of which is given by Barbour in his work on *Reptiles and Amphibians* (19). A yet more perfect example is that of the little Pine-wood Tree-frog *Hyla femoralis*, which bears a brown, bark-like disruptive uniform comparable to that worn by many moths. A photograph well illustrating its effective disguise (which includes the familiar ocular stripe and abrupt contrasts of tone), showing the frog snugly stowed away in its daytime nook, partly hidden behind a projecting flake of pine bark, has been published by Harper (229) who gives an interesting account of the species in Georgia. What we may note especially here is the close association of the frog with the pine bark which it resembles, for Harper states that no other amphibian of North America seems to be so closely associated with pine trees. 'In the Okefinokee region I have seldom found it very far from a pine. In the depths of the swamp it may be absent over considerable areas where these trees do not occur; but let a few straggling pines appear, and there its notes are likely to be heard.'

Among lizards a similar type of coloration is typical of several tree-dwelling Iguanid genera in the New World: it is repeated in their Old World Agamid counterparts: it occurs again among the almost cosmopolitan Gekkonidæ—whose bark-like representatives are well illustrated by *Hemidactylus richardsoni* in West Africa (Fig. 67), by *H. leschenaulti* in Ceylon, by *Phyllurus lichenosus* in Queensland, and by *Aristelliger præsignis* in the West Indies: and it is exhibited again in the plumage of Tree-creepers, Wrynecks, Owls, Nightjars, Frogmouths, and other bark-haunting birds.

IV. SPECIAL RESEMBLANCE TO LICHEN

As regards appearance, such bark-like types as we have considered lead up to, and intergrade with, other types which in their most specialized form resemble in high degree the lichens growing on wood or on walls. The resemblance is literally superficial, rather than structural—that is to say, it is generally due to the most ingenious and deceptive disruptive patterns, which give the optical impression of irregular processes and deep interstices—even when painted, as they often are, on the flat canvas of a moth's wing or on the ovoid abdomen of a spider—rather than to actual excrescences and irregularities in the animal's form. From the standpoint of camouflage these cases are therefore of the greatest interest.

Lichen-like species are not confined to any particular continent or country: they may be seen on the limestone walls of a Wiltshire garden or on the slopes of an extinct volcano in Lanzarote; in the luxuriant rain-forests of South America, or on the rocky summit of a Scottish mountain. Nor are they restricted to one phylum or to a few families. Wherever lichen forms a characteristic feature of the environment, different animals are found associated with it for purposes of feeding, of shelter, or of predation; and many of these—including such a diverse assemblage as phalangids and spiders; mantids, stick-insects, and grasshoppers; moths and caterpillars; weevils and longicorn beetles; geckos and tree-frogs—are decorated in colour (and sometimes modified in form) so that they appear to resemble it, and are most difficult, and often almost impossible, to detect in their natural roosting, feeding, or hunting grounds.

FIG. 67.—*Hemidactylus richardsoni*

Lack of space prevents any but a brief reference to a few examples. British Lepidoptera, both larvæ and imagines, present a number of striking cases—notably, as caterpillars, the Black Arches (*Psilura monacha*), the Scalloped Hazel (*Gonodontis bidentata*), and the Brussels Lace (*Cleora lichenaria*) (Geometridæ). The latter, pale green in colour with interrupted and irregular black markings, bears a very deceptive resemblance to its food-plant *Usnea barbata*, a lichen commonly growing on trees and fences, and, as pointed out by Poulton, often insinuates itself among the irregularities of the lichen, so as to be almost completely indistinguishable (496).

Among British moths, perhaps the two species most remarkable for their resemblance to green lichens are the Merveille du Jour (*Agriopis aprilina*), and the Scarce Merveille du Jour (*Diphtera orion*) (Noctuidæ). Both of these handsome insects have the fore wings green in ground-colour, disrupted in the former with white-edged black markings, and in the latter with white stripes crossed by irregular black bands. These moths are associated with the branches and trunks of oak and other trees upon which they rest by day. Other species, such as the Marbled Beauty (*Bryophila perla*) (Plate 29), frequently rest upon the old lichen-covered walls where the larva feeds, and where its cream fore wings, variegated with slaty-grey and with irregular black lines, reproduce the patterns of greyish lichen, with its irregular patchwork of creamy high-lights and deep shadows.

(1) **The Effectiveness of such Resemblances**—The eye—or rather the brain behind it—is very easily deceived by resemblances such as these. Well do I remember one occasion when, intending to record its cryptic likeness, I had arranged my camera tripod some twelve inches in front of a Marbled Beauty that had settled on an old wall near Bradford-on-Avon. After carefully focusing the insect, and having attended to the diaphragm and shutter, I looked up before making the exposure to be sure that the moth was still in position—when I discovered, much to my disappointment and disgust, that I had evidently disturbed it while making the final adjustments to the camera. At any rate, the moth had vanished. To make sure of this, however, I subjected the stone where it had been resting to a close and most careful examination, verifying the exact position with reference to the axis of the camera, but I could see no sign of the moth. Just as I had begun to convince myself that I had lost my subject and was about to turn and replace the dark slide, I suddenly *recognized* what I must repeatedly have *overlooked.* My *Bryophila* was there all the time: it had never moved, and was ‘ staring me in the face ’ in full view. Surely I had never been so easily and completely taken in. But that, of course, is the function of disruptive coloration, and as I once more examined the insect I felt less inclined to admonish myself for blindness than to admire afresh the deception caused by a device so naïve and so effective (see Plate 29).

No useful purpose would be served by multiplying instances of the kind. The photograph of that remarkable weevil, *Lithinus nigrocristatus*, on Plate 43, speaks for itself. Any one who is doubtful of the cryptic efficiency of a disruptive pattern would do well to study this reproduction and identify the *two* beetles on the bark. Another good example is furnished by the remarkable tree gecko *Uroplates fimbriatus* (Plate 42). Unfortunately my illustrations of both these (unlike the large majority in this book) are taken from museum specimens. However, no field naturalist imagines that such specimens are better concealed, because artificially placed on a fragment of bark in a show-case, than they would appear if seen in a state of nature. The fact is that the wild animal —with its resting attitude adapted to its conditions of life, with its coloration unfaded, and its immediate environment unlimited—is far *better* concealed than its dead and dried remains are likely to be. Every one is familiar with the show-case exhibits of the famous leaf butterflies *Kallima.* Well, this is what Wallace says of them *in nature* : 'The concealment produced by this wonderful imitation is most complete, and in Sumatra I have often seen one enter a bush and then disappear like magic. Once I was so fortunate as to see the exact spot on which the insect settled ; but even then I lost sight of it for some time, and only after a persistent search discovered that it was close before my eyes' (646). As examples of disruptive lichen-like patterns photographed *in the field*, and illustrating this point, we may refer to the Oak Beauty (*Pachys strataria*) on Plate 11, and to the Phalangid (*Phalangium opilio*) on Plate 43. The latter presents a wonderful example of disruptive coloration. The back is ornamented with a plum-coloured stripe, which deepens laterally into sepia at its irregularly indented margin. Immediately beyond this sharply defined margin the colour changes abruptly to cream, deepening on the sides into lichen-grey. The sudden transition from the deepest tone (sepia) to the lightest (cream), combined with the irregular form of the pattern along which the transition occurs, produce an effect that renders the creature wellnigh unrecognizable, even when it is resting in full view.

Considering the general abundance of lichen on tree-trunks and boughs, and on walls, it is scarcely surprising that its appearance has so repeatedly been adopted for purposes of disguise by all manner of animals. Moreover, as a background against which an animal may readily be concealed, lichen is peculiarly apt—on account of its irregularity of contour, its intricacy of pattern, and its tonal contrasts, as well as its natural abundance.

(2) **The Relation between Coloration and Habitat**—Even when not reposing upon or among the plant that it resembles, a lichen-like form resting on a tree or rock may easily escape notice. But it is significant that such animals normally act their part on the appropriate stage, that is to say, they are in general associated with their model—in just the same way that we normally find bark-like forms resting on trees, weed-like animals living among sea-weed, coral-like creatures among coral. Conversely, we may look in vain in the sea for animals resembling the excrement of birds ; nor shall we commonly find there forms looking like bark or blossoms, any more than we shall see creatures that simulate corals living on tree-trunks ; or sea-weed, on ground herbage.

This important relation between the object imitated and the natural habitat of the imitator may be seen in a somewhat different light by considering the appearance of a number of related animals in relation to their respective haunts and habits. For instance, to take an example from the Lacertilia: one of the most beautiful cases of lichen-resemblance of which I have personal acquaintance in the field is that of the lizard *Agama atricollis.* In a belt of rain forest at Amatongas, in Portuguese East Africa, where I came across this fine Agamid, it was essentially arboreal in its habits, and could be seen sunning itself on tree-stumps or logs, or running on the rough trunks of great trees, where its coloration harmonized wonderfully with lichen-encrusted bark. Its ground-colour varies from brown or olive to silvery-grey, broken by irregular patches of silvery-green and sepia, by scattered blue-green and yellow scales, and by a conspicuous jet-black patch on the shoulder: the head colour ranges from olive or grey to blue or emerald: the tail is olive or grey, broken with silvery bands. No one who has observed the species in nature can fail to appreciate the remarkable effectiveness of its concealing coloration, which embodies all the varying hues of forest leaves, moulds, and lichen-covered bark with its silvery high-lights and black shadows. Now a similar colour-scheme is exhibited by tree-dwelling lizards belonging to several families in different parts of the world. Among Iguanidæ, for instance, it is seen in the arboreal *Anolis ortonii*, of the Amazon valley; and among Gekkonidæ (as already mentioned) in the Madagascar *Uroplates fimbriatus.* This type of coloration is typical of bark-haunting forms, whereas it does not generally occur in species frequenting, say, the foliage of trees, or grass or ground herbage, or sandy wastes. On the contrary, the Agamid, Iguanid, and Gekkonid species, typical, for instance, of deserts—like *Moloch horridus*, of Western Australia, *Phrynosoma cornutum*, of Arizona, and *Palmatogekko rangei*, of South-West Africa—are dressed in the drab and dusty garments of their environment.

V. SPECIAL RESEMBLANCE TO LIANAS

We have remarked in an earlier chapter that cryptic coloration renders many tree-snakes more or less difficult to detect in nature. But certain of them excel in this respect, having become exceedingly attentuated and vine-like in appearance—a specialization that reaches its highest development in the species of *Oxybelis* in Central and South America, of *Thelotornis* in tropical Africa, and of *Dryophis* in South-east Asia. Snakes belonging to the above genera must in certain respects be regarded as unique—on account of their extraordinary slenderness, cryptic coloration, and highly specialized arboreal habits.

Only those who have seen them in their native haunts can appreciate the marvellous way in which appearance and habits combine to create a deceptive resemblance to green tendrils or dead vines twined loosely among the foliage. A beautiful example is presented by *Oxybelis acuminatus.* This snake, which may be green, grey, or brown in colour, has a narrow, pointed head, excessively attentuated body, and long, tapering prehensile tail. Whilst in the rain-forests of the Lower Amazon I have marvelled at the successful camouflage exhibited by this animated liana : the first specimen which I came across near Pará was to me a revelation of the art of aggressive resemblance. With a total length of three feet eleven inches, of which the tail accounted for one foot seven inches, the body at its thickest point slightly exceeded a quarter of an inch in diameter. In other words, the animal was 160 times as long as its greatest width. Greyish-brown in colour, variegated with silvery-grey patches and minute sepia markings, and with its individual scales overlapping so closely as to be indistinguishable, the creature reproduced in remarkable detail the colour, texture, and general form of a liana.

These snakes are sometimes in the habit of stopping with the fore body —perhaps a foot or more in length—stretched forward horizontally and held motionless in space, a feat which must require great muscular effort and control. Occasionally when in such an attitude they impart to the body a swaying motion, which adds to the deceptive appearance and recalls the antics of the leaf-insect *Phyllium* when instinctively imitating the movement of a leaf disturbed by a breath of wind.

It is difficult to think of any animal more perfectly adapted to its environment and conditions of life. Length, lightness, and great muscular strength combine in enabling this wonderful, whip-like creature to thread its sinuous way, smoothly, noiselessly, and with perfect precision, through the broad-leaved luxuriance of tropical foliage ; to scale tree-trunks festooned with their untidy burden of parasitic and epiphytic plants, or glide with ease and grace along lateral branches ; to project the front of its body far from any support as it spans the gap between adjacent boughs ; to dart away, if alarmed, swift as an arrow in flight, scarcely touching the twigs through which it drives a path ; or remaining motionless, to fade from view—indistinguishable from the tangle of twining vines and grey lianas that trail everywhere in the confusion of its forest home.

Ditmars (145) has referred to the concealing coloration of a related species, *Oxybelis fulgidus*, as follows : 'The author had four of these specimens in a cage containing a green bush, and there was frequent amusement in asking friends to count how many there were. Right under one's eyes it was difficult to differentiate their bodies from the stems and foliage and few observers could be induced to say there were more than two.'

The genus has a tropical African counterpart in Kirtland's Tree-snake (*Thelotornis kirtlandii*), a splendid species which agrees with *Oxybelis* in its excessively elongated body and slender whip-like tail, its cryptic colour-scheme of variegated greens and browns and greys, and its essentially arboreal feeding habits and manner of life. No one who has seen the animal in its natural surroundings can doubt the efficiency of the anticryptic coloration—an adaptation typical of many other African genera, such as *Chlorophis*, *Philothamnus*, and *Dendraspis*, but nowhere in East Africa seen in such perfection as in the present species, whose coloration, form, and feeding habits represent the extreme of arboreal specialization.

In tropical Asia the same role is played by species of *Dryophis*, such as *D. prasinus*, of Borneo, whose commonest variety is bright green in colour. According to Shelford, it is ‘the most beautiful and graceful creature imaginable. . . . To see one of these snakes gliding amongst foliage is to realize the meaning of the phrase “poetry of motion”.’ The nearly allied *D. mycterizans*, from India, a species growing to a length of over six feet, and intensely green in colour, has been described by Wall (645) as usually reclining on the topmost boughs of bushes, where it would generally pass for a green twig, and escape notice. Wall also remarks on its ‘wonderful turn of speed over the foliage’, and states that he has seen its pursuers running along a hedge find some difficulty in keeping up with it. Such potential speed, when combined with cryptic habits and coloration so perfect, must render the animal a formidable adversary to the birds, lizards, and other snakes on which it lives.

VI. SPECIAL RESEMBLANCE TO EXCREMENT

Among the whole range of special resemblance, one of the most singular classes of examples is furnished by certain animals which bear a striking and intimate resemblance to the excrement of a bird. A classical instance of this kind relates to a spider, *Ornithoscatoides decipiens*, which was discovered in West Java by Forbes. Since, however, the device is here mainly alluring in function, we shall refer to it in detail on a later page.

Many insects, belonging to different groups and inhabiting different parts of the world, illustrate special resemblances of the same sort, but essentially protective in function, and it is instructive to notice how the deceptive appearance itself is brought about in a variety of entirely different ways.

Certain Geometrid and Drepanid moths—white in colour with blackish, brown, or grey markings—habitually expose themselves with the wings extended and closely applied to the surface of the leaves on which they rest. ‘In this position’, writes Poulton (496), ‘they forcibly suggest the appearance of birds’ excrement which has fallen from a great height, and has therefore become flattened into a wide patch.’ *Problepsis ægretta* (Plate 45) is a beautiful example.

In other cases the resemblance is to a dropping of more solid consistency, and hence of cylindrical form, as opposed to those which we have considered, in which the imitated excrement is more fluid and flattened. This effect is reproduced by several moths, which rest with the wings wrapped round the body after the manner of a cloak. Such are the small South American *Stenoma* described and figured by Mrs. Brindley (232), and the British *Olethreutes salicella*, and *Cilix glaucata* (see Plate 45).

Sometimes it is the caterpillar, rather than the adult insect, which is perfected to this end. An extraordinary case of the sort, described by Colonel A. Newnham, is cited by Poulton (513). Newnham’s drawings and description indicate that the insect is probably a Notodontid larva. He writes: ‘I came across the larva in question in the month of August or September 1892, at Ahmadabad on a bush of Salvadora, I think. . . . I was stretching across to collect a beetle and in withdrawing my hand nearly touched what I took to be the disgusting excrement of a crow. Then to my astonishment I saw it was a caterpillar half-hanging, half-lying limply down a leaf. The chief thing that struck me about it was the apparently unnecessary perfection of the resemblance. The Russian proverb "Nature dura" (Nature is a fool) occurred to me, because it seems so much simpler and efficacious for the larva when at rest to conceal itself under the leaf.

'Another thing that struck me was the skill with which the colouring rendered the varying surfaces, the dried portion at the top, then the main portion, moist, viscid, soft, and the glistening globule at the end. A skilled artist, working with all the materials at his command, could not have done it better.'

The lower 'glistening globule', indicated in Newnham's drawings and shown by Poulton to resemble perfectly 'a droplet formed by the liquid part of the excrement and still attached by a slender stalk to the more solid parts', is actually reproduced by a median prominence on the caterpillar's back, the head being tucked in so that this prominence forms the lower extremity of the 'dropping'.

An instance of the same kind in Britain is afforded by an early larval stage of *Acronycta alni.* Another very interesting case has been recorded by Carpenter from Uganda (87). On one leaf of a tree he found a company of young caterpillars of the Bombycid moth *Triloqua obliquissima.* The stony-grey larvæ became chalky-white after the first moult. As at this stage they 'always crowded closely together and fed on the flat surface of the leaf (an unusual habit for Bombycid larvæ)', the group closely simulated a patch of excrement.

In the Homopterous *Naiacoccus serpentinus*, a Scale Insect from Lahore, India, a similar general effect is attained in an entirely different way: in this case, it is the whitish twisted masses of egg sacs which simulate excrement.

The coloration of certain beetles also falls into this class. Two good examples are afforded by the Elaterid (*Alaus hieroglyphicus*), from Uganda, and the Curculionid (*Alcides trifidus*) from Japan. The former, an elongated insect wearing a somewhat irregular white and sepia-colour scheme, represents in a very realistic manner the dropping of some large bird or lizard. The latter, oval in shape, is greyish-white with a black saddle which serves both to break up the weevil's apparent form and to give a general resemblance to an excreted pellet. In yet other cases, as with certain beetles, the excrement resembled is not that of a vertebrate, but of a caterpillar (87). Referring to the genus *Chlamys*, Dr. H. E. Hinton informs me that he has come across instances of the kind in Mexico, in which it was easier to detect the deception by feeling whether the suspected object was hard or soft, than by inspection. As instances he mentions the Mexican *C. stictica*, the Chilian *C. apricaria*, and the Brazilian *C. arcula.* He tells me further that when disturbed they remain quiescent in the so-called 'death-feint' so commonly seen in other cryptic organisms.

I have gone into these resemblances of different animals to droppings somewhat fully because it is only thus possible to show clearly how remarkably effective the resemblances are in creating a deception—in deceiving, not indeed the eye of casual spectators who know nothing and care less for the features, colours and meaning of natural objects, but the eyes of trained observers—experts and naturalists whose very knowledge, experience and powers of discrimination render the illusion the more significant.

I will illustrate this point by referring briefly to two further cases. The first was kindly given me by Dr. C. B. Williams, who wrote in answer to an inquiry: 'In the district round Amani N.E. Tanganyika a small moth resembling a bird-dropping was not uncommon. On one occasion I observed what I thought to be one on a leaf, but after a close examination from a distance of only a few inches I discovered (to my own satisfaction) that it was after all only a bird-dropping. Just as I turned away the said bird-dropping flew off!'

A similar but converse experience is described by Mrs. Brindley. She had collected half a dozen excrement-like larvæ of a large Swallow-tail Butterfly, on a vine in British Guiana, and brought them into the house for examination. 'A few minutes later', she says, 'I saw what I supposed to be one of these caterpillars accidentally dropped, lying on the doorstep, and picked it up. However, it turned out that I was quite deceived, and that the object was really excrement, dropped by a captive trumpeter tethered near the house' (232).

A remarkable feature in certain of these cases is the detailed accuracy of the imitation, even to the reproduced appearance of the lower dried-up, or still fluid, part of the dropping—which is effected, by the fine-textured white web film of *Ornithoscatoides decipiens*, and by a median dorsal prominence in the Indian caterpillar. It is perhaps not surprising that H. O. Forbes and Colonel Newnham, the two naturalists who discovered these specialized examples, both considered the appearance unnecessarily perfect. (The same view has also been expressed in reference to the other detailed special resemblances, such, for instance, as shown by many leaf-like Orthoptera and Lepidoptera.) But, as pointed out by Poulton, 'the class of enemies which could learn that a cocoon is thinner where it is attached to a leaf and can best be opened by pecking through the leaf was unlikely to be evaded by the simple expedient of resting on the under surface. Free exposure on the upper surface, with the disguise already explained, was likely to be far more advantageous, when the object resembled is both unpleasant and very common in similar situations, and the animals which resemble it extremely rare' (513). It is also to be noted that these and most other very detailed examples occur in tropical countries where the interspecific warfare between prey and predator goes on incessantly at high pressure.

Regarding the function of the resemblances, we have to bear in mind that while excrement is not normally devoured by birds (though for sanitary purposes many birds habitually eat the droppings of their fledglings or remove them from the vicinity of the nest), it is, on the other hand, attractive to different insects—bugs, flies, butterflies, and others—which visit excrement for the sake of its contained moisture. Thus in spiders the imitation may doubtless serve a double function—alluring and concealing; it may serve both to attract prey and also to deceive enemies. But in Lepidoptera, whether larvæ or adults, and in plant-feeding weevils and other Coleoptera, only the latter purpose can be served. We must admit, however, that actual evidence, apart from strong *a priori* considerations, is scanty, and further observations, supported by experiments, on these extremely interesting excrement-resembling creatures are greatly needed.

VII. SPECIAL CRYPTIC APPEARANCES EFFECTED BY WIDELY DISSIMILAR MEANS

Under the heading of resemblances to leaves, to lichen, and to excrement, we have seen how the same end has been achieved independently by widely dissimilar means in different animals. Indeed, this fundamental principle of convergence pervades all classes of adaptive coloration phenomena. The *appearance*, and the *effect on the observer*, is the thing which counts. The methods by which the appearance is attained do not signify, except as a means to that end.

(1) **Resemblances to Stipules**—This point is strikingly brought out by the following instance of two widely unrelated animals—a bug and a caterpillar—both inhabitants of the rain forest of British Guiana, and both protected by a special resemblance to a plant stipule. The first, a solitary Membracid (*Lycoderes hippocampus*), has been described by Mrs. Brindley. This insect has a black pronotum, which is produced dorsally into a long horn. Below it the wings are transparent, and thus allow the green abdomen to be seen through them. It was found feeding in the axils of leaves, where, she says, it was ‘ the perfect likeness of a withered and partly skeletonized stipule ’ (232).

A very different arrangement has been described and figured by Hingston in a caterpillar which constructs a somewhat curved, conical case, made out of brown vegetable hairs, within which it dwells. The caterpillar clings to its plant, *Cephælis tomentosa*, through an opening at the base of the cone, in which position the structure looks exactly like one of the stipules growing on the stem. ‘ Case and stipule ’, he writes, ‘ are the same shape and size ; they are attached to the plant in the same way and incline from it to the same degree ; their colour too is absolutely identical owing to both being covered in the same brown hairs. Case cannot be distinguished from stipule until it begins to move ’ (265).

(2) **Resemblances to Broken Twigs**—Two further examples which beautifully illustrate how similar effects may be produced by different means may be mentioned. Among the various natural objects imitated by different animals, branches, or twigs with one end broken off, figure as models. Certain moths are wonderfully made up to play this part. One of these is the large *Duomitus leuconotus* (Cossidæ) from India and Ceylon. This moth flies late at night, resting by day with the wings folded closely in against the sides of the body. In this attitude, the crest-like tuft of cream-coloured hairs on its thorax, and the similarly coloured tuft on its head ending abruptly in front, look like the splintered end of a broken twig, of which the beautiful grey wings, with their blackish marbling and irregular creamy-white spots arranged in a striking disruptive design, apparently form the weather-worn, lichen-covered bark.

Less perfect, though yet effective as a stick-simulator of this type, is the more familiar Buff-tip Moth, *Phalera bucephala* (Notodontidæ). The violet-grey variegated fore wings, which in the resting insect are folded in a roof-like manner at the sides of the body, resemble fairly closely the outer part of a decayed twig, while the oval ochreous patch on their slightly incurved ends reproduces the appearance of a woody broken-off stump. It will be seen that in *D. leuconotus* the effect of a fractured end is produced by hair-like scales on the head and thorax, and is therefore anterior in position : in *P. bucephala* an analogous effect is reproduced by the incurved extremities of the fore wings, and is therefore posterior in position.

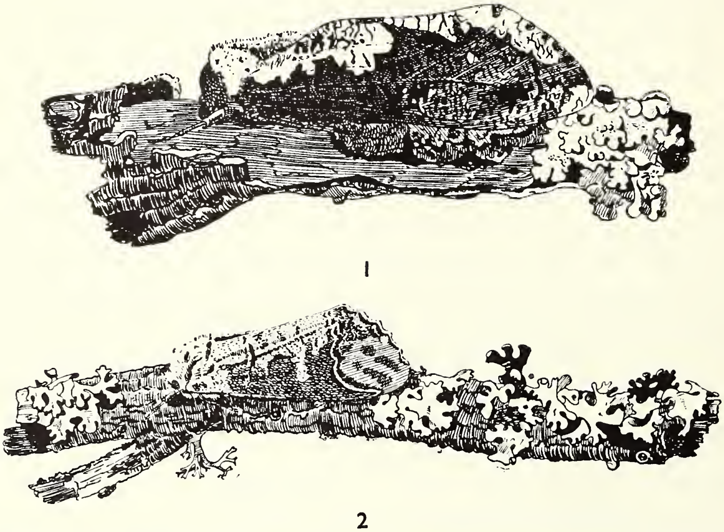

FIG. 68.—Special resemblance to broken twigs : 1 *Duomitus leuconotus* ; 2 *Phalera bucephala*

(3) **Resemblance to Growing Twigs**—More frequently the similarity is to a twig growing out from its parent branch rather than to one that has become detached ; and it is a singular fact that this special type of deceptive resemblance has been perfected by a number of totally distinct insects. The best-known instance is, of course, presented by various Geometrid larvæ, which rest with the body erect and inclined outwards at an angle from a stick of the food plant.

Now a precisely similar effect is attained in an entirely different manner by the Phasmid *Parasosibia parva*, whose singular resting attitude has been described by Cappe de Baillon, Favrelle, and de Vichet. This insect rests on a branch with its head downwards, the antennæ and front legs stretched forwards, and the second pair clasping the support. The whole of the body behind the mesonotum is inclined outwards at an angle, rigid and straight, with the legs closely applied to the body. Here, then, the fore part of the insect performs the duty which is carried out by the posterior segments of the caterpillar, the latter having its head directed upwards, the former its abdomen.

This situation takes on additional significance when we examine the resting attitude of the Australian Phasmodid grasshopper *Zabrochilus australis.* I have recently received from Mr. A. J. Nicholson a photograph of this species from life. As with *Parasosibia parva,* an inverted position is adopted, the fore feet and antennæ of the grasshopper lying together and being closely applied to the stem—precisely as with the Phasmid. But here the comparison ends. For the lateral ' twig ' is formed by the tegmina alone, these being so constructed that they cannot be closed down against the body. The latter, together with the hind legs, are directed backwards in close contact with the branch (Fig. 69).

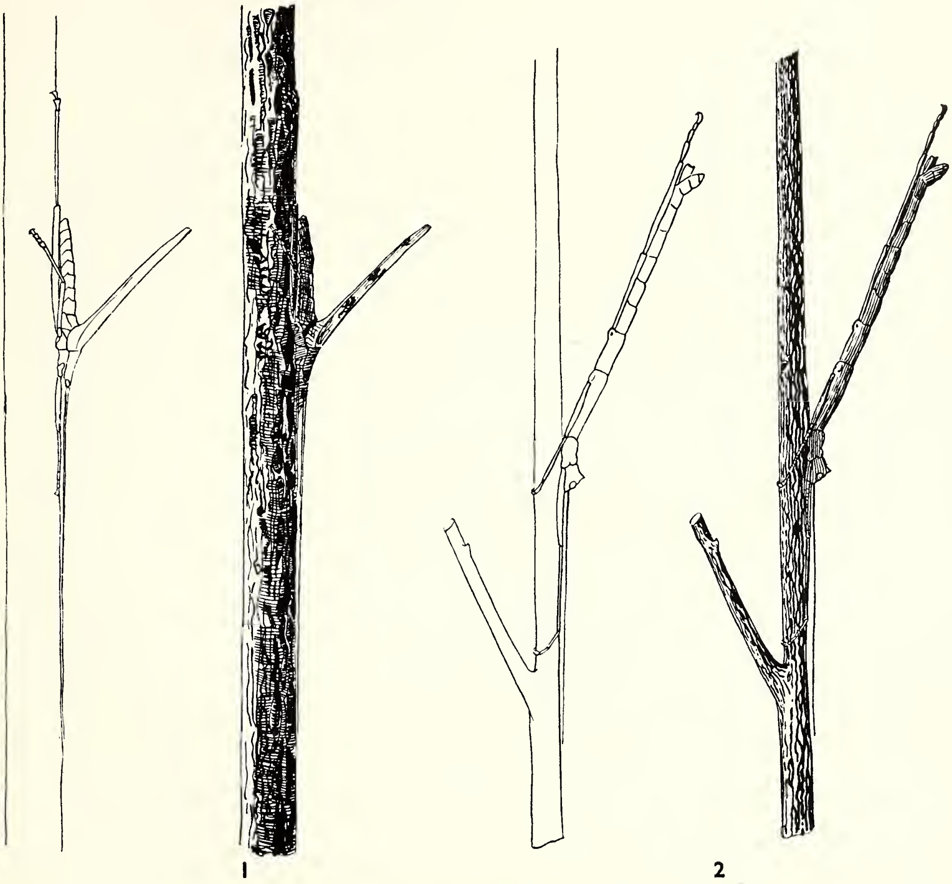

FIG. 69.—Special resemblance to growing twigs, showing cryptic resting attitude: 1, of the grasshopper *Zabrochilus australis* (*based upon a photograph by* A. J. NICHOLSON); and 2, of the stick-insect *Parasosibia parva* (*after* CHOPARD)

VIII. DISSIMILAR CRYPTIC APPEARANCES FOUND WITHIN PARTICULAR GROUPS OF ANIMALS

Many cases have already been mentioned of *widely different appearances occurring among animals of close affinity.* This is really a special application —in terms of adaptive coloration—of the principle of adaptive radiation, by which is meant the superficial difference in form and structure of related animals due to adaptation to different modes of life, as shown chiefly by the divergent methods of locomotion and of feeding evolved within particular classes and orders.

(1) **Cryptic Adaptive Radiation in Phasmidæ and Mantidæ**—In its application to concealment or deception in nature those highly curious and interesting Orthoptera, the Phasmidæ, well illustrate this principle. With the possible exception of Reduviid bugs, it is probably true to say that no family of insects exhibits so great variety of form or diversity of appearance. Among the different genera and species are many which look like stems, twigs, or sticks of various descriptions: such forms may be green, or brown, or grey in colour; broad and bark-like—as in *Cotylosoma dipneusticum*, of Fiji; large-bodied and branch-like—as in *Cyphocrania gigas*, of Amboina; or extremely attenuated, with limbs and bodies smooth and slender, resembling the young stems of plants—as in *Carausius margaritaceus*, of Annam; or, like the Brazilian *Acanthoclonia sævissimus*, dusky-hued, rough-textured, and studded with sharp, thorn-like spines. Others, again, such as *Aruanoidea grubaneri*, from Perak, resemble stems of grass; or pieces of lichen-covered bark, as in *Prisopus piperinus.* Others, of irregular form, are moss-like in appearance—as *Epicharmus marchali*; while the well-known 'leaf-insects', such as *Phyllium crurifolium* in Ceylon, live up to their popular reputation in resembling leaves of various hue—reddish-yellow, bright green, or russet.

It is significant that where the two sexes differ in their powers of flight, it is the male whose wings are more fully developed, while the females are larger, more sluggish, and more frequently flightless. Probably correlated with this difference between the sexes is the further fact that the deceptive likeness to various plant structures is often much more marked in the female than in the male.

Other Orthopterous families, such as the Mantidæ, Acridiidæ, and Tettigoniidæ, show a like adaptive radiation of form to resemble various plant products. Among the first, for instance, are tree-haunting types of bark-like appearance (*Amorphoscelis annulicornis* and *Majanga basilaris*); desert-dwelling species resembling sandy ground (*Eremiaphila turcica*); while others look like sticks (*Leptocola giraffa*), grass-stems (*Mantis religiosa*), lichen (*Blepharopsis mendica* —nymph), leaves (*Chœradodis ståli*), or blossoms (*Hymenopus bicornis* and *Gongylus gongyloides*).

(2) **Cryptic Adaptive Radiation in Tettigoniidæ and Acridiidæ**—Many grasshoppers, both 'short-horned' (Acridiidæ) and 'long-horned' (Tetti-

goniidæ), diverge widely in their varied procryptic resemblances. Certain of the latter, for instance, bear the most extraordinary likeness to fresh or dead leaves, both linear and broad in form, and to grasses. Among Acridiidæ adaptive radiation of form and appearance is more striking. There are short, stout-bodied species, like the desert-dwelling *Eremocharis insignis*, from Algeria, which as nymphs resemble stones (Plate 44). Another type, looking wonderfully like the withered grass on which it lives, is well illustrated by the little straw-coloured *Acrida turrita* which I have taken at Maspalomas, in the South of Gran Canaria—an insect I could never find unless I happened to see it move. Many other species, like *Prionolopha serrata* from the Lower Amazon, and *Acrida sulphuripennis* from the Lower Zambesi, resemble fresh green grass. Others, such as *Cannula linearis*, simulate stumps of burnt grass. Others again, such as the Sumatran *Systella rafflesii*, have reproduced the resemblances to broader leaves more commonly imitated by various Tettigoniid species, and are extremely compressed in form and leaf-like in appearance. While yet another group, including such slender, attenuated forms as the South American *Cephalocœma lineata*, vie with Phasmids as stick-simulators.

Though we have only touched on the subject here, enough has been said above to indicate how striking is the adaptive divergence of coloration, form, and function within single families, in bringing about special procryptic and anticryptic resemblances to different natural objects which are inedible to an insect's enemies, or innocuous to its prey. Similar phenomena might be traced in many other orders and families—for instance, the protective resemblances of Flatid bugs to bark, blossoms, or foliage; of Membracid bugs to thorns, seeds, or stipules; of beetles and butterflies, of moths and caterpillars, of spiders and crabs, snakes and geckos, frogs and fishes to such diverse objects as coral, sea grass and seaweeds, lianas and lichen, leaves and grass, flakes of bark and broken branches, soil, seeds, flowers, cocoons and excrement, as well as to other animals.

IX. SPECIAL RESEMBLANCES IN THE SEA

Passing from an aerial to an aquatic environment, there also we find parallel phenomena. Just as different members of the terrestrial and arboreal faunas are modified in form, coloration, and habit so as to resemble all manner of natural objects occurring in their normal surroundings—twigs, lianas, bark, buds, seeds, thorns, leaves, lichen, and what not; so in the sea innumerable instances are known of special resemblances—often attaining a remarkable degree of perfection—by different marine organisms to shingle, algæ, sea grass, sponges, anemones, corals, crinoids, and other objects of their environment. In these pages it will only be possible to refer to a few cases which are selected not merely because they are of interest on their own account, but because they illustrate principles and confirm conclusions suggested from similar studies in other environments.

As might, of course, be expected, our examples come mainly from in-shore waters of coast or coral reef, or from special environments such as that provided by floating sargasso weed—all environments exceptionally rich both in abundance and variety of animal life, and, incidentally, of potential models for simulation. We should not expect deep-sea forms to exhibit special resemblances to natural objects since neither they themselves nor their surroundings can be seen in the eternal darkness of the abyss, except by the uncertain light of luminescent organisms. Nor do we commonly find instances of special resemblance among pelagic forms whose lives are spent floating or swimming in the open waters of the ocean, where is to be found no substratum and no hiding-place.

(1) **Special Resemblance to Cœlenterata**—Protective resemblances are familiar to every zoologist who has studied the shallow-sea fauna. In his delightful work *A Naturalist in Indian Seas*, Alcock mentions several interesting cases of the kind. For example, on a common branching Alcyonarian (*Spongodes pustulosa* or some very closely related species), whose individual polyps were a bright pink colour, he found no less than four species of Crustacea—an *Alpheus*, a *Galathea*, a *Porcellana*, and a little Spider crab *Hoplophrys oatesi*, all of which, he states, were coloured in life greyish-white with bright pink spots, so that they were invisible so long as they remained quiet in their living refuge. *Pteroeides elegans*, another Alcyonarian belonging to a different order—the Pennatulacea or ' Sea-pens '—was grey in ground-colour, profusely marked with little blackish rings. This species was closely attended by three species of Crustacea which lived among its ' leaves '—all of them, he states, coloured and spotted exactly like the living citadel in which they dwelt.

The above cases illustrate once more the familiar principle of convergent adaptive coloration—of dissimilar animals assuming a common cryptic livery in adaptation to the same surroundings. An instance which well illustrates the converse principle—of similar forms varying in appearance in adaptation to different surroundings—and in which the related Gorgonacea or ' Sea-fans ' play the part of environmental model, has been described by Osborn (449*a*). At Beaufort, in North Carolina, an orange-yellow Sea-fan (*Leptogorgia virgulata*), occurring in shallow water, was attended by the Gastropod mollusc *Ovulum uniplicatum*. Both the shell of the mollusc and the folds of skin that surround it in the expanded state were of precisely the same orange-yellow colour. Osborn states that the *Ovulum* was abundantly found in association with *Leptogorgia*, but was never met with apart from it. Another *Leptogorgia* found in ten fathoms of water, of the same general habit, but very differently coloured, being deep-rose or purplish in hue, mottled with white round the openings of the polyps, was also seen on examination to harbour in large numbers a form of *Ovulum uniplicatum*. But here the mollusc was again coloured so as to harmonize perfectly with its host, having the shell red-brown, and the surrounding skin-folds deep-rose in colour, *mottled with white spots*.

As compared with many other groups of animals, molluscs afford relatively few instances of protective resemblance—among which it may therefore be pertinent to refer here to the Gastropod *Lamellaria perspicua*, whose adaptive coloration has been described by Giard (in Plateau, 474). When found on granite, it is grey in colour, with white, brown, and black markings; but when associated with Tunicates, it again faithfully reproduces the colour of its support—uniform red on *Leptoclinum fulgidum*, yellow on *L. gelatinosum*, while it has also been found imitating two other species, namely, *L. durum* and *L. asperum*.

Among the cœlenterates which are imitated by animals associated with them, we must also mention sea-anemones and corals. The former, themselves well protected from attack by their stinging-cells and unpalatable nature, are used as a harbour of refuge, and sometimes as an actual retreat, by various crabs and fishes that are known to enter into curious and more or less intimate partnerships with them. Some of these cases have been discussed under the heading of Adventitious Warning Coloration, where we find various animals, themselves relatively defenceless, benefiting from the proximity of an aposematic partner not only by a borrowed means of physical defence, but also by a borrowed means of psychological warning.

In other cases, the coloration of the anemone is itself closely imitated by animals domiciled upon it. Thus in the Great Coco Islands Alcock observed several kinds of shrimps living among the tentacles of a huge blue-spotted species. Like their animated environment, they were spotted and banded with blue, and invisible as long as they kept under shelter (2). It is clear that we have here a condition closely akin to true protective mimicry.

Living corals, as well as the weathered coral shingle, are likewise imitated by different in-shore animals—notably coral-haunting fishes. A Gastropod mollusc *Cypræa pustulata*, which occurs on corals in Panama Bay, has, according to Mortensen, the skin-folds set with small, branching protuberances, coloured exactly like the coral-polyps (417). Alcock found several species of small flat-fishes in Indian waters which, he states, were so curiously dappled and mottled as to defy detection on the coral shingle where they rested: he refers especially to *Samaris cristatus* of the Ceylon coast as ‘ one of the most perfectly concealed species . . . whose effective toning surpasses description ’ (2). Another beautiful example—of which Franz gives a figure in colour—is that of a small Japanese Serranid fish observed by Doflein to be associated with the coral *Astræa*, both fish and coral wearing the same red and yellow dress (185).

(2) **Special Resemblance to Echinodermata**—At Murray Island Potts (487) found a Crinoid (*Comatula parvicirra*), with which were associated as commensals two species of Alpheid, two species of shrimps, a *Munida*, an Amphipod, and an Isopod among Crustacea; various Myzostomids and a Polynoid polychæte among Annelida; and certain Ophiuroids: in most of these cases, he says, the coloration showed some relation to that of the host: and of the Alpheids in particular he states that their colour varied greatly and corresponded roughly with that of the host, which was also very variable—the same variations occurring in both.

Alcock has similar instances from the Indian Seas: a *Galathea*, banded with violet and blue, was found living on a Crinoid striped in exactly the same fashion. In another case, Crustacea striped in alternate bands of yellow and

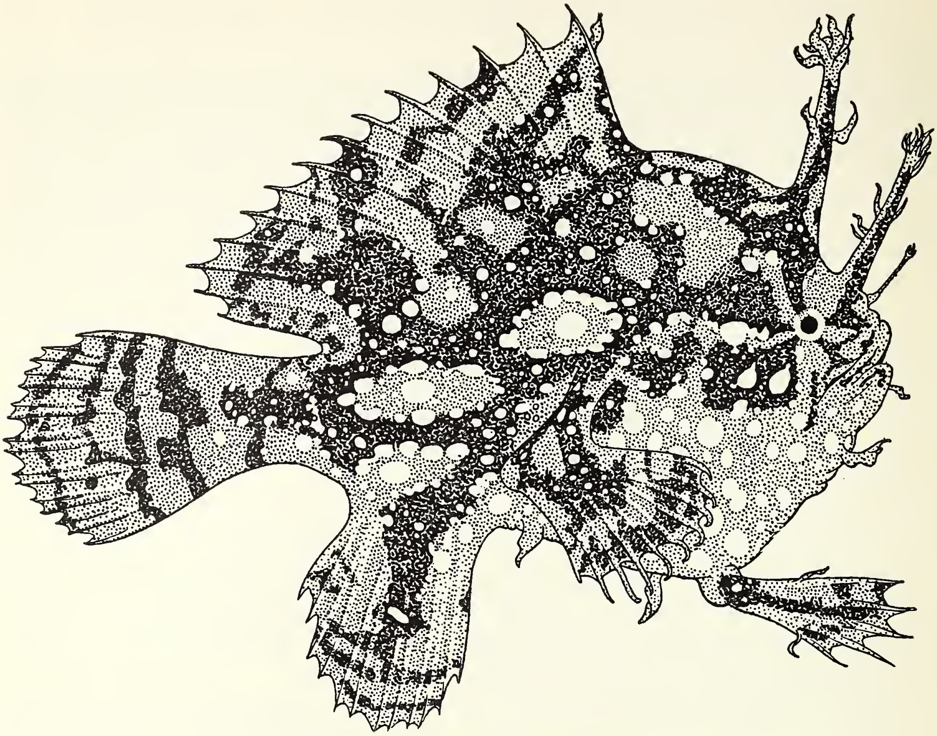

FIG. 70.—*Antennarius marmoratus*

FIG. 71.—*Pterophryne tumida*

purple were taken sheltering on the fronds of a similarly striped Sea Lily (*Actinometra*), while in a different area the same species was utilized as a place of refuge by sea worms which once more reproduced the yellow and purple banding of their Crinoid partner (2).

(3) **Special Resemblance to Algæ**—Just as leaves constitute an important type of model for special resemblances on land, so do marine algæ in the sea. The green, brown, or red sea-weeds of the coast are inhabited by a very rich and varied fauna, including many species which bear a close cryptic resemblance to the particular alga with which they are associated; and the same applies to the floating pelagic Gulf Weed, whose highly peculiar fauna is especially noteworthy for the high percentage of more or less effectively concealed forms, which include besides Mollusca, Crustacea, and Annelida, a number of small fishes such as the Gurnard *Dactylopteris volitans*, the Pipe-fish *Syngnathus pelagicus*, and the Frog-fishes *Antennarius marmoratus* (Fig. 70) and *Pterophryne tumida* (Fig. 71). The last are pelagic members of the Antennariidæ, bizarre in appearance, being adorned with fleshy protuberances and weed-like filaments,

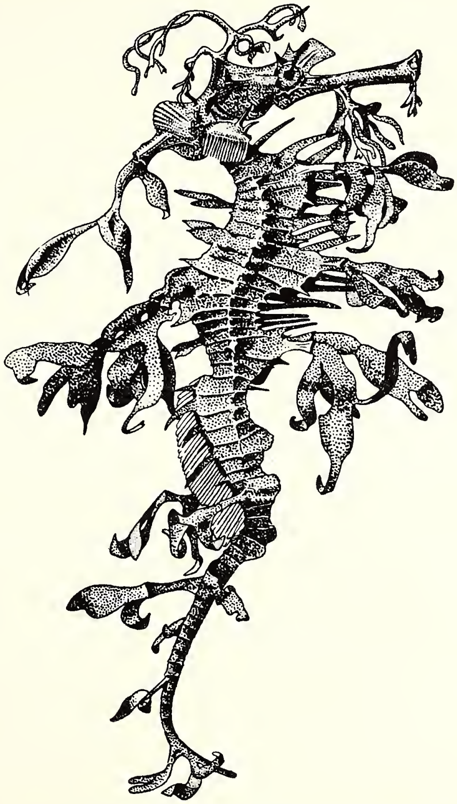

FIG. 72.—Sea Dragon (*Phyllopteryx eques*)

and wearing the typical Sargasso uniform of yellow, with irregular brown bands and small white spots representing incrusting organisms growing on the weed.

An interesting Crustacean belonging to the *Sargassum* fauna, recently described by Dr. Robert Gurney, is the prawn *Hippolyte acuminata*. In addition to wearing the usual cryptic dress common to so many of the weed animals, this little prawn has its waisted body banded with light and shade in such a way that *it appears to be broken up into two parts*, each of which bears a certain resemblance to the vesicles of *Sargassum* (219).

Among the in-shore weed-like crustacea, perhaps the most beautiful example of special protective resemblance is afforded by a little crab *Huenia proteus*, whose carapace simulates in form and colour a segment of a frond of *Halimeda*, the weed with which it is associated.

Even more singular and specialized is that animated piece of sea-weed, the so-called Sea Dragon (*Phyllopteryx eques*), of Australian waters (Fig. 72). One can scarcely imagine a less fish-like fish than this extraordinary Sea-horse with its fantastic outline distorted and broken up by numerous filaments—developed from its head and tail, back and belly—which stream out in the surrounding water and create a most deceptive resemblance to weed. The filaments themselves, as may be seen from the accompanying illustration, are variously shaped. Branches of what appear to be a fine species of weed sprout from the chin and the back of the head; broader leaf-like fronds of a larger weed are simulated by processes springing at intervals from the dorsal and ventral surfaces; while a series of flattened plumeless spines, mainly but not confined to the ventral surface, simulate sprouting algal shoots.

2. ADAPTIVE BEHAVIOUR IN RELATION TO SPECIAL CRYPTIC RESEMBLANCE

> The act of movement means life, and life interests us, for we are living beings ourselves. Dead things are abhorrent to us, and we put them out of sight.
>
> ALFRED EAST

Under various headings in this book I have already laid some stress upon the essential part played by special instincts and particular attitudes in producing cryptic and aposematic effects. If such specific habits contribute so largely to the success of general cryptic resemblances, they become doubly important when we pass from the phenomena of concealing and advertising to those of deceiving coloration. For here we are dealing with appearances which are neither general nor arbitrary, but rather specific and realistic. And in the field of deception, or imposition, mere make-up is not enough. If the disguise is to be complete, animals must *act* as well as *look* the part they are destined to play. We have now to consider the subject of special resemblance in terms of the special behaviour which is so vital a factor in matters of disguise and deception.

I. SPECIAL PROTECTIVE RESEMBLANCE EFFECTED BY GREGARIOUS HABITS

In various groups of insects, gregarious resting or feeding habits are generally associated with conspicuous coloration, whose effect on an observer is intensified by the aggregation of individuals. There are, however, certain notable exceptions, in which gregariousness has just the opposite effect, by bringing about a deceptive appearance to some familiar object such as a cluster of flowers, or the dropping of a bird, and thus enhancing self-effacement rather than self-advertisement.

I have referred elsewhere (p. 331) to the caterpillars of the Bombycid moth *Triloqua obliquissima*, which, as observed by Hale Carpenter in Uganda, crowd together and feed on the flat surface of a leaf, where they combine to resemble a patch of excrement. Mrs. Brindley has described a forest-dwelling Membracid bug of the genus *Bolbonota*, whose peculiar breeding habits give rise to a deceptive appearance : ' The nest is a crescentic structure made of a white waxy substance in which the eggs are embedded, and several are built in a cluster against a twig. The female sits in a cavity on the upper surface of the nest, which is several times larger than her body ; and the whole colony is easily mistaken for one of the crops of small white fungi sprinkled with bits of bark which are common objects among the undergrowth ' (232).

Perhaps the most striking instance of deceptive resemblance due to gregariousness is afforded by Homopterous bugs of the genus *Flata*, whose habit of clustering together on the stems of plants when at rest gives them a remarkable resemblance to certain flowers. In 1896 Professor J. W. Gregory published an account of *Flata nigrocincta*, a species which occurs in two forms, green and red respectively, and which he found at Kibwezi, in British East Africa, clustered upon upright stems, with the green individuals above and the red beneath, an arrangement which closely simulated the flower-spikes of a Foxglove or a *Tinnæa*—the green uppermost specimens representing the unopened buds, those beneath the open flowers (217).

Such grouping according to colour has very rarely been observed (the colour arrangement is usually quite promiscuous), and Gregory's statement and coloured figure of this imitation flower-spike have attracted much interest and some criticism.[1] It is certainly so remarkable as to require careful examination, though his observations were to some extent confirmed in 1912 by Dr. A. C. Parsons, who observed a nearly related species, *Phromnia* (*Flata*) *superba*, in Northern Nigeria. Some thirty or forty of the insects had settled on a nearly leafless branch, with their heads all pointing the same way (upwards) and ' the colour graduated from green at the top of the twig to a deep dove colour that would indicate the oldest blossoms below '. In a letter he states that he mistook the insect cluster for a most beautiful dove-coloured pea flower, and it was not until he had gathered it, with a view to painting it on his return to camp, that he realized how he had been taken in—as the ' blossoms ' flew up in a cloud about his head !

While this colour arrangement does not appear to be at all general, there is abundant evidence both of the insects' gregarious instincts, and of the resemblance which the insect congregations bear to blossoms and buds. Hinde found *Flata nigrocincta*, in British East Africa, resting on horizontal twigs and with the colours intermixed, but states that both he and his wife recognized a strong superficial likeness between the mixed groups of insects and the flowers and buds of a leguminous plant with which they were perfectly familiar ; and that they have mistaken the insects for the flowers, and conversely the flowers for the insects (258).

An Indian species, *Phromnia* (*Flata*) *marginella*, has been observed by Imms in the Himalayan foot-hills of Kumaon. This insect, which also occurs in two forms—pea-green and pinkish-buff respectively—was found resting in closely packed groups, likewise with the heads all pointing in one direction, on the twigs and branches of forest trees. Clusters of the green form are described by Imms as bearing a considerable resemblance to leaf or flower buds just about to open, while the buff-coloured examples appeared very like unopened petals (280). In *Siphanta acuta*, an Australian Flatid which has been figured by Tillyard (625), the roof-like wings are coloured bright green with pale venation.

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[1] I am indebted to Sir John Graham Kerr for the information that Gregory subsequently told him the illustration was erroneous as regards the difference in *size* of the individual insects ; but in other respects Gregory stood by the correctness of the figure.

A correspondent, Miss M. L. Parker Smith, has recently sent me a drawing of a blue form which she observed many years ago in the Botanical Gardens at Kandy. According to Mr. Ernest Green the species figured is *Hansenia glauca*, a Flatid allied to *Phromnia* (*Flata*) *marginella*, which is apparently peculiar to Ceylon, and which commonly rests, as figured by Miss Parker Smith, clustered along the stem of certain *Eugenia* trees upon which the larva feeds.

Observations in the field indicate that single individuals of *Flata* appear more conspicuous to human eyes than when the insects are clustered together, and it is interesting to note that their gregariousness is no mere passive aggregation of individuals that have never been scattered since birth, for according to Hinde, imagines which have been dispersed in flight soon begin to collect again into groups—and this instinctive habit of combining for mutual protection is shared by the white waxy larvæ (258) which resemble, when clustered, groups of white blossoms (280).

II. SPECIAL RESEMBLANCES ENHANCED BY ADAPTIVE MOVEMENTS

Adaptive attitudes and behaviour, of a kind appropriate to the animal's appearance and conditions of life, may indeed be said to form a fundamental factor in the phenomena of special cryptic resemblance. The subject, which is one of great interest and significance, and which offers wide scope for further experiment and observation, especially, perhaps, in tropical forests and in-shore waters, is one which we cannot pursue here, beyond pointing in conclusion to certain cases of deceptive movements.

Concerned as we are here with resemblances to motionless, or at any rate to sessile or floating objects of various kinds (as opposed to active animals which frequently serve as models in cases of true mimicry), the *place of rest* and the *position of rest* are, next to form and coloration, all-important. Occasionally, however, deceptive movements of a cryptic (as opposed to a warning or bluffing) nature form part of the disguise—especially in different leaf-like forms.

It has been recorded that the flight of certain cryptic butterflies resembles the flutter of falling foliage. Thus Mortensen states that he very often had the impression that several brown-coloured butterflies from Panama resembled falling leaves when in flight. In fact, he was often uncertain whether he was looking at a butterfly in flight or a falling leaf (417). Piepers records similar observations (471).

Much more remarkable, however, are the deliberate adaptive movements made by resting insects. The leaf insect *Phyllium* will occasionally suspend itself beneath a twig or leaf-stalk by two or three legs only, and slowly rotate its body to and fro, so as to suggest the motions of a leaf just ready to fall, suspended by a thread and spinning in the breeze.

An excellent instance, recorded by Hingston from British Guiana, is that of an immature Mantid which he found on the bark of a tree. It was clinging to its support head downwards, with its thorax applied to the trunk and its leaf-like abdomen reflected and hanging down over its back. In this position Hingston states that the head and legs corresponded to a leaf node; the straight thorax to the leaf-stalk; and the flattened expanded abdomen, with its corrugated margin and grey-green colour, to the actual leaf. ‘This attitude and resemblance were remarkable enough, but still more impressive were the movements of the insect . . . though there is not much wind on the forest-floor, yet the leaves are not always quite still. They tremble, and the Mantid behaves so as to simulate the trembling in a manner that was staggering by its perfection. It kept all the time swaying its abdomen from side to side, not rhythmically, but in an irregular manner, sometimes gently, at other times vigorously, just as a leaf is made to move when touched at one time by a puff of air and at another by a distinct breeze. The insect was always varying these movements. At one moment it was a wide swing, at another a series of delicate quiverings, then it would turn its abdomen almost half-way round and sway it back again. It was all done with an irregularity and perfection of resemblance that was simply astonishing’ (265).

Movements of the same kind are practised by various leaf-like Lepidoptera, such as *Kallima philarchus*, of Ceylon, which usually rests head downwards on the trunk of a tree (90). In this attitude it was observed by Green (215) to sway gently from side to side: ‘It might then’, he writes, ‘be mistaken very easily for a detached leaf that in its fall has hitched up in a cobweb and is being shaken by the breeze.’

In the water similar effects are known, the resembled movements here being those of water-logged, rather than wind-blown foliage. I have already referred (see p. 313) to the leaf-simulating *behaviour* of the little fishes *Monocirrhus polyacanthus* and *Platax teira*. Writing of the latter's leaf-like appearance, Mortensen points out: ‘From a figure alone it would certainly not be possible to infer that this would be the habit of the fish . . . but on seeing the fish in its natural surroundings it is unmistakable; it is a most admirable case of protective resemblance, no less admirable than the numerous cases of butterflies mimicking dead leaves. It is true, the resemblance in the shape of the body and in the coloration is not nearly so perfect as is generally the case in butterflies; but the movements of the fish outweigh completely the lack of perfectness in shape and colour, and the combined result of shape, colour and habits of the fish is a very perfect disguise as an old Mangrove-leaf swaying for the movements of the water’ (417).

Similar adaptive behaviour has been recorded by Mortensen of certain young fishes—Serranids, Monacanthids, and a species of *Tetrodon*—resembling small fragments of wood among which they were swimming in the Bay of Panama. These fish were generally floating about *on their side*, and Mortensen states that the resemblance between the young fishes and the wooden fragments (both of which he has figured) was so perfect that he found it nearly impossible to distinguish the fishes except when they started to swim (417).

Finally, I wish to refer here to an observation by Professor Walter B. Barrows (21*a*) relating to cryptic swaying behaviour on the part of the American Bittern (*Botaurus lentiginosus*). The bird was seen to alight in a lily pond, and on being approached assumed the well-known erect and rigid attitude. 'As we stood admiring the bird,' he writes, 'and his sublime confidence in his invisibility, a light breeze ruffled the surface of the previously calm water and set the cattail flags rustling and nodding as it passed. Instantly the Bittern began to sway gently from side to side with an undulating motion which was most pronounced in the neck but was participated in by the body and even the legs. So obvious was the motion that it was impossible to overlook it, yet when the breeze subsided and the flags became motionless the bird stood as rigid as before and left us wondering whether after all our eyes might not have deceived us.

'It occurred to me that the flickering shadows from the swaying flags might have created the illusion and that the rippling water with its broken reflections possibly made it more complete; but another gentle breeze gave us an opportunity to repeat the observation with both these contingencies in mind and there was no escape from the conclusion that the motion of the Bittern was actual, not due to the shadows or reflections, nor even to the disturbance of the plumage by the wind itself. . . . This was repeated again and again, and when after ten or fifteen minutes we went back to our work, the bird was still standing near the same spot and in the same rigid position although by almost imperceptible steps it had moved a yard or more from its original station.'

III. SPECIAL PROTECTIVE RESEMBLANCES IN RELATION TO THE TIME OF REST

We have now to consider a class of facts which are in a sense the very opposite of those just dealt with, namely, *adaptive stillness*, as opposed to *adaptive movement*. In another part of this work I have discussed the relation between concealment and immobility, and have more than once had occasion to stress the significance of stillness as part, and an essential part, of the business of concealment. It will be realized that the movements described in the last section are movements of a very special type—they are movements (so to speak) not of the animal, but of the plant which the animal so closely resembles. And as such they undoubtedly assist in the deceptive appearance.

But with ordinary movements of insects and other animals as they feed, or move from place to place, the matter is very different. Whenever such movements occur, all else that makes for concealment or deception is foredoomed to failure: then, neither harmony of colour, nor obliteration of shade, nor extinction of form, nor all of them together, can have great power to prevent detection by a watchful eye. *Compared with stillness, cryptic coloration is relatively unimportant; but combined with stillness, it is all important.*

Broadly speaking, it may be said that animals which obtain concealment by special protective resemblance are crepuscular or nocturnal in their habits. That is true, for instance, of the well-known twig-like Geometrid larvæ, innumerable procryptic moths, and other forms. On the other hand, species whose special cryptic resemblance is mainly aggressive, rather than protective, in function are frequently, perhaps generally, diurnal feeders. This is certainly the case, for example, with insects such as cryptic mantids and with those beautiful liana-like snakes which we have already mentioned. But it is characteristic of anticryptic as well as procryptic forms, that they are able to remain, and habitually do so for prolonged periods, absolutely motionless, so that whether as hunters, or as the hunted, the most is made of the particular cryptic appearance.

Moreover, it frequently happens that such well-concealed animals instinctively arrest all movement in sudden times of danger, or when an enemy or intruder appears. As will be remembered, *Podargus*, the bark-like Frogmouth of Australia, behaves in this way. Another striking instance of the same thing is furnished by the little stump-tailed forest Chameleon (*Rhampholeon boulengeri*), from the Ituri Rain Forest, Belgian Congo—a species which, as already mentioned, bears a close likeness to a dead leaf, and may remain motionless for hours (558).

Another point of considerable interest concerns the periods of activity in certain partially diurnal forms. There is evidence to show that various tropical cryptic insects have a midday period of activity coinciding with that when birds and other enemies are relatively inactive. Thus Annandale (6) found that the Phasmid *Lonchodes* was only conspicuous when the sun was at its hottest and brightest, and that the majority of Malayan Phasmidæ were most active in the middle of the day, being inclined to remain concealed in the early morning and late afternoon when enemies are most active. In a locality where several species of Phasmids were common and easily disturbed at other times, he states that it was impossible to find them early or late in the day: during six months' stay in Lower Siam he never discovered any specimens late in the afternoon, and the only individual seen in the early morning 'was clinging to a blade of grass, with its front legs stretched out rigidly in front of its head, and the other two pairs lying close along the body. . . . The curious paired process which terminates the abdomen in the genus to which this individual belonged (*Myronides*) was clasped round the stem of the grass, so as to conceal the junction between animal and plant. . . . The stick insect remained absolutely still while the grass was broken off.'

IV. SPECIAL RESEMBLANCES IN RELATION TO THE PLACE OF REST

It is important to remember that such animals are under natural conditions typically associated with the objects which they resemble. Obviously, it is easy enough to point to exceptions: but in general terms, whether we have regard to particular species as a whole, or to individuals, the association between the dissembler and the thing resembled is close: and, what is even more significant, this environmental correspondence is most intimate where the mimetic resemblance is most perfect—as shown, for instance, by different caterpillars which feed and dwell upon the lichen which they so well resemble, and by that remarkable and varied fauna which is so intimately associated with the Sargasso weed. In such cases the animals are never normally seen apart from the surroundings which they simulate.

Certain remarkable cases of the kind are known among marine Mollusca. For instance, the Nudibranchiate *Archidoris tuberculata* closely resembles in colour the common shore sponge *Halichondria panicea*, upon which it usually feeds, the resemblance being increased by a layer of dermal spicules in the mollusc, so that, as pointed out by Garstang, an enemy would be doubly deceived in a resemblance which both to the eye and to the touch represented something known by experience to be inedible (201). Another Nudibranchiate, *Tritonia plebeia*, is salmon-pink in colour, and feeds on the Actinozoon *Alcyonium digitatum*, to which it closely approximates in form and colour (206).

Archidoris johnstoni, a pale creamy white Nudibranchiate, has been described by Garstang as bearing the most exact resemblance to a small piece of the sponge *Halichondria panicea* var. *papillaris*—the appearance (depending as much upon attitude as coloration) being perfected by the half-retracted gill-plumes which form a perforated cone accurately simulating the osculum of the sponge (201). The same authority mentions the parallel case of another species, *Eolis papillosa*, which resembles an anemone, *Sagartia parasitica*—' the dorsal papillæ of the former corresponding to the tentacles of the latter '.

Another very interesting example of the same sort described by Garstang in his valuable observations on the ecology of Opisthobranchiate Mollusca (202) is that of the Tectibranch mollusc *Aplysia punctata*, which shows wide colour variation according to age. Small individuals are bright rose-red; full-grown individuals are olive-green. Specimens kept under observation were found to change from the immature rose-red, when its colour is exactly that of the alga *Delesseria sanguinea*, through a brownish-red stage (a month later) exactly that of *Iridæa edulis*, to a deep red-brown, and finally to the olive-brown adult coloration resembling that of littoral *Laminaria* and *Fucus*. Under experimental conditions in the laboratory the change was found to be correlated with growth *under uniform environmental conditions*. In nature ' an *Aplysia* migrating with growth from deep water to the shore would pass through algæ coloured first red, then brown, and finally olive-green ', and these, as Garstang points out, are the stages of its own colour changes.

This correspondence between coloration and station is not merely a passive relationship. There is evidence, in at least certain species, of adaptive habits and escape reactions which lead such animals to rest upon or return to the appropriate background. For instance, a North American grasshopper known as *Trimerotropis saxatilis*, which according to Folsom is found only on rock surfaces, is beautifully camouflaged when resting on lichen by a disruptive pattern of yellow, black, and green—similar in effect to that worn by many another lichen-like animal; and this author states that where, as in Southern Illinois, the grasshopper occurs among lichen-covered rocks, it does not alight haphazard, ' but habitually flies from one patch of lichens to another ' (178).

Swynnerton has observed in butterflies of the genus *Charaxes* an accurate choice of surroundings in harmony with the procryptic underside coloration, both habitually for all-night rest and sometimes for temporary rest. The underside of *C. candiope candiope* well harmonizes with dry leaves, most perfectly with those of its food plant *Croton sylvaticus*; and in its normal attitude with body and legs closely adpressed to the branch beneath which it is suspended, wings downwards, this and related species look marvellously like withered leaves (610). Longstaff also gives instances of butterflies, when alighting, selecting backgrounds which match their own colour (353).

A parallel case from a different group of animals and from a widely dissimilar environment is given by Mast, who showed that Flounders will select backgrounds which match their colour, though they do not discriminate in regard to pattern (398). A striking instance of the habit is given by Alcock (2), who refers to a fish from the Andaman Islands as follows: 'Under almost every rock . . . you may find a sea-perch, *Epinephelus hexagonatus*, whose livery of dark, close-set hexagonal spots has a decided resemblance to the surface of an Astræid coral: you cannot get this fish to leave the protection of the rock; so much so, that a large specimen which Dr. Prain and I wounded (and afterwards landed successfully), went straight to its doom in a clump of coral, when it might have betaken itself to the open sea beyond our reach' (2).

The prawn *Hippolyte*, whose powers of colour change have been exhaustively treated in an important memoir by Gamble and Keeble (199), also exerts powers of selection with respect to different coloured weeds, selecting as a place of rest red or green weed matching its own individual requirements.

As a final example we may mention experiments by Garstang (202) which indicate that the green Nudibranch mollusc *Hermæa dendritica* avoids red weeds upon which it would appear conspicuous, but not green ones upon which it is concealed. Individuals kept under observation for a fortnight in water containing green algæ (*Enteromorpha*, *Ulva*, and *Bryopsis*) and red algæ (*Antithamnion*, *Rhodymenia*, and *Spondylothamnion*) were seen to rest on each of the green weeds, especially on *Bryopsis*, *but never on the red ones.*

V. SPECIAL RESEMBLANCES IN RELATION TO THE ATTITUDE OF REST

Many excellent examples are given by Poulton of the procryptic habits, attitudes, and appearance of twig-like Geometrid larvæ (496, 506). Although such caterpillars present what are undoubtedly some of the most perfect known examples of special protective resemblance, limitations of space prevent us from considering them here, especially as one or another species of these 'loopers' is familiar to nearly everybody. Points to be noted in passing are that the resemblance to a twig of the food plant is often extremely exact—the larval head, for instance, being 'modified from the usual shape to one which suggests the end of a twig' (496) and the body bearing humps and excrescences and other features which combine with the cryptic coloration and texture to produce a deceptive effect; that the larvæ are nocturnal or crepuscular in their feeding habits, habitually resting motionless by day for hours together in attitudes closely simulating the arrangement of real twigs with the body held outwards at an angle from its support; and that these attitudes, which over long periods of stillness involve considerable bodily strain, are often rendered possible by the use of threads to support the front of the body, while the posterior end of attachment appears in certain cases to grow out and be part and parcel of the branch (see p. 110).

Closely comparable—in an entirely different group of animals—is the procryptic attitude habitually adopted by small weed-dwelling, weed-like Tectibranch molluscs such as *Aplysia punctata*, which have been observed by Garstang to rest attached by the posterior portion of the foot, with their bodies extended, and with their tentacles and pleuropodia (the latter generally compressed or rolled together) simulating stunted branches of weed—a position in which he states they will remain motionless for hours together (202).

Special cryptic attitudes are adopted by a number of leaf-like or weed-like fishes. The habits of *Monocirrhus* and *Platax*, whose resemblance to a leaf depends as much upon behaviour as upon structure, have already been described. Certain species which live among eel-grass adopt attitudes which bring their bodies into proper relation to the green blades which they simulate. An interesting example of instinctive orientation is provided by the Trigger-fish *Monacanthus* (Fig. 73), which swims in a horizontal position, but on reaching a clump of grass turns head downwards, and fixes itself in a vertical attitude with its sucker mouth (37). In this position the attenuated tapering body with its mottled green coloration is well camouflaged in such surroundings. It is interesting to notice that a similar result may be produced in an opposite manner by certain Pipe-fishes (*Syngnathus*) which not infrequently come to rest vertically in *Zostera* with the head uppermost. We may recall in passing that such habits are closely comparable with those of different moths, which when at rest on a tree-trunk adopt a position which is at right angles to that natural for members of their group (see p. 100).

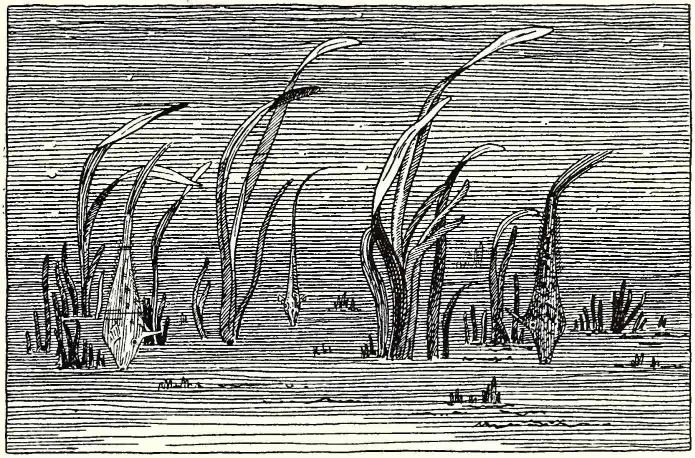

FIG. 73.—Slender Trigger-fish (*Monacanthus scriptus*), in cryptic attitude among Eel-grass (*Thalassia*). (*Redrawn after* BEEBE)

I am indebted to Mr. N. B. Kinnear for drawing my attention to literature describing the cryptic habits and appearance of the American nightjar *Nyctibius griseus*, whose remarkable protective position and behaviour at the nest led Goeldi to consider it one of the most interesting facts in natural history (209). This wonderful bird, which rejoices in the popular name ' Poor-me-one ', habitually selects the top of an upright stump as a receptacle for its egg, which usually occupies a small hollow just, and only just, large enough to contain it. Two nests recorded by Muir and Butler (429) were in almost identical situations on stumps of the Bread-fruit tree (*Artocarpus incisa*). In both, the stump selected had thrown up a new leader just below the point of fracture; and at both the birds sat facing this in such a way that when viewed from behind they came into line and blended with the grey stem.

Subsequently the species has been recorded by Belcher and Smooker (41) nesting on bamboo, on the top of broken-off stems about 1½–2 inches in diameter, and 40–50 feet from the ground. In every instance, the parent takes its station by the egg or young, sitting bolt upright in the most un-bird-like attitude indicated in text figure 74, which is based upon one of Muir's photographs (429). Thus posed, the coloration, the stiff attenuated posture, with the tail closely applied to the side of the stump, and the eyes nearly closed, and the absence of movement, all combine to render the bird marvellously like a continuation of the stump itself, no matter from what angle it may be seen. Indeed, the ' Poor-me-one ' becomes a veritable observation post, similar to those imitation tree-stumps used for the purpose in France during the War. Butler states that the bird also always appears to rest by day in the same cryptic attitude on a stump, which it adopts as a breeding disguise.

It is most interesting to compare with the above the nesting arrangements of the Tawny Frogmouth (*Podargus strigoides*): for here a similar result is produced in a very different manner. The main facts have been described by Mellor (in Mathews, 401), who remarks that the nest is placed ' between a fork of a tree that lies in a horizontal position, the bird thus being able to sit on the nest with its tail lying along the bough and its head projecting between the fork of the bough from which place it can watch everything below; it lies very flat on the nest, and the head, with the bristles about the bill, makes the bird look like a piece of broken dry wood. . . . In this position it lies as though lifeless, and will only fly off when you climb close to the nest.'

When we consider these adaptations, the singular fact emerges that we have here a series of modifications of structure and instinct providing a striking parallel to those developed on a smaller and more exact scale among twig-like Geometrid larvæ. Is it not significant that in two groups of animals, so dissimilar in affinity, structure, and habits as birds and caterpillars, almost the same method of concealment should have been arrived at by a series of precisely analogous phenomena, involving for its perfection in each group the combined effect of special cryptic coloration, rigid adaptive attitudes, instinctive immobility, and nocturnal habits—a method, moreover, which is the best possible under

FIG. 74.—Poor-me-one (*Nyctibius griseus*) on nest, showing special protective resemblance and cryptic attitude

the existing circumstances, namely, disguise as an actual portion of the plant on which it rests by day ?

The correlation between adaptive behaviour and procryptic appearance pervades group after group of animals, and is nicely illustrated by the attitudes in which different short-horned grasshoppers carry their limbs and antennæ. In the following cases I shall refer, for the sake of brevity, only to the latter. *Omura congrua* is a stick-like species from British Guiana. The deceptive resemblance to a stick is here assisted by the antennæ, which in the resting insect *are stretched forward and kept close together*, thus producing in front the linear contour of the 'stick'. *Acrida turrita* is a remarkable buff-coloured species which bears a most perfect likeness to the dead grass with which I found it associated in the Canary Islands. In this grasshopper the antennæ *are held erect but diverging from one another at an angle*, which gives them the precise appearance of young leaves at the end of a shoot—a resemblance which is intensified by their flattened and tapering form, as may be seen in the accompanying photograph (Plate 44).

Eremocharis insignis is in its wingless immature stages a short stoutly built species bearing in life a close resemblance both in colour and configuration to a rough and weathered rock fragment. Now the interesting point arises, what can this insect do with its antennæ ? Obviously neither stick-like nor grass-like appendages will be advantageous here, and any processes protruding from the 'stone' would tend to reveal the insect to an observer. However, the difficulty is surmounted by an instinctive reaction. Normally the antennæ are extended, but when the insect is in danger, these tell-tale organs *are instantly lowered, and laid flat against the front of the face*, where they at once become inconspicuous and part and parcel of the simulated stone.

Another group showing the most varied and remarkable cryptic devices is that comprising the spiders. Generally speaking, spiders are relatively defenceless creatures—actively sought after for food by a host of enemies both invertebrate and vertebrate. They are relentlessly persecuted by various Pompilid and Sphegid wasps, and by Ichneumons. They are preyed upon by Asilid flies, by dragonflies, and by Cicindelid beetles. And they are devoured by a multitude of small insectivorous vertebrates, including frogs, toads, and tree-frogs, salamanders and lizards, monkeys and shrews, and especially by birds. It is hardly surprising to find, therefore, that spiders have evolved types of coloration, of attitude, and of behaviour which in correlation with their form and habitat combine in different ways, as wonderful as they are various, to create deceptive resemblances both in the artificial surroundings of their snares, and in the natural surroundings of bark, and leaf, and twig.

Innumerable instances may be found in the writings of Peckham (463), Hingston (261, 265), McCook (381), and other naturalists who have studied the group. Here we can only mention one or two in passing. For instance, it is a common practice with spiders of slender build to stretch their elongated bodies and legs along the stems of plants, in which position they become quite inconspicuous. *Tetragnatha extensa*, whose long narrow body is cylindrical in shape, and green, yellow and grey in colour, rests stretched out at full length on a stem, with its first and second pairs of legs put forward in a straight line and the third and fourth pairs directed backwards in the same way. Hingston has described how this spider, when alarmed, *runs from its snare* to assume the cryptic posture. The Peckhams also observed *T. grallator* run from the web to a branch, where the spider stretched itself in the manner characteristic of the genus.

VI. SPECIAL PROTECTIVE RESEMBLANCE EFFECTED BY SPECIALLY PREPARED SURROUNDINGS

Of great interest under this head are certain spiders whose habits have been carefully studied by Hingston (265). Various spiders which habitually sit in the centre of a cartwheel snare manufacture and display in the snare an artificial framework or background against which the owner blends or into the configuration of which it fits. Special colours, special structures, special attitudes, and special habits combine to produce concealment of a most effective type. In composition and design these devices vary enormously. They may consist of insect or of vegetable debris, of silk, of packets of insects rolled in silk, or of a mixture of silk and insect fragments, or of pieces of bark, or the owner's cocoons: they may form a circular carpet in the centre of the web, or a cluster of packets or a string of pellets, or a diametrical band, or thread or ribbon.

One point to which I wish to draw attention here is the remarkable correlation between the *colour* of the protective device and that of the spider which constructs it. The grey-brown *Cyclosa tapetifaciens* from British Guiana constructs in the centre of its snare a flat grey-brown carpet composed of tiny insects and vegetable fragments: *Argiope filiargentata*, a small pure white species from Trinidad, weaves in a similar position a vividly conspicuous pure white screen of zigzag threads. In the case of *Cyclosa globulifaciens*, a mottled grey-brown species found on the Essequibo River, the similarly coloured blending device consists of clusters of packets of dead insects rolled in silk sheeting; *Azilia*, from British Guiana, is darker in colour and makes its somewhat similar blending device of bits of bark and lichen cut from a tree whose brown colour exactly harmonizes with that of the spider. *Cyclosa caroli*, from Trinidad and British Guiana, a grey-brown species with a tinge of yellow, constructs a band of silk in which are mixed insect fragments, and Hingston tells us again that the spider is exactly the same colour as the band. In another example of the same species found in the egg-laying season the band was represented by a cocoon chamber identical in colour with that of its owner. *Cyclosa caudata*, a related species described from the United States by McCook, is greyish-white, mottled with small black markings; this spider, like the last, fixes a string of whitish cocoons in the snare, and in this case, as Hingston points out, the blackish markings necessary to complete the resemblance to the spider are supplied by the attachment of insect fragments to the white silk. In *Cyrtophora bifurcata*, another American species which strings its cocoons in the snare, these cocoons are dark green in colour, and the spider, itself green, ' looks like a cocoon at the end of the string'. These cases are the more remarkable in that spiders as a rule are not like their cocoons, and it is only those kinds that hang them in the webs that possess this close resemblance to them.

One pellet-making species described by Hingston from the Guiana forests must be mentioned as a further example of the way in which similar ends are effected by entirely different methods. *Cyclosa tremula*, unlike most pellet-making species, does not match the colour of its pellets. It is a small conspicuously black and white species. 'The sharp difference in colour between spider and pellet, though at first sight undermining the principle of protection, turns out to be an exception that proves the rule. The spider is black and white; the pellet is brown. But the moment I touched the leaf to which the snare was anchored, immediately the spider underwent a transformation. It raised itself a little from the snare, then threw its body into an extremely rapid and delicate vibration which had the result of changing its colour. What must happen is that, as a result of the rapid quivering, the black patches and the white patches on the spider's body come to occupy alternately each other's place. As a consequence the white and black colours become fused to the eye, and the spider appears to be brown, exactly the same colour as the pellets. We have here, therefore, a delightful illustration not only of a spider making a special concealing device, but, by its movements, altering its colour in order to blend with the colour of that device.'

A major factor in producing the required optical obliteration is the attitude adopted by the spider. In *Ariamnes gracillima*, observed by the same writer in British Guiana, the shape of the body is excessively slender, and the spider is in the habit of slinging its silken cocoon, which is also very long, narrow, and cylindrical, by threads beneath a branch, and of taking up a position at the lower end with its body in alignment with the cocoon. 'Spider and cocoon', he writes, 'become one continuous object which any one would take for a piece of thin straight stick. It thrust its front two pairs of legs on to the cocoon; its third pair gripped the end of the cocoon; its fourth pair went straight back along the sides of its abdomen and clutched the anchoring thread. All this helped to create the stick-like appearance. In addition, it kept its body straight and rigid and its legs in perfect line with its body when stretched out fore and aft. It was very unwilling to abandon this position. When I forced it away from the cocoon it came back after five minutes, crawled down again to the lower end of the cocoon and took up the stick-like position once more' (265).

Again, this is what Hingston says of a dead-leaf brown spider, *Labdacus prolatus*, whose habits he studied in British Guiana: 'The spider had secured a dry leaf, folded it longitudinally and united the edges with silk. This it had slung by means of eight threads attached to its upper end. It hung vertically and was free to swing in all directions. The spider sat on this suspension-leaf. Its body was pressed down low and tight; its front pairs of legs were stretched straight forward; its hind pair straight backward. The result was that it became just a ridge on the dead leaf and practically invisible against its background.

The seat was just a little longer than the spider. The spider sat on it absolutely immobile. When alarmed, it did not try to escape ; on the contrary, it pressed itself even tighter to the leaf and remained absolutely still. It behaved as though it understood that immobility and harmonization were the foundations of its defence ' (265).

It is interesting to compare with the above certain cryptically coloured caterpillars whose appearance, manner of feeding, and position of rest combine to produce a curious effect which is, in a sense, the converse of the usual arrangement whereby an animal resembles its surroundings : namely—that of causing its surroundings to resemble itself. Many years ago Wilhelm Müller described a remarkable South American caterpillar belonging to the genus *Anæa*, which gnaws the leaf of its food plant in such a manner as to leave uneaten a number of rough models of itself attached by one or two stalks to the mid-rib. It then takes its station on the mid-rib beside them. The deceptive effect is the more remarkable in view of the caterpillar's coloration, which is green above and dark below, so disposed that the green comes into contact here and there with the mid-rib while the interrupted darker tones blend with the darker background. Thus only the green part of the caterpillar is conspicuous, and that part simulates one of the leaf remnants still attached by two narrow stalks to the mid-rib.

In recent years Hingston (265) came across a caterpillar in the forests of British Guiana whose similar habits present certain features of great interest. The caterpillar, belonging to the genus *Siderone*, was found in the darkest part of the forest on a long-leaved plant of the genus *Pithecollobium*. Having bared the mid-rib for about a third of its length at the distal end, Hingston states that the larva had *cut off five small bits of leaf and anchored them to it by a few silken threads*. These were approximately the size of the caterpillar—green and fresh in appearance and evidently recently cut : the caterpillar was seated on the mid-rib near its extreme tip, and was of the same colour as the leaf fragments. The device concealed it perfectly. Subsequently Hingston came across an older example of this caterpillar—seated as before near the end of its gnawed mid-rib. But this leaf was more eaten ; the fragment attached to the mid-rib was withered and brown ; and the caterpillar itself had changed from the fresh green of its early stage to a deep brown colour exactly like that of its changed surroundings.

3. ADVENTITIOUS CONCEALING COLORATION

> Macbeth shall never vanquished be, until
> Great Birnamwood to the Dunsinane hill
> Shall come against him.
>
> SHAKESPEARE

Results similar to those described above are often achieved in a strikingly different manner, namely, by the use of a covering of foreign objects. Many animals habitually masquerade in garments borrowed from their surroundings; sedentary species using local material, while various wanderers instinctively reclothe themselves from time to time from their more extensive wardrobe. Others construct shelters within which they live, or borrow ready-made shelters from their surroundings.

The phenomena of Adventitious Resemblance present several features of interest. In the first place, as a method of obtaining effective concealment and of avoiding recognition, the device is perhaps unrivalled. Some species when suitably attired, or sheltered, are quite indistinguishable from the miscellaneous objects which compose their normal surroundings; and they can, of course, be suitably disguised wherever they happen to live.

We see here many beautiful examples of cryptic appearance brought about by, and absolutely dependent upon, highly specialized *behaviour.* Such instinctive reactions which lead animals to cover themselves with adventitious clothing until completely disguised in appearance, or to build cryptic or protective shelters in which to live, can hardly be explained except in terms of the need for concealment from the eyes of enemies or prey.

The present phenomena also well illustrate how the different functions of cryptic coloration tend to merge with one another through series of cases. Thus with different animals, adventitious materials provide for some a means of concealment from enemies; for others a method of ambushing, or of approaching prey undetected; and for others again, of decoying or attracting prey to their doom.

While in typical instances the dressing and shelter-making habits are clearly correlated with the above-mentioned functions of concealment, various cases—as we shall see—show every degree of gradation with other and entirely different methods of protection, leading to the borrowing of protection from aposematic partners; to the use of fortified hiding-places; and to the habit of burrowing.

I. CONCEALMENT AFFORDED BY MASKS OF ADVENTITIOUS MATERIAL

Among insects this habit is widespread. Not only is it found in several families belonging to a number of distinct orders; but it may also occur in the larval, pupal, or imaginal state; or indeed it may persist in all three. Hingston (265) has described a number of excellent examples from various groups. One is a predatory Neuropterous larva of the genus *Hemerobius*, found living among moss on the bark of forest trees in British Guiana. 'The larva was completely hidden, being covered over with a hillock of moss perhaps 50 to 100 times as big as itself. Only the tips of its front legs and the ends of its pointed jaws projected from under the edge of the heap. On other occasions it covered itself with lichen. . . . One which I met with was a perfect circle; it was made out of tiny bits of lichen and . . . was an exact image of the round lichenous patches that occur so commonly on forest trees.' The larva of *Chrysopa*, another predatory Neuropteron, dresses itself with the remains of dead ants; and if these are removed, the insect has the instinct to reclothe itself with them. The same writer found that the predatory bug *Acanthaspis* is in the habit of heaping on its back desiccated insect fragments. Thus concealed, it cannot be doubted that the insects are the better able to approach and surprise their prey. The device is, in fact, scarcely different in principle from that recently used by police officers who, when detailed to keep a watch on a London house, ingeniously concealed themselves in a tradesman's carrier tricycle. In this familiar and inoffensive vehicle they were taken to the scene from which, without exciting suspicion, they were able to make their observations and capture their victims. Such tactics offer wide scope in the field of deceptive aggression, whether in peace or war, and as every one knows, were made famous by the exploits of the Greek heroes who concealed themselves in the gigantic hollow horse at Troy, and thus gained admittance to the city.

Several beetles have adopted the same cryptic device for protective purposes. *Chœtophorus cretiferus* whitens itself all over with chalk from its immediate surroundings. *Limnius œneus* covers itself with sand (265). The British *Georysus pygmœus*, which occurs along the margins of streams, habitually covers itself with a thick coating of mud and thus becomes entirely concealed from observation. An excellent example taken by the writer in South Africa is *Eurychora modesta*, whose wide flattened back is thickly plastered with mud pellets, so that the beetle is quite unrecognizable until it moves. Dr. H. E. Hinton tells me that certain Orobatid mites, such as *Damœus geniculatus*, likewise plaster mud on to their backs.

Many marine organisms mask themselves with dresses of leaves and weed, or with sponges, cœlenterates, ascidians, and other local material. Thus the Amphipod *Atylus* decorates itself with sea-weed. Dixon (151) has described the habit in the British crab *Hyas araneus*, which disguises itself very perfectly. He states that when moved into a new environment, this crab promptly assumes a new disguise to suit its changed surroundings. Three specimens—all dressed alike, when obtained, in short sea-weeds—were placed respectively among stones covered with *Sertularia abietina* and *Hydrallmania falcata*; among small shells and fine gravel; and among specimens of the crinoid *Antedon rosaceus*. 'In the morning', he says, 'each of them had clothed himself to suit his environment. No. 1, who had been placed among the corallines, had arrayed himself with a dense shrubbery of *Sertularia abietina* on his back, with the finer branches of *Hydrallmania falcata* on his legs. . . . No. 2, who had been placed among the small shells and fine gravel, covered himself with these materials, and no. 3, who was given as a companion to the crinoids, broke off portions of their arms and fastened them on his back, using the *cirri* to conceal his legs.'

Frequently spines are used as pegs upon which to hang the cryptic clothing; and the deliberate manner in which the dressing is done is inconsistent with any view other than that which explains it in terms of the need for a disguise. The process in *Stenorhynchus* and *Inachus* has been described by Bateson as follows: 'The crab takes a piece of weed in his two chelæ, and neither snatching nor biting it, deliberately tears it across as a man tears paper with his hands. He then puts one end of it into his mouth, and, after chewing it up, presumably to soften it, takes it out in the chelæ and rubs it firmly on his head or legs until it is caught by the peculiar curved hairs which cover them. If the piece of weed is not caught by the hairs, the crab puts it back in his mouth and chews it up again. The whole proceeding is most human and purposeful. Many substances as hydroids, sponges, Polyzoa, and weeds of many kinds and colours are thus used, but these various substances are nearly always symmetrically placed on corresponding parts of the body, and particularly long plume-like pieces are fixed on the head, sticking up from it' (25). Bateson further states that if a *Stenorhynchus* is cleaned, it will '*immediately* begin to clothe itself again with the same care and precision as before'.

The habit finds a parallel among Lepidopterous larvæ. Shelford has described a Geometrid caterpillar from Borneo which adorns itself with flower buds, attached to spinous processes of its body. Similarly, the larva of the British Blotched Emerald Moth (*Euchloris pustulata*) constructs a camouflage screen by fixing leaf fragments from its food plant on to the hooked bristles of its body. This it does as soon as it leaves the egg in July, while after hibernation it fits out in a fancy dress of scales or husks of oak-buds (583). The device is, of course, essentially the same as one widely practised during the Great War for the concealment, not of caterpillars, but of caterpillar-tractors, battery positions, observation posts and so forth.

It is not to be imagined that such applications of a natural phenomenon by man are in any sense new. From times immemorial they have been practised by primitive hunting tribes. Basedow has described how the Australian aboriginal used to place a large lily leaf over his face when approaching waterfowl. Two holes were cut for the eyes to look through, and thus concealed he was able to swim out over a lagoon towards some geese, working cautiously right up until he was within grasping distance, when he could simply pull a bird under by its legs and strangle it (22).

Near the Gulf of Maracaibo in Venezuela a somewhat similar method is employed by natives for catching duck. A number of scraped-out gourds are set floating on the lake. When the waterfowl have become accustomed to them they allow them to float freely among them. ' The Indian then takes a similar gourd and puts it over his head, having previously cut a couple of holes through which he can see. He slips quietly into the water, and makes his way towards the ducks, taking care to keep the whole of his body submerged. As soon as he gets among them, he grasps the nearest duck by the legs, jerks it under the water, and ties it to his girdle, where it is soon drowned. He then makes his way to another duck, and, if an experienced hand, will capture as many as he can carry, and yet not alarm the survivors ' (676).

Sometimes, again, mud is used as a cryptic covering. In this way Australian hunters can approach grazing Kangaroo in open country within spear-throwing distance without being detected. On some types of ground his own swarthy colour gives him natural protection. But Basedow (22) points out that he has learned the value of artificially colouring himself with the mud of the particular terrain he is about to cross—on a blue mud flat he paints himself a slaty blue, whilst on lateritic soil he applies red ochre.

II. THE TRANSITION FROM ADVENTITIOUS CONCEALMENT TO ADVENTITIOUS ADVERTISEMENT

The little Indian fish *Minous inermis* affords a highly specialized example of adventitious resemblance. It belongs to the Scorpæonidæ, a family composed mainly of species leading a more or less cryptic existence among coral or rocks, where they creep about on the sea floor, or hide themselves in crannies. In such surroundings they are well concealed both by their disruptive dress, and by the floating frond-like cutaneous filaments with which many species, like the Sea Scorpion (*Scorpæna mystes*) and the Lion-fish (*Pterois volitans*), are adorned. In the present species, however, there is no cutaneous camouflage scheme to simulate the weeds or zoophytes encrusting a rock fragment. Instead, the fish is infested with a growth of living polyps of the hydroid *Stylactis minoi.* What is so singular in this symbiotic association is its mutually obligate nature, a point to which Alcock drew attention in 1902, when he stated that the fish had never been found without a coat of these polyps, nor had the polyps ever been seen anywhere but on this particular fish (2). When in 1928 Gudger reviewed the data, he found that no fewer than twenty-nine specimens of the fish (presumably all ever taken) from widely distant stations in Indian and Japanese waters, were all infested, and that so far as was known, the hydroid had never been found except on *M. inermis* (218).

A somewhat similar partnership exists between the Japanese Hermit Crab *Eupagurus constans*, and a hydroid zoophyte *Hydractinia sodalis* which grows over and conceals the hermit's shell-dwelling. Such cases intergrade with others in which adventitious material has an aposematic, rather than a cryptic, function : in which, that is to say, the covering is positively distasteful and repellent to predatory enemies, rather than merely of no interest as food. Such, for instance, are the well-known associations between crabs and sea anemones. An extreme example is presented by the Hermit Crab *Eupagurus cuanensis*, which is found with its borrowed shell surrounded by a bright orange-coloured sponge (*Suberites domuncula*) known to be highly distasteful to fishes. Such animals trade upon the unpalatable reputation of their partners. Their defence lies not in a cryptic costume, but in an adventitious advertisement. This use of colour has already been considered in an earlier section.

III. THE TRANSITION FROM ADVENTITIOUS CONCEALMENT TO ADVENTITIOUS SHELTER

The amount of masking material used varies widely with different animals. Some are content, as we have seen, with one or two tattered rags. Others completely cover themselves with adventitious trappings. Moreover, the habit of using flimsy materials which provide only visual protection passes imperceptibly into the employment of heavy cover which affords physical security. The first involves a psychological factor, reducing visibility, the second a physical factor, reducing accessibility.

We may note in passing that a similar transition in the use of cover has been evolved in modern warfare—for example, in defence against air attack, where protection may be derived from camouflage, or from shelter; from a layer of paint, or a layer of concrete.

(1) **Concealment Afforded by Specially Constructed Shelters**—With wild animals, as with civilized man, every gradation between the two extremes is found. In Borneo, the crab *Dorippe astuta* was seen by Shelford (572) to carry a leaf over its back. 'So close was the resemblance', he writes, 'between one of these leaf-covered crabs and a water-logged leaf washing to and fro in the gentle bottom-currents, that the closest scrutiny was needed to detect the presence of the crab.'

A beautiful example is provided by caterpillars of the Brazilian moth *Saccophora*. Bates has described how this insect forms a leaf of Melastomæ, its food plant, into an elongated bag, open at both ends, in which it hides. Since the weight of this leaf-dwelling would become insupportable for the contained caterpillar, the case is attached by threads to leaves near which the insect is feeding (24)—a labour-saving device recalling the habits of twig-like Geometrid larvæ which use threads to support the weight of their own bodies when waiting motionless in strained cryptic attitudes during the long hours of daylight.

A somewhat parallel arrangement obtains with certain birds whose nests, while of course serving primarily as a cradle for the eggs and young, are frequently extremely well concealed owing to the type of material used in their construction—as seen, for instance, in the Chaffinch's beautiful compact nest of lichen and moss welded to the fork of a lichen-clad apple tree, and in the more remarkable leaf nursery made by the Tailor-Bird (*Orthotomus longicaudus*).

A further step in the use of adventitious coverings has been made by various insect larvæ and pupæ, which construct for themselves more or less elaborate protective shelters. This is seen, for instance, in the cryptic cocoons, made of bark or wood fragments, which encase the pupæ of *Cerura* and *Cilix*. Caterpillars of Psychid moths—the so-called ' basket worms '—build cryptic cases which are remarkable for their variety of form, composition, and structure. Made of silk, or leaf fragments ; or of leaf stalks, grass stems, or small twigs, bound into compact baskets, they provide habitations not only for the larva and pupa, but also in the case of the female for the adult insect. In many instances they form a truly marvellous ' hide ' for their owners. For example, *Thyridopteryx sierricola*, from Sierra Leone, masquerades within a shelter of dead leaves which render it absolutely invisible and unrecognizable. In *Apterona* the case is entirely of silk and closely simulates a snail shell.

Similar are the cylindrical cases made by caddis worms out of small bits of stick, stones, leaves, shells, and other material. But while these protective habitations undoubtedly add to the difficulty of recognition, their main function appears to be no longer one of concealment, but of shelter. This development, whereby animals utilize adventitious material as a protective armour, reaches a climax in certain marine Gastropod molluscs, such as *Xenophora pallidula*, whose shell is both concealed and strengthened with extraneous shell, rock, and coral fragments incorporated in its growing edge, so that the whole structure becomes reinforced to a remarkable extent, and so perfectly concealed that it is impossible to recognize if from above as the tenement of a living animal.

(2) **Protection Afforded by Appropriated Shelters**—In the cases just considered, the shelter is constructed or manipulated from adventitious materials by the animals' own activities. A modification of this expedient is seen in many animals which seek for, and appropriate, ready-made shelters of various kinds, such as the hollows of trees, which are used as nesting-sites by Nuthatches, Titmice, Owls, Woodpeckers, and other birds. Examples might be cited from almost any group of animals.

For instance, it has been known from antiquity that Hermit Crabs live in the discarded shells of Whelks and other Gastropod molluscs, having the abdomen soft and spirally twisted in accordance with the shape of their portable shelters. The group Paguridea, to which these creatures belong, includes a few which have retained the symmetry of the body. Among them, the habits of *Pylocheles miersii* are of special interest in the present connexion. These somewhat lobster-like Hermit Crabs are native to the Andaman Sea, where they inhabit hollow pieces of bamboo. When the animal is withdrawn into its cylindrical house, the two chelæ are applied together, and like a cork in a bottle, exactly stop up the entrance.

Among animals which have adopted this mode of life, the climax has been attained by certain ants, belonging to the genus *Colobopsis*. These insects nest within hollow stems or bamboos, or within excavated wood, and hide the entrance to their home in a manner so remarkable that their habits read almost like fairy-tales. The duty of porter, or janitor, is performed by a caste of large individuals having the head especially modified to function as a door (Fig. 75). It is quite circular in front view, and abruptly truncated, so that it forms an admirable stopper, just the right size and shape to fit the entrance. Moreover, the arrangement is perfect even as to colour, for the frontal part of the janitor's head imitates the appearance of the stem in which the nest is situated—being yellow in the Brazilian *C. paradoxus* which inhabits yellow bamboos, and brown and sculptured in the European *C. truncatus* which usually nests in the hard dry twigs of willow trees (183).

This remarkable device has been described by Forel, from whose work I quote the following passage : 'It was not till after many a fruitless search that I discovered at Vaux near Morges, about 1872, the nest of our European *Camponotus* (*Colobopsis*) *truncatus*. On the withered branch of an old pear tree I saw a number of workers of this species running towards some centre—a mystery to me—situated in the middle of the bark, while no other assemblage of the kind could be seen, either near the foot of the tree, or about the top. Knowing nothing about the matter at the time, but stimulated to exceptional keenness by the ill success of my endeavours to find the home of the *Colobopsis*, I began to observe their movements with concentrated attention. All of a sudden, I saw a very small round hole stand out against the bark, and through this a worker promptly slipped in. But, immediately after, the black hole disappeared again, and I saw nothing but the brown rough bark of the pear tree. . . . Shortly afterwards, a second worker behaved in the same way, slipping into another little hole situated

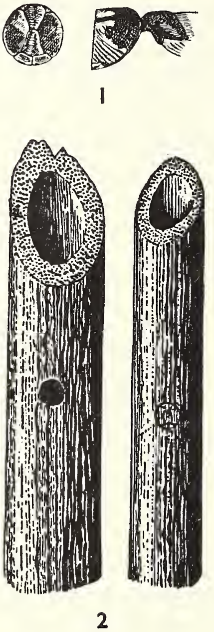

FIG. 75.—1 *Colobopsis paradoxus* var. *janitor,* front and lateral views of the janitor's head. 2 Entrance to the nest of *C. culmicola* in bamboo : open (left) ; and closed by the head of a janitor (right). (*Redrawn after* FOREL)

near the first, and appearing and disappearing in the same way. But this time I fixed the exact spot, and seizing one of those pins which an entomologist always carries about him, I buried its point cautiously in the hole, which immediately reappeared. I then slowly withdrew the pin and saw the brown, truncated head of a soldier advancing once more to take its place as doorkeeper, whence my action had driven it away for a moment.'

IV. THE TRANSITION FROM ADVENTITIOUS CONCEALMENT TO BURROWING HABITS

Finally, as we have already mentioned, other examples illustrate a transition from the dressing to the burrowing habit. For instance, *Ceratophrys cornuta*—a huge-mouthed, toad-like creature from Brazil—is in the habit of half-burying itself in the ground among herbage where its position, cryptic coloration, and stillness combine to render it almost invisible. In the absence of vegetable cover, these grotesque animals throw lumps of soil over their backs with their feet, and lie thus in ambush, as Gadow remarks, ' waiting for some unfortunate creature to pass into the trap represented by the enormous mouth, which opens and shuts with lightning-rapidity and with an audible snap ' (see Plate 9).

Other animals pile on the adventitious covering so as to be nearly, or completely, buried beneath their surroundings, as happens with numbers of flat-fishes which scatter sand over their bodies and leave little more than the eyes exposed. The protective value of this habit is well seen in the case of shrimps, who are thus able to escape the keen eyes of their enemy, the Wrasse. Bateson (26) says of the latter : ' Its vision is so good that it can see a shrimp with certainty when the whole is buried in grey sand, excepting the antennæ and antenna-plates. It should be borne in mind that if the sand be fine, a shrimp will bury itself absolutely ; digging with its swimmerets, kicking the sand forwards with its chelæ, finally raking the sand over its back and gently levelling it with its antennæ, but if the least bit be exposed, the wrasses will find it, in spite of its protective coloration. Shrimps put into the wrasses' tank at night escaped for some days, hence they must retire to the sand before daylight is strong enough for the wrasse to see them. The knowledge of night and day is therefore of paramount importance to a shrimp, as it is not safe for it to hunt until darkness has come.'

The combination of burrowing habits and adventitious concealment reaches the limits of perfection in certain tropical trap-door spiders, which close and conceal their burrows with a camouflaged door. These doors are tough and thick, being made of alternate layers of silk and earth. Hinged at one side, the edges are bevelled so that the lid fits the tube perfectly, like a shallow cork. And when, as usually happens, the outside has been covered by the spider with leaf fragments, moss, lichen, or other local materials, the site of the closed doorway is almost undiscoverable.

CONSPICUOUS LOCALIZED CHARACTERS

4. DEFLECTIVE MARKS

> The field-naturalist, properly instructed, crowns the work of the comparative anatomist and the physiologist, though without the necessary education he is little more than an empiric, even should he possess the trained cunning of the savage on whose knowledge of the habits of wild animals depends his chance of procuring a meal.
>
> ALFRED NEWTON

IN these two sections I shall deal with certain types of coloration which I have grouped together here for purposes of comparison, and which, though differing very widely in their nature and function, have the following features in common—we are treating of characters which are essentially *conspicuous in appearance, localized in distribution* and *directional in function*—that is to say, of structures, patterns, and behaviour which tend to reveal and to draw attention especially towards or away from one part of an animal (or, it may be, to one member of a species), in such a way that the animal (or species) may thereby benefit. The nature of the advantage to be gained by this spatial focusing of the observer's attention is twofold. It may, on the one hand, lead to the capture of food (where the advertising element has an aggressive function) or it may, on the other hand, make for safety (where the localized character has a protective function). In the former type, we shall see operating the principles of Special Aggressive Resemblance (anticryptic) and Alluring (pseudepisematic) Coloration ; in the latter, the principles of Deflection (parasematic), Confusion (flash colours), Warning (aposematic), Bluff and Mimicry (pseudaposematic). While several of the above categories intergrade and overlap with others (thus illustrating the difficulty—perhaps I should say impossibility—of arriving at an entirely satisfactory classification of such phenomena) typical examples of each type are clearly distinct.

I have endeavoured to give below a comparative account of these localized advertisements and of the several functions which they serve ; to stress the principles upon which the different appearances depend ; and to show how in the several classes of cases dealt with, similar or closely analogous devices have often been independently evolved in widely dissimilar groups of animals.

I. CHARACTERS WHICH DEFLECT THE ATTACK OF ENEMIES FROM THE MORE TO THE LESS VITAL PARTS OF THE BODY

We have already alluded, when dealing with concealment of that most conspicuous organ, the eye, to the fact, that of all objects which may come into the visual field, those which are round in shape are (other things being equal) the most striking, the most easily seen and recognized. We saw, consequently, that the eyes of many animals, conforming as they do more or less in appearance to a disc, are masked or hidden by a variety of devices, which in certain cases are extraordinarily ingenious and effective.

Now, at first sight it would seem something of a paradox that natural processes which have effected as one of their main results the apparent obliteration of animals' eyes, should at the same time, and with even greater precision and accuracy, endow the same or other creatures with imitation eyes, or ' eye-spots ', yet such is the case. Dummy eye-like elements are found throughout a wide range of animals : they adorn the feathers of different birds ; lizards and snakes display them on their scaly bodies, sightless they stare out from the wings of mantids, moths, and butterflies ; from the bodies of spiders and grasshoppers, bugs and beetles, frogs and fishes.

Accepting, as we must, the demonstrated fact that such round, target-like structures possess the maximum of visibility, their occurrence and recurrence as bold elements in the coloration of forms belonging to many different groups is a phenomenon that must claim our special attention.

If the advertising colour patterns worn by different animals are biologically significant (which we have every reason to believe is the case), then one may reasonably suppose that these units—which at their best embody the very essence of visibility—have some special biological meaning.

Poulton originally ascribed a protective function to the eye-spots beneath the wings of certain butterflies (*Cœnonympha*, *Thecla*), believing that they divert the attention of enemies away from vital parts and direct attack on non-vital parts of the body, thus increasing the insect's chance of escape (496)—a view which is supported by several lines of evidence, and abundantly confirmed in the subsequent observations of many naturalists. The position of the spots themselves, which are commonly situated near the hinder margin of the hind wing, or in the conspicuous apex of the fore wing, in each case far distant from the body, is significant. More significant is the fact that butterflies possessing such markings are frequently found with V-shaped beak-injuries or imprints at or just beside the eye-spots (see Plate 45). Further important evidence refers to special structures and postures and movements (to be considered later), which in their highest development cause part of the butterfly's hind wing to be mistaken for the head. Sometimes, as shown by Mortensen in the case of certain Central American Lycænidæ, the directive function of the eye-spot is strongly enforced by the whole undersurface pattern of the wings, which in *Thecla phaleros* (Fig. 24) is especially remarkable. Here a series of broad black and white bands cross the fore wing, continue without interruption on to the hind wing, and converge towards the false head, with its false eye and antenna, at the hind extremity of the hind wing. Such an arrangement, which provides a most interesting application of the principle which I have described elsewhere as coincident disruptive coloration (114), Mortensen compares to the honey guides in flowers. In the present case it does undoubtedly serve to lead the eye of an observer away from the insect's head and to direct it unfailingly towards its false head.

Swynnerton's important investigations on the defences of *Charaxes* in Rhodesia (610) provide valuable testimony on the directive function of wing markings in nature. Taking advantage of numerous butterflies of the above genus which daily visited bunches of bananas hanging in his verandah, he carried out a series of experiments with marked individuals. Conspicuous ' eye-spots ' were painted on the underside of 51 specimens. Wing injuries or beak imprints subsequently sustained by these individuals numbered 47 : of these, 36 implicated ' eye-spots ', and of the remaining 11 most were conceivably attempts to reach an ' eye-spot '. Considering the attacks from another point of view, 25 of the injuries were found to involve both pairs of wings, while 22 were unilateral. Allowing for coincidence and for the fact that the hind wings are not always quite closed when the insect is at rest, Swynnerton concluded ' that the majority of the attacks were made on the butterflies when settled ' and ' that the majority of those " settled " attacks were, probably, directed by the " eye-spots " and other painted markings '. Extended observations also indicated ' that these markings did confer some protection on the individuals to which they were applied '.

Turning now to an entirely different class of animals, it is highly probable—as tentatively suggested by Poulton many years ago—that the tails of certain lizards have an analogous function (496). I have referred elsewhere to the protective value of autotomy in this group, many species, belonging to different families, readily casting off the tail when that member is seized. Every one who has collected lizards knows that a considerable percentage of freshly captured specimens show lost, or regenerated, extremities which prove ' an enemy hath done this '. Now, quite apart from the fact that the tail is the part most easily, and therefore most likely to be, seized by a pursuer, it is a striking fact, which so far as I am aware has not been noticed in the present connexion, (1) that in many species this organ is more brilliantly coloured than the rest of the body and (2) that in other species it is more brilliantly coloured in the young than in the adult. For instance, the handsome arboreal Lacertid *Holaspis guentheri*, which I have taken in the rain forest at Amatongas, Portuguese East Africa, has the tail coloured a beautiful, intensely vivid azure, in striking contrast to the black and bronze body stripes. In another family, the East African Scincid *Mabuia quinquetæniata* has a very similar general colour-scheme when young, but in this species the blue tail coloration disappears with advancing age. In South Africa the Lacertid *Eremias namaquensis* illustrates the same point, though here the tail is distinctly reddish in juveniles, later changing from rufous to sandy grey and thus taking on the general hue of its sandy surroundings. Quite apart from the fact that many lizards which especially practise autotomy have brilliantly coloured tails which will therefore appear all the more conspicuous when gyrating in the mouth of a predator (19), I refer here particularly to the *directive* function of the organ, whose relative conspicuousness *before capture* diverts attention from the lizard itself to that part of its body which may so readily be dispensed with, and replaced.

Curiously enough, comparable phenomena occur in certain snails of the genus *Helicarion* in the Philippines and *Stenopus* in the West Indies. Here again, the ' tail '—in reality the posterior part of the foot—is both more conspicuous than the rest of the body, and is easily shed and afterwards regenerated (564). Semper records that about 10 per cent. of the individuals of one species (*Helicarion gutta*) had shed the part. However, since the snails, unlike the butterflies and lizards which we have considered, are incapable of escaping by speed, the cases are not analogous; possibly here the conspicuous area may have a warning (aposematic) rather than a directive (parasematic) function—like that of the conspicuous ' tussocks ' in many Lymantriid caterpillars.

An interesting extension of the principle here described is presented by the curious food-relations of Skuas to other sea-birds which provide them with food. Auks, Gulls, and Terns are relentlessly pursued by these pirates until forced to vomit up their latest meal. Since Skuas occasionally attack birds directly as prey, instead merely of commandeering food from them, it is easy to conjecture how this habit of throwing the cargo overboard may have developed as a ready means of escape. The device is, in fact, comparable in this respect to the tail-shedding habit of lizards.

II. CHARACTERS WHICH DEFLECT THE ATTACK OF ENEMIES FROM THE MORE TO THE LESS VULNERABLE MEMBERS OF THE SPECIES

An extended application of the deflective principle is seen in another class of phenomena, where the local conspicuousness has a *social* rather than an *individual* significance. The gaudy coloration of most species of male ducks (Anatidæ) during the breeding season differs strikingly from the highly cryptic plumage of the females. Now Mottram has suggested that such coloration may be valuable in deflecting enemy attack away from the more vulnerable, and biologically more valuable, female, during the critical nesting period, at a time when the male is biologically less important, for in most cases he plays no part in incubation or nursery duties, which necessarily devolve upon his mate (425).

Dr. Julian Huxley (278) cites a most interesting case, mentioned by Dr. Stresemann, which by analogy supports the above interpretation. In certain species of Ptarmigan (*Lagopus*) the change from white winter plumage is deferred in the male until the females in their cryptic summer plumage have completed incubation. As a result the males become relatively much the more conspicuous sex during the nesting period, and thus are sacrificed to predatory enemies such as Eagles in proportionally greater numbers. Dr. Stresemann has also suggested that the bright coloration of most male ducks has a ' social parasematic ' or deflecting function. These cases are closely analogous to those of the gaudy-tailed lizards already discussed: in the latter a conspicuous, but relatively unimportant, part of the individual, and in the former a conspicuous, but relatively unimportant, member of the species is sacrificed.

Conditions similar to the above are also found in the relations between parent and offspring, rather than between male and female. I refer here to the well-known tactics, familiar to all observers of birds in nature, by which a parent endeavours to decoy intruders away from the vicinity of nest or young. Here it is not conspicuous coloration, but conspicuous and symbolical antics, which deflect the enemies' attention. Gilbert White speaks of the way in which 'a partridge will tumble along before a sportsman in order to draw away the dogs from her helpless covey'. The female Reed-Bunting (*Emberiza s. schœniclus*), disturbed at her nest, will first slip silently from it, and then appear a few feet before the intruder's path, falling on this side and that, fluttering and going through all kinds of antics, as though severely injured. In such cases, the display begins at a distance from the nest, and attention is directed to the place where the nest is not, just as in the eye-spots of butterflies the attention is directed to the place where the head is not. Every countryman has watched Lapwings attempt to beguile away intruders on the nesting territory with demonstrations in which both visual and auditory effects play a part. The birds fly conspicuously to and fro, uttering their plaintive notes, which while drawing attention to themselves, at the same time warn the chicks to lie low.

This habit is fairly widespread among birds that nest in exposed places, and it is sometimes used as a last resort even by cryptic species like Nightjars, when forced to leave the nest: for example, Beebe has described deflective tactics in the South American Dusky Nightjar (*Caprimulgus nigrescens*): 'When frightened from its egg it limped away like many another species and crouched in a conveniently exposed spot to attract the attention of the hunter to itself and from its home' (35). While photographing at a nest of the Nightjar in Norfolk recently, this wonderful principle was very beautifully demonstrated to me by the brooding bird. On being disturbed, she slipped silently from her two eggs, which were just due to hatch, and flew to an old elder branch lying on the ground fifteen yards from the nest-site. Here she perched—not *along* the branch in the usual cryptic attitude, but *across* it—and proceeded to fan her tail widely, at the same time bringing her wings forward in front of her and spreading them until the tips pointed directly downwards. After exhibiting every available square inch of her fanned-out plumage in this way for several seconds, she slipped off the perch and came towards me, shuffling along the ground and then halting with the wings and tail expanded flat on the flinty earth. When tired of these demonstrations, she flew around uttering the harsh and oft-repeated alarm notes and now and again alighting to rehearse the display of feathers on the branch or bare ground.

A point to be noted is that actions of this kind are not merely conspicuous and hence deflective, but they simulate a *wounded* bird, and hence invite or encourage pursuit.

Jourdain (296) gives a complete summary of the subject in his paper on *The so-called 'Injury-feigning' in Birds*, to which the reader is referred for fuller information.

III. CHARACTERS WHICH MISDIRECT THE ATTACK OF ENEMIES BY MISREPRESENTING THE POSTURE OF THEIR PREY

We must now consider briefly certain cases where deflective (parasematic) markings have a special and additional significance, which reaches its extreme development among Lycænid butterflies. I refer to the deceptive appearance of a false head situated at the posterior extremity of the hind wing in species of *Thecla*—an appearance often elaborate and perfect, which is brought about by the combined effect of adaptive structure, coloration, attitude, and movement. The structural modifications have as their main feature peculiar prolongations of the hind wings which simulate antennæ. In some species such as *Thecla phaleros* these are long and thread-like: sometimes they are white and slightly enlarged at the tip. At the base of this pseudo-antenna is a conspicuous eye-like spot. When at rest, the butterflies close their wings, in which position the false head appears actually far more conspicuous than the real head. At the same time, the deception is strengthened by adaptive movements of the hind-wings, which are moved alternately up and down, so that the false antennæ cross and recross each other conspicuously, and are in constant movement, while the real antennæ are inconspicuous and *motionless* (417). The resemblance to a head is further increased in Central American species of *Thecla*, and in Indian species of *Aphnæus*, *Pratapa*, and *Rapala* by having a conspicuously coloured lobe at the anal angle of the hind-wing bent outwards nearly at right angles to the plane of the wing. *Talicada nyseus*, another Lycænid, was observed by Longstaff (352) at Kandy to settle with its head directed downwards—a habit which has an obvious bearing on the deceptive appearance. The same observer found that the British *Lycæna icarus* rested with the head downwards twelve out of fifteen times. In Panama *Gynæcia dirce*, a species which usually rests on tree-trunks, is said by Mortensen to rest always with the head downwards. This butterfly, like species of *Thecla* already mentioned (p. 75), has an under pattern of lines which converge towards the false head. Planter records that a ' double-headed ' species of *Deudoryx* even moves backwards as well as forwards (cited Mortensen, 417).

Here then we have an elaborate system of structures, patterns, and instincts which combine *to produce the impression of a head at the wrong end.* In such cases the previously discussed function of directive eye-spots will be intensified, and with the additional advantage that when alarmed the insect will dart off in an unexpected direction.

Precisely similar conditions are found in certain vertebrates, such as the Chætodontid fish *Chætodon plebejus.* The head of this fish is crossed vertically by a bold black, white-bordered band, which, running through the eye, effectively obliterates that organ as previously described. Near the base of the tail there stares out a large, conspicuous eye-spot. Observations by Haddon (in Marshall, 395) at Thursday Island in the Torres Straits, reveal the interesting fact that this species had the habit of swimming very slowly tail first: but when disturbed it darts rapidly off to safety in the opposite direction. Mr. Robert Gibbings tells me that *C. capistratus* adopts the same tactics. Here again modifications of pattern and of habit tend to misdirect attack and so in effect facilitate escape. The present example is of particular interest in that the real eye is obliterated and a false eye substituted in one and the same animal (Fig. 76). Several other fishes belonging to different families possess very conspicuous eye-spots on various parts of the body, but usually towards the tail end, as seen, for instance, in *C. unimaculatus*, *Chelmo muelleri*, *Cichlasoma festivum* (Fig. 33), and *Antennarius notophthalmus* (Fig. 77). Similar very conspicuous eye-spots occur on the hind part of the body in several frogs belonging to different families, for

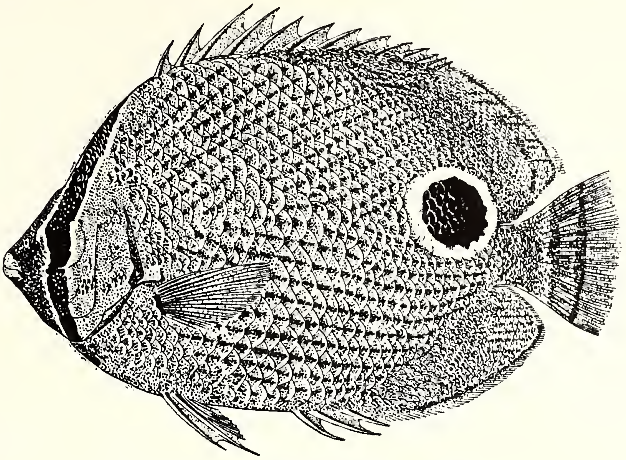

FIG. 76.—*Chætodon capistratus*

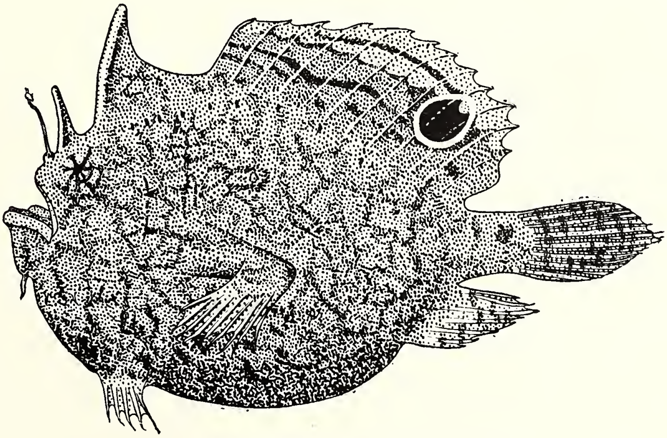

FIG. 77.—*Antennarius notophthalmus*

example, *Mantipus ocellatus*, *Paludicola fuscomaculata*, *Gastrophryne elegans*, *Eupemphyx nattereri* (Plate 46). In certain of these, there is here also a tendency for the real eye to be camouflaged and for the false eye to be by far the most conspicuous element in the whole colour-scheme, but in the absence of observations on their habits and relationships in the field it is inadvisable at present to speculate on any biological function which these markings may serve.

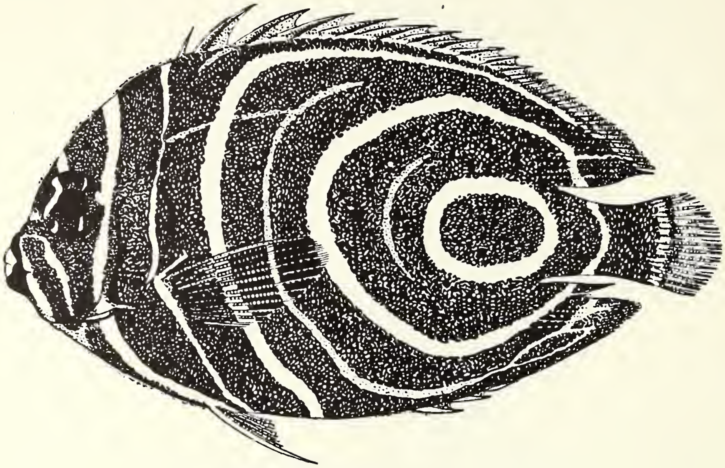

FIG. 78.—*Pomacanthus imperator* (immature)

IV. CHARACTERS WHICH MISDIRECT THE ATTACK OF ENEMIES BY MISREPRESENTING THE WHEREABOUTS OF THEIR PREY

In another interesting class of cases all the visible parts of the *resting* animal are obliterated by a cryptic colour-scheme which clothes the exposed surfaces. But there is also present an advertising colour-scheme, disposed on parts of the body, which are normally concealed, but which momentarily flash into conspicuousness when the animal *moves*, revealing a brilliant badge of scarlet, vermilion, orange, yellow, or blue (Fig. 79).

The Red Underwing Moth (*Catocala electa*) (Noctuidæ) provides a well-known example. When this insect is at rest the fore wings are folded back so as to overlie and completely hide the hind-wings. The former—grey, with a delicate figured pattern of black—constitute a most effective cryptic dress when the moth is resting by day against bark: the latter—red, with bold black markings—are highly conspicuous when the moth is in flight. Several other species of Noctuid, such as the familiar Large Yellow Underwing (*Triphæna pronuba*), with its black-bordered yellow hind-wings, illustrate the same point. But this is more clearly seen in various tropical species, such as *Mormia neonympha*, from Mesopotamia, or *Dermaleipa juno*, from India. Both these species have the fore-wings cryptically coloured, ashy in the former, chestnut or ochreous in the latter, while the hind-wings are very brilliant—bright cadmium yellow, with a broad black border in *M. neonympha*; and black, with the terminal area vivid crimson in *D. juno*.

Colour-schemes of this type are fairly common in a number of Lepidopterous families. In the forests near Pará there are several species of Hawk-moth (Sphingidæ) which wear similar bright colours on parts normally covered, namely, the hind-wings and abdomen, while the fore-wings are decorated with the most beautiful and effective cryptic tones and patterns which conceal the insects when resting in the daytime. For instance, *Isognathus scyron* and *I. menechus* both have the hind-wings yellow, with a sepia border—in fact their general colour-scheme is broadly similar to that of the Yellow Underwings. *Pholus vitis*, also from Pará, carries a carmine patch on the inner angle of the hind-wing: *Protoparce diffisa* has both pairs of wings cryptic, but wears a conspicuous series of orange spots on the sides of its abdomen. In a related family, Syssphingidæ, similar devices are found: for instance, in the light buff-coloured *Syssphinx molina*, from Brazil, the hind-wings are reddish, each with a conspicuous central black spot.

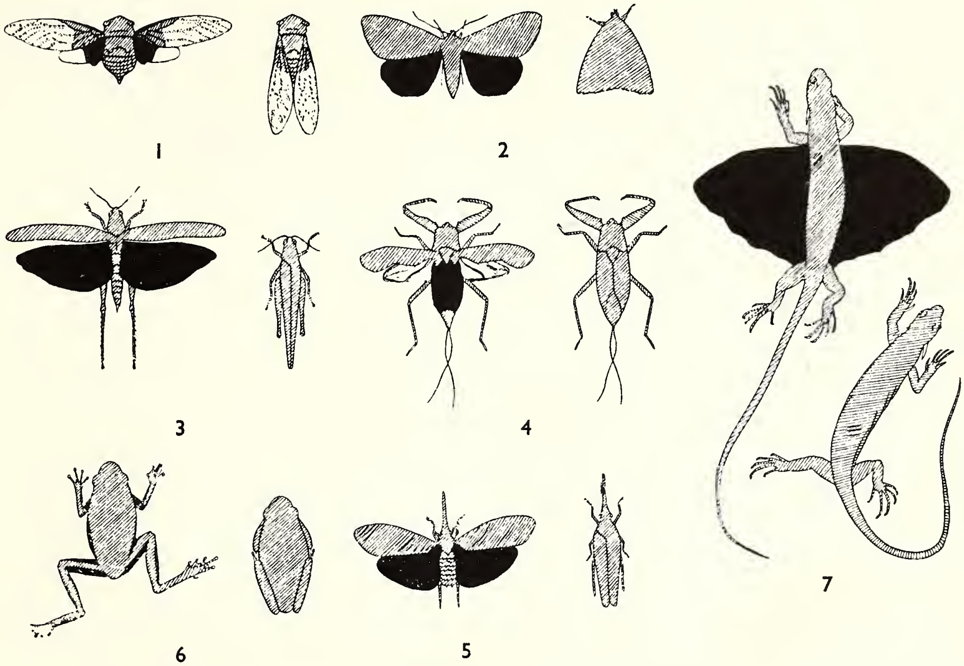

FIG. 79.—Examples of flash coloration in a variety of animals, the parts conspicuously displayed are drawn in black: 1 *Hemisciera* (Homoptera); 2 *Catocala* (Lepidoptera); 3 *Ornithacris* (Orthoptera); 4 *Laccotrephes* (Heteroptera); 5 *Fulgora* (Homoptera); 6 *Phyllomedusa* (Anura); 7 *Draco* (Lacertilia)

Many butterflies, including some of the most cryptic species, such as *Kallima*, illustrate the same principle: but here, in correlation with the quite different resting attitude (in which the wings are folded together over the back), the bright hues are frequently disposed on the upper surfaces of both wings, while the *under* surface of both pairs, rather than the *upper* surface of the fore-wings, are dressed in cryptic attire.

Such animals are Nature's quick-change artists. The sudden transformation from a concealing to a revealing colour-scheme requires but an instant of time; and the bright dress is as instantly laid aside when movement is done. What, then, is the function of these conspicuous parts, which flash out during movement and vanish again, like a conjurer's rabbit, when the creature alights? It is generally believed that these so-called 'flash colours' serve to confuse or misdirect an enemy in the pursuit of prey. Certainly for human eyes it is easier to mark the exact spot where bird or insect has alighted if its colour is persistently cryptic both in flight and at rest than one which unexpectedly flashes into conspicuousness on the wing, and then, as movement ceases, as suddenly melts into the landscape. It is the sudden disappearance of colour *combined with the equally sudden suspension of movement* which tends to mislead the eye and to render the animal's exact whereabouts on alighting all the more difficult to detect.

It must be admitted that in the present state of our knowledge the precise biological meaning of flash colours is not clearly understood: here is a point urgently needing the confirmation and proof of experiment and observation. However, it can hardly be doubted that in nature flash colours have an escape significance—a view which finds much indirect support both in their *wide occurrence in the animal kingdom*, and in their *actual distribution on the surface of the body*—as will be apparent from the following considerations.

It is significant to find that the same device which occurs in Lepidoptera such as *Catocala* and *Triphœna* has been evoked independently in at least two other orders of insects, the Hemiptera and Orthoptera, and in several different families. Among Homopterous bugs, one of the most striking cases of flash colours with which I am acquainted is that of a forest-dwelling Cicada, *Hemisciera maculipennis*, from the Amazon valley. Most Cicadas have the wings quite transparent and colourless, but in the present species the innermost, or proximal, portion of each hind-wing is decorated with a vivid splash of vermilion which extends nearly half-way along the wing. This colour would, of course, be perfectly visible through the transparent fore-wings in the resting insect, were it not for the fact that a patch of about equal area on these wings is pigmented with opaque olive-green, so that when the wings are folded the cryptic green area closes like a shutter so as just to hide the red areas on the wings beneath.

In several other tropical species both pairs of wings are wholly pigmented, and in such cases it is common to find colour-schemes similar to those of moths already considered, the fore-wings being soberly coloured in greys or greens or browns, and the hind-wings (seen only during flight) highly painted in crimson, orange, or yellow, as seen respectively in the Indian species, *Gœana atkinsoni*, *Balinta octonotata*, and *Platypleura mira*. Moreover, a similar arrangement turns up again in another family of Homopterous bugs, the Fulgoridæ, where we

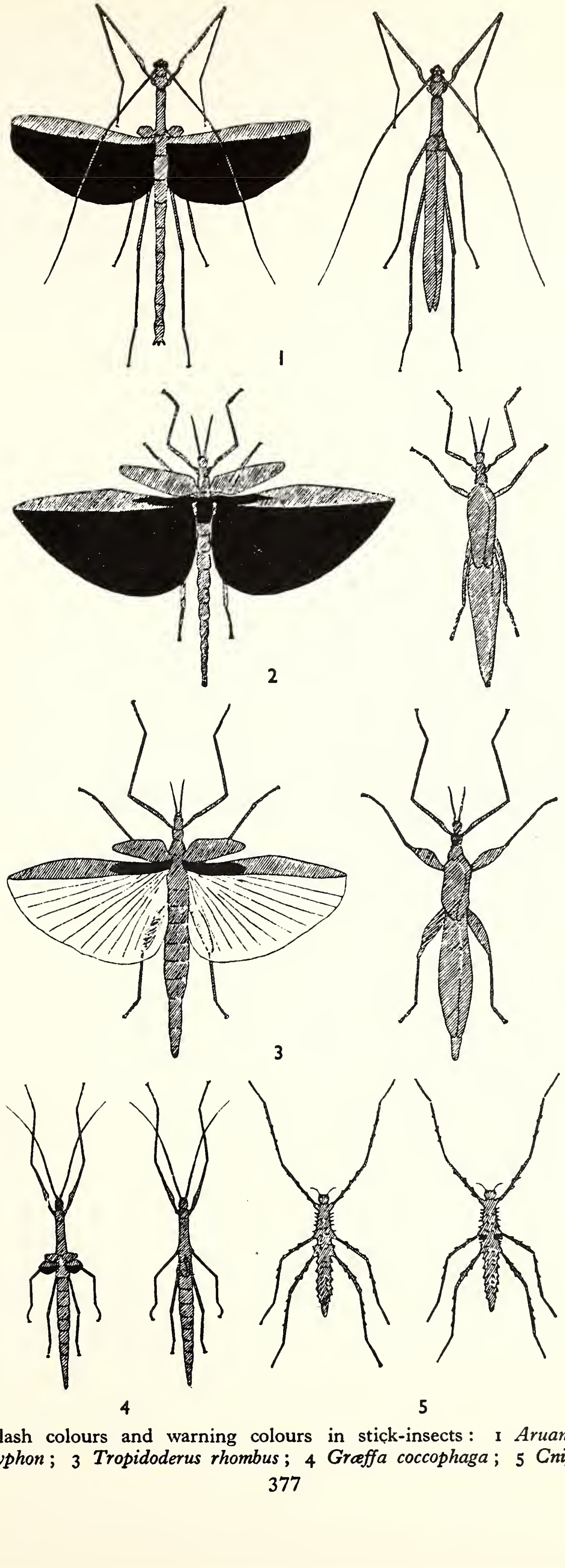

FIG. 80.—Flash colours and warning colours in stick-insects: 1 *Aruanoidea grubaneri*; 2 *Podacanthus typhon*; 3 *Tropidoderus rhombus*; 4 *Græffa coccophaga*; 5 *Cnipsus rhachis*

have cryptic species whose tegmina overlie vividly hued hind-wings—yellow and black in *Fulgora spinolæ*, blue and black in *F. intricata*.

Again, in certain sombre-hued Heteropterous bugs, what appear to be red flash colours are found, not on the wings, but on the upper surface of the broad abdomen, where they are covered by wings and tegmina in the resting insect, but conspicuously exposed in flight—an arrangement which occurs, for instance, in the genus *Mictis* (Coreidæ) and in *Nepa* and *Laccotrephes* (Nepidæ). Members of the latter family—the water scorpions—live in mud and reeds at the bottom of ponds; but when, as often happens, the water dries up, they are capable of flying considerable distances in search of new quarters.

Many species of grasshoppers (Acridiidæ) have the membraneous hind-wings (which are normally folded fanwise out of sight beneath the tegmina) gaily coloured: in *Œdipoda miniata* of Southern Europe they are bright crimson, with a blackish border; in *Titanacris carinata*, a fine green species from the Amazon, they are purple. In the Fataga Valley of Gran Canaria, on the slopes of Teneriffe, and in the barren tracts of Fuerteventura, I have repeatedly been struck by the effectiveness of this type of coloration in grasshoppers such as abound in these districts, but which are rarely seen until a flaming wing proclaims the presence of an insect fluttering to a safe distance, to vanish, invisible, the instant it alights on the lava or pumice or lapillæ of basalt, with which all its exposed surfaces blend. Many forest-dwelling grasshoppers of the Amazon basin, including some gigantic species, illustrate the same contrast between their cryptic resting and conspicuous flying liveries. Dr. Julian Huxley has reminded me of the fact that flash-coloration in grasshoppers is often associated with a zigzag flight and with a sudden change of direction before coming to rest—habits which undoubtedly contribute to the efficiency of this type of coloration.

Instances of the same principle occur in the Phasmidæ, certain species of which present an adaptive series illustrating the correlation between colour disposition and structural features (Fig. 81). There is a tendency in this family for the upper wings, or tegmina, to be reduced, or entirely wanting. In such cases it is obvious that the lower wings, which are often brightly coloured, cannot be concealed by the method obtaining in various moths, mantids, grasshoppers, cicadas, and other insects which fold the hind-wings beneath the fore-wings. Yet flash coloration, carried on the fan-like hind-wings, is found, even in such Phasmids, and is made possible by adaptive modifications in the wing membrane itself.

In extreme cases of the kind, where the tegmina are almost or completely absent, that part of the hind-wing which lies uppermost in the folded state is often coloured quite differently from the rest of the organ, while at the same time it lacks the narrow radiating fan-like folds of the membranous part. It therefore takes the place of the missing tegmen, which it resembles both in texture and appearance, and in its function of protecting the wing and screening its bright colours. *Aruanoidea grubaneri*, from the Malay Peninsula, is a case in point. With the wings folded the insect appears bright green and doubtless harmonizes well with grass and foliage. With the wings spread, however, it is seen that these organs are a beautiful rose-pink colour, except for a narrow strip of bright green which extends along the anterior margin of the wing from base to extremity, and which effectively serves to eclipse the brightly hued membrane that lies neatly folded beneath it until the wing is extended in flight.

Where, on the other hand, the tegmina are well developed, so as to cover more or less of the basal part of the wing when folded, the flash coloration frequently extends on to the base of the anterior area also. Thus, in the Australian *Podacanthus typhon* the anterior margin of the hind-wing is green and tegmen-like distally, where it is exposed in the resting insect; but proximally, where it is covered (at rest) by the tegmen, it is strongly pigmented with the pink coloration of the remainder of the membrane; and a patch of the same colour is worn upon the thorax. A similar arrangement is found in *Tropidoderus rhombus*, where the basal anterior wing margin carries a bright patch of red on an area closely coinciding with the extent of the somewhat abbreviated tegmina: in this species, however, the membranous part of the hind-wing is almost colourless.

It will be understood that in the species considered above, the hind-wings, whether partially covered by tegmina or not, are themselves well developed, and the conspicuous colours which they bear are so disposed as to be shown in flight and concealed in the resting insect. A singular and very interesting case in such a series as we have described is presented by an almost wingless form known as *Cnipsus rhachis*, from the New Hebrides. This Phasmid, greyish-brown and spiny in appearance, has both tegmina and wings extremely abbreviated, and is, of course, flightless. Seen at rest, the insect appears highly cryptic, but Mr. Bushby tells me that when irritated it is in the habit of raising its tegmina so as to display its minute hind-wings, which are coloured a very vivid carmine. The sudden flashing out on the animal's back of these two flaming red spots, which in their saturated brilliance appear to be almost luminous, is decidedly startling, and it is clear that we have here a remarkable intimidating mechanism, whose function is to prevent attack by bluff, rather than (as in the previous examples) to frustrate it by flight.

It is not difficult to reconstruct the steps by which such a change of protective technique—from flight, through flash, to threat—may have taken place. Many large-winged Orthoptera use the hind-wings solely for flight. When, as often happens, such wings become brightly hued, they take on an additional and allæsthetic function—that of concealment by deception. It is well known that other orthopterous insects, as already mentioned, though possessing well-developed wings are yet reluctant to fly, relying instead upon the effect of a warning display. Reduction of the wings, while materially affecting their capacity for flight, will not seriously damage their value as visual signals: thus a condition may be reached when locomotion becomes entirely subordinate to threat, until flight is no longer possible. This apparently is the stage reached by *Græffa coccophaga*, of Fiji, which forms a link in the series reaching its climax in *Cnipsus rhachis*.

We have here an excellent example of functional substitution—the previously predominant function of the wing as an organ of flight falling into abeyance and being replaced by other functions, at first subsidiary, but later becoming dominant and essential. Parallel functional changes are found in the Mantidæ, as shown, for instance, by the large-winged *Pseudocreobotra wahlbergi* (Fig. 81), which carries a warning device on the tegmina ; and by the flightless *Eremiaphila braueri*, where both wings and tegmina are reduced in size and purely sematic in function.

Turning now to an entirely different group of animals, we find an analogous arrangement in Oriental ' flying ' lizards of the genus *Draco*. Here, again, it is the wing membrane which bears the ' flash colour '. This structure, supported as it is by a series of modified ribs, can be spread open or closed back at will, like an umbrella. In *Draco maculatus*, from Indo-China, the ' wings ' are reddish or orange above and pale yellow below ; in *D. indochinensis*, from Annam, they are reddish-brown above, marked with four transverse black bands, and lemon-yellow below ; in *D. norvilli*, from Assam, they are banded with scarlet ; in *D. dussumieri*, from Southern India, purplish-black with lighter markings. Normally the membranes are folded in at the sides of the body, where they are quite inconspicuous. It is only when expanded in use that the colours are momentarily revealed as the lizard sails rapidly in an inclined plane from branch to branch, to be eclipsed instantly as it alights. It must be borne in mind that these colours are probably used for display by the males in courtship or rivalry, though at present there is scanty evidence available on the subject. However, there can be little doubt that in escape from predatory foes their function is analogous to the more familiar flash phenomena so well exhibited in grasshoppers and other insects.

Flash colours are not to be confused with symbols shown in *display*. It is true that, as with *Draco*, they may serve both functions in the same animal. But warning, threatening, or courtship displays depend upon a definite display reaction directed *towards* the enemy, rival, or mate. Flash colours, on the other hand, are exhibited in *escape from* an enemy. Their function is not to intimidate, or to stimulate, but to misdirect or confuse. Such colours are not situated upon surfaces of the body which for exposure require a deliberate display reaction —as, for instance, in *Bombinator*, which wears them on its belly, or *Pseudocreobotra*, which wears them on its fore-wings. They are essentially distributed upon parts which will be exposed (and where they will constitute the ' flash ') during the normal escape reaction. To operate effectively in nature, the ' flash ' must be associated with movements that are *sudden* and *swift*, and hence with the organs of movement. In all the cases mentioned hitherto, the exposure of conspicuous colours occurs simultaneously with the act of *flight* or *gliding*, and the conspicuous areas are, in general, confined to wings that are spread during movement, and covered by wings that are folded during rest.

In certain other cases the colours are associated with the act of *leaping*, as seen in different cryptic Anura, such as the Hylid *Phyllomedusa hypochondrialis*. This little tree-frog, whose biology has been studied by Budgett (67) in the Paraguayan Chaco, is a nocturnal species, remarkable for its powers of changing colour (which may be green, grey, or brown) to harmonize with its surroundings. When at rest, nothing is seen but the upper surfaces of the body as it crouches, most inconspicuously, on a leaf, with its legs folded closely in to its sides. However, during movement, or when seen at night in its active state by lantern light, it presents a very different picture, for the flanks, the hinder surface of the forearm, and the hinder and inner surfaces of the hind-limbs are coloured a brilliant scarlet, marked with transverse bars of black, while the soles of the feet are a deep purplish black. *Hylambates maculatus*, a Polypedatid frog which I came across in Portuguese East Africa, has the flash coloration similarly disposed, the sides of the thigh, the inner side of the tibio-tarsus, and a small area behind the forearm extending to the arm-pit being adorned with flaming vermilion of great brilliancy, which is completely hidden in the normal resting attitude.

An application of the distractive principle somewhat comparable to that seen in flash colours is furnished by animals which retreat under cover of a barrage flung in the face of the enemy at the moment of their departure. The effect of the discharge, whether visual or olfactory, is temporarily to disable, to delay, to dazzle or to distract the pursuer.

The Squid's dense smoke-screen of sepia is a wonderfully efficient device for eluding capture, especially when, as often happens, the production of the black cloud is accompanied by a sudden change in the direction of flight. A remarkable modification of this device is found in certain deep-sea Squids, which discharge a luminous cloud into the darkness of the abyss, to confuse or dazzle pursuers.

Different in detail, though similar in function, is the luminous discharge of certain *Acanthephyra*-like shrimps observed at great depths by Beebe (38). When startled by bumping against the window of the bathysphere, ' a rocket-like burst of fluid was emitted with such violence that the physiological effect was that of a sudden explosion. This occurred time and again at the lower levels, and I learned to distinguish two separate types of discharge, one uniformly luminous, the other dimmer but interspersed with dozens of brilliant stars and pinheads. For an instant the shrimp would be outlined in its own light . . . and then would vanish, leaving behind it the confusing glow of fluid.'

Olfactory, rather than visual, distraction associated with sudden escape reactions occur among various animals which discharge the contents of the bladder, cloaca, or crop, when surprised or hard-pressed by a predator. Various frogs and toads forcibly empty the bladder, squirting the urine over their adversary as they leap or run for safety. The Eider Duck emits a shower of evil-smelling excrement when flushed from its nest by a dog. Fulmar Petrels vomit up oil under provocation, and according to Coward may eject it at an intruder for three feet or more.

5. DIRECTIVE MARKS

> Beware of false prophets, which come to you in sheep's clothing, but inwardly they are ravening wolves.
>
> MATTHEW VII. 15

It will be relevant here to draw attention to a type of adaptive coloration whose function is of a converse nature, and relates to aggression rather than protection. Hitherto we have considered conspicuous features which *tend to deflect the attack, or to divert the attention of enemies away from their prey.* But localized markings may also subserve a directive, rather than a deflective, function. In this capacity they may be aggressive—reaching a climax in the sphere of allurement; or protective—in the sphere of bluff.

I. CHARACTERS WHICH DIVERT THE ATTENTION OF PREY FROM THE MOST DANGEROUS PART OF THEIR ENEMY

Just as with prey it is the head which it is especially necessary to conceal—to facilitate escape by flight, so with predators it is the head which it is especially necessary to conceal—to facilitate capture by ambush. Now in certain aggressively concealed predators, it is interesting to find that the head-end of the body is, relatively to the rest, especially well concealed. Among fishes, for instance, this is well seen in the case of the Angler (*Lophius piscatorius*). Although the whole animal, with its flattened form and cryptic disruptive coloration, is remarkably well concealed on the sea floor, it is anteriorly, where the head and terrible jaws are camouflaged by a curtain of innocent-looking weed-like lobes, that the aggressive colour-scheme reaches its zenith. Precisely similar conditions are found in the quite unrelated Carpet Shark (*Orectolobus barbatus*). Here, again, in a fish that haunts, and hunts from, the sea bottom, we have a creature whose variegated coloration harmonizes beautifully with weed-covered rock surfaces, and which wears on the head and round the mouth, but nowhere else, the deceptive weed-like processes that doubtless serve to dispel suspicion in small fishes, which perhaps may even fly for refuge into the very jaws of death.

The Star-gazers of the Atlantic and Mediterranean coasts, belonging to the genera *Astroscopus* and *Uranoscopus* (Uranoscopidæ), are sluggish, stout-bodied fish, which bury themselves in the sand under the surf, and capture their prey by ambush. Correlated with these habits, the eyes are dorsal in position, the upper surface of the fish is flattened, and the jaw is vertical so that the mouth opens on the upper surface of the head. When the fish lies beneath the sand, with little more than the eyes exposed, the cleft of the mouth is obscured by fringes of closely set filaments lining the lips.

The same habit has arisen independently in a totally unrelated group known as Sand-fishes (Trichodontidæ), of the northern Pacific. Like the Star-gazers, these fishes submerge themselves in the sand, and they, too, have labial fringes, which doubtless act like little curtains in concealing the slight movements of the mouth during respiration.

In such cases, then, we have (in distinction to those previously considered) cryptic features which tend to deceive prey as to the most dangerous part of their enemy. What looks like an extension of the same principle is the local colour play recorded by Holmes in *Sepia officinalis*. When the cuttlefish is manœuvring into position preparatory to striking its prey, brilliant changes of colour pass over the arms and head. Holmes has suggested that this play of colour may serve to distract attention from the long ejectile tentacles, which suddenly shoot out with lightning speed from pockets within the outer ring of eight short tentacles where the display is taking place. 'For the impression of movement given by the waves of colour is much more striking than the movement involved in the appearance of the tentacles' (269).

II. CHARACTERS WHICH ALLURE PREY TO THE MOST DANGEROUS PART OF THEIR ENEMY

From cases like those just considered, it is but a step to localized alluring elements, which deceptively suggest something attractive to prey. For instance, in addition to the cryptic frills of *Lophius piscatorius* just mentioned, the fish also carries on its head a line and lure—in reality a modification of the first ray of the dorsal fin, which, situated well forward on the snout, is elongated, flexible, and bears at its extremity a flattened flag-like appendage whose swaying movements in the water attract investigation by the small in-shore fishes upon which the Angler feeds.

Related Ceratoid Anglers of the deep sea likewise possess alluring apparatus —often, as in *Lasiognathus saccostoma*, of a remarkably elaborate nature, and including a stout fishing-rod, long line, hooks, and bait—but the latter, as an adaptation related to the eternal darkness of the abyss, generally 'takes the form of a bulb of varying size which can be made luminous at will and acts as a lamp to attract other fishes to destruction' (446).

We may remark here that lights are well known to attract marine organisms such as Amphipods, squids, and fishes; and indeed the fact has a scientific application which was apparently first made use of by the United States Fish Commission in 1884. A few years later Herdman (239) showed conclusively the effect of a brilliant light in attracting free-swimming animals. Two tow-nets, one with a battery of lights fixed in its mouth and the other without lights, were let down to three fathoms at night. When hauled in half an hour later, the former contained an abundant assemblage of organisms, especially Crustacea; the control net contained practically nothing.

It is interesting to find that certain Star-gazers possess a lure associated with the mouth. Of a Mediterranean species, *Zaleoscopus tosæ*, Norman writes: ‘At times it protrudes from its mouth a little red filament, which represents a membranous process of the valve of the lower jaw. This is made to move about on the sand, crawling, wriggling, contracting and expanding—in short, imitating to perfection the movements of a small worm.’ A second species, from the West African coast, uses a broad white membranous flap, for the same purpose (446).

Among Reptiles, certain Chelonians possess specially modified processes believed to serve a precisely similar function. In the rivers of Brazil there lives a large turtle, the so-called ‘Matamata’ (*Chelus fimbriata*) of cryptic bottom-dwelling habits, whose rugged carapace, broad, flat-topped head, and unusually long, laterally folded neck well equip it for a life of stealth and ambush. About the mouth and beneath the throat of this grotesque creature are a series of red filaments, flattened and fleshy. According to Ditmars, some of the filaments are voluntarily movable (146) while the more slender ones sway with every movement of the water, and their conspicuous colour and worm-like form and motions doubtless serve as lures to fishes and frogs.

A parallel case is known in the unrelated Alligator Snapping Turtle (*Macrochelys temminckii*), a powerful mud-coloured form inhabiting North American rivers. Ditmars (146) states that the dull yellow head and shell exactly match the coffee-coloured waters of the lower Mississippi, where the reptiles lie motionless on the bottom in wait for unwary fish. This species likewise entices prey to their destruction, employing for bait a remarkable appendage, attached to the inside of the lower jaw, close to the tongue. ‘This’, says Ditmars, ‘is a well-developed filament of flesh, white and distinct from the yellowing mouth-parts and resembling a large grub. . . . More striking, however, is the reptile’s power to keep this appendage in motion, giving it the aspect of crawling about in a small, circular course’ (143).

According to Pycraft (532) the tail in the young of certain Pit Vipers (Crotalinæ) such as the Copper-head *Agkistrodon contortrix*), the Water Moccasin (*A. piscivorus*) and the Fer-de-Lance (*Bothrops atrox*), is used for a similar function. As juveniles these species have the last inch or so of the tail coloured a brilliant sulphur yellow. When offered food, captive specimens have been observed to set the tail-tip writhing and twisting, thus producing a generalized deceptive likeness to a worm or insect larva which may well form an irresistible attraction to the curiosity of lizards, frogs, and toads.

What appears to be an excellent illustration of localized alluring colour among birds has been described by Beckham (cited Keeler, 305), who writes of the King-Bird, *Tyrannus tyrannus*: ‘Several years ago, in May, I saw one of these birds occupying an exposed perch on a pear tree in bloom, about which many bees were darting. Several times I observed that the bird caught the insects without leaving his perch by quickly turning his head and grabbing them. My attention being thoroughly aroused, I noticed that many of them seemed to fly directly towards him ; the majority appearing to shy off at a short distance and change their course, but very few that came within reach escaped him.' While thus feeding, the orange-red crown was fully displayed, with the crest held erect, and doubtless may have been mistaken for a flower.

The same author refers to a similar occurrence witnessed by Nutting in Nicaragua, where *Muscivora mexicana*, perched upon a twig, was seen to wave its curious and conspicuous fan-shaped crest after the fashion of a flower blown by a gentle breeze, and thus to attract insects within reach.

An example among invertebrates is furnished by a little British crab, *Hyas coarctata*, whose habits have been observed by Dixon (151). In this case concealment of the body is adventitious, the crab clothing itself with a shrubbery of algæ, corallines, crinoids or other foreign material, until only the pink claws are exposed. Thus dressed, and swaying gently about in a mass of weed, it decoys and seizes the small fish attracted within striking range of the brightly coloured chelæ. Observations of alluring devices in actual operation are unfortunately only too rare, and I therefore quote in full Dixon's valuable statement : ' A few days after we obtained the *Hyas* we put a number of gobies into the tank. These little fish had their curiosity at once aroused by the red and white tips of the *chelæ* moving among the groves of Sertularians, and swam up to observe such an interesting phenomenon. The moment one came within his reach the *Hyas* suddenly closed all his extended legs like a spring trap, and generally succeeded in making a capture of the poor goby, who was forthwith thrust head-foremost into the mouth of his voracious captor. One *Hyas* caught and ate fourteen gobies within a week. We believe, therefore, that the polished white and red tipped chelæ, the two terminal joints of which are never concealed by the decorations, are held aloft by the crab as a kind of bait, and that the rhythmic motion is added to make the bait still more attractive. It is needless to remark that the capture of the fish is rendered much more easy by the way the crab has himself disguised, so that he is almost unrecognizable among his surroundings.'

A special case is presented by certain intestinal parasites which depend upon being swallowed by a vertebrate host for the completion of their life-cycle. The ' fluke ' *Distomum macrostomum* occurs in the intestine of Blackcaps, Sparrows, and other passerine birds. The eggs, discharged with the bird's excrement, are scattered upon leaves and herbage, and if swallowed by the snail *Succinea putris*, hatch as minute active larvæ in the snail's gut. After penetrating the alimentary canal, the larvæ undergoes metamorphosis and grows rapidly until it has permeated the snail's tissues as a shapeless sporocyst. Branches of the parasite growing in the head sprout into lobes in the snail's tentacles. These now take on a most conspicuous appearance, being much distended, banded with green and white, and tipped with vermilion. Moreover, they become motile and pulsate rapidly. In short, these branches act as an attractive advertisement to birds, which peck off the snail's tentacle, and with it the fertile branches of the sporocyst containing large numbers of young flukes. Curiously enough, the adult bird is immune to infection and digests the Distomes, but if the tentacle is offered as food to a nestling, the young ' flukes ' are liberated in the gut and complete their development. Here, then, we have a type of alluring coloration comparable to that commonly found in the plant kingdom in the display of fruits, since its function is not to allure prey with an imitation bait, but to bribe a predator with a real meal. It is also significant that red is once again the colour used to appeal to an avian population.

III. CHARACTERS WHICH ATTRACT THE ATTENTION OF ENEMIES TO THE MOST DANGEROUS ATTRIBUTE OF THEIR PREY

The markings to which I must now very briefly refer belong functionally to the important warning (aposematic) type which has already been discussed in detail. There are, however, certain aposematic phenomena which must be included here as having a local and directive function. In the previous section we have considered animals possessing *locally conspicuous marks—whose function is to lure prey to the most dangerous part of their enemy.* In the present section we have to consider cases of precisely the opposite nature, that is to say, animals possessing *locally conspicuous marks—whose function is to warn and educate enemies by drawing attention to the most dangerous part of their prey.*

This is seen, for instance, in the Weever Fish (*Trachinus vipera*), where the intense black colour of the dorsal fin is also the site of two intensely poisonous spines; and in the fish *Hepatus achilles*, where the general body colour is black, against which there stands out in strong contrast a scarlet spot round the caudal spine. In these cases a local advertisement is associated with a local armament, and the one attracts special attention to the other.

Garstang has drawn attention to the directive function of the highly conspicuous and highly distasteful papillæ of certain Nudibranchiate Eolids such as *Facelina coronata* and *Eolis alderi*: here the bright coloration is confined to the papillæ, which besides being unpalatable owing to the presence of stinging nematocysts, are easily detachable, and can be regenerated to their full size in two or three days. Hence he regards them as of value in facilitating the education of enemies, besides giving the individuals themselves an additional chance of escape (201). This view is supported by the animal's reaction if touched, when the head is telescoped inwards, while the papillæ ' rise up from their recumbent position and become very prominent, like the quills of a porcupine ' (202).

Other instances of the same principle are seen in the sea-anemone *Actinia equina*, where intense blue patches beneath the tentacles are associated with batteries of nematocysts (174); in the marine Terebellid *Polycirrus aurantiacus*, whose defensive tentacles become brilliantly phosphorescent when the animal is irritated; and in different Lymantriid caterpillars with their defensive dorsal brushes or ' tussocks ', which are conspicuously coloured—white in the Scarce Vapourer (*Orgyia gonostigma*), black and white in the Dark Tussock (*Dasychira fascelina*), yellow in the Pale Tussock (*D. pudibunda*), Reed Tussock (*Lælia cœnosa*) and Vapourer (*O. antiqua*)—besides being prominently situated, easily detachable, and deterrent in effect against enemies. In all such cases the psychological advertisement, whose function is to prevent attack, and the physical armament, whose function is to defeat attack, are embodied in one and the same organ : in each case the most conspicuous part of the prey is also the most dangerous or disagreeable.

Many years ago Marshall (395) suggested that the posterior white spots on various Carabidæ are directive in function. Such beetles depend for protection upon their power of ejecting strongly acid liquids from behind. With the smaller species, this discharge enables the insects momentarily to disconcert their enemies, and so gives them an opportunity of escape. 'Under these circumstances, it is evidently of importance that an attack from an enemy should be directed to the anal portion of the body in order to ensure its receiving the discharge.'

Larger species, belonging to the genus *Anthia*, are extraordinarily conspicuous insects, and in some, like *Anthia sexguttata*, the posterior spots may also have some directive function. According to Marshall, they adopt a very characteristic attitude when alarmed, raising the body high on the legs, so that the liquid can be ejected upwards. 'Their acid secretion is very powerful', he writes, 'and causes a strong stinging sensation when it touches the skin of the face or the more tender parts of the hands, and as it can be projected to a distance of some four or five feet, the insect would have to be captured with considerable caution even by an enemy which might be aware of its powers.'

Finally, there are a number of cases in which the organ concerned is specially displayed before an enemy or rival—as, for instance, in the show of teeth by Mandrills and by many Carnivora, in the erection of spines by Porcupines, and in the show of arms by the East African crab *Sesarma meinerti* (108).

IV. CHARACTERS WHICH ATTRACT THE ATTENTION OF ENEMIES TO AN APPARENTLY DANGEROUS ATTRIBUTE OF THEIR PREY

Instances such as those mentioned above grade into others in which target markings are symbolical of dangerous attributes which are, in fact, not present ; we have passed from signs that are aposematic to those which are pseudaposematic ; from the realm of warning to that of bluff.

Such terrifying masks, in which the essential feature is a pair of gleaming eye-spots, occur in a number of insects belonging to widely different groups. Hingston (265) has given a vivid account of certain examples found in forest-dwelling insects from British Guiana. One of these, a Cassidid beetle (*Pseudomesomphalia contubernalis*), was a flattened, broad-winged form, black in colour, from whose wing-cover stared out two bright yellow eye-spots which, in the living insect, 'seemed to peer forth like yellow penetrating orbs each with a black pupil'. Another was a weevil (*Heilipus ocellatus*), which wore on each wing-case a conspicuous eye-mark in the form of an oval ring of bright yellow, enclosing an area of dense velvety black. Another example occurred in a grasshopper (*Ommatolampis perspicillata*), a green, flightless form, each of whose rudimentary wings were largely occupied by a target-like pattern, with a conspicuous circular bull's-eye and yellow marginal rim.

It is significant that in each of these insects, a bug, a beetle, and a grasshopper, the same striking pattern and arresting colour-scheme has been evolved. ‘ In each case ’, as Hingston has it, ‘ a black pupil glares out from a yellow iris.’ Now the identical device is found in other forms, such as certain Lepidopterous larvæ already mentioned, in which the coloration is intimately associated with an instinctive display reaction, whose display towards, and effect on, enemies indicate sufficiently clearly its intimidating function. The effect of such eye-spots will doubtless be found to vary with different enemies: to some it may merely suggest a general but concentrated warning signal; to others, it may perhaps be interpreted in terms of a vertebrate eye. But the point to which I would draw attention here is the nature of the advertisement itself.

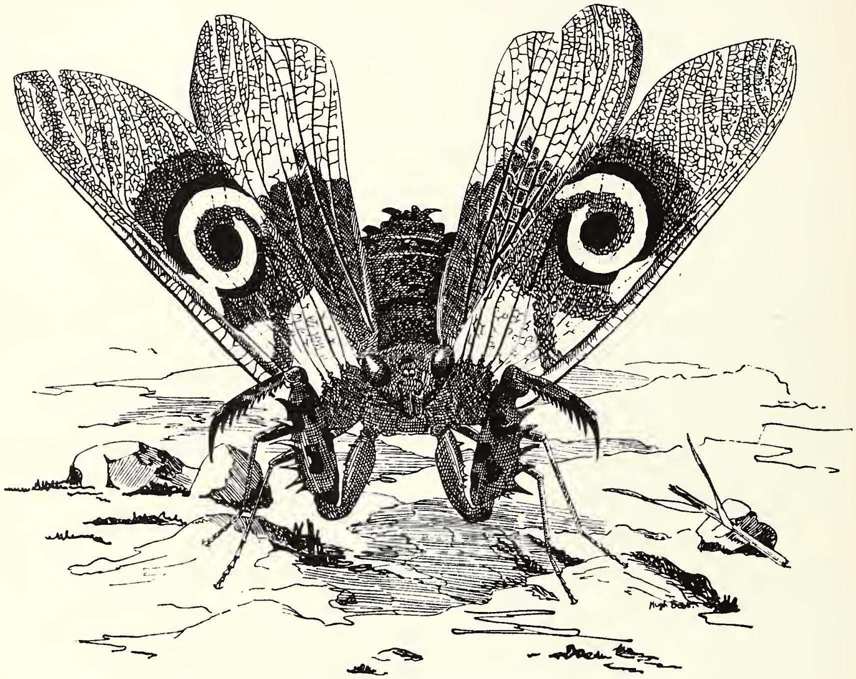

FIG. 81.—Warning display of *Pseudocreobotra wahlbergi*

Finally, there are the markings, often glaringly conspicuous and piercing, whose function is to alarm or intimidate enemies by mimicry. These depend for their effect upon crude resemblances, or caricatures, suggestive of a formidable foe. The most remarkable examples are undoubtedly those in which the intimidating elements take the form of false eyes, which at their best are exaggerated in size, conspicuous in colour, and penetrating in appearance. Several cases of the kind have already been mentioned under the heading of warning displays: such are the ocelli on the fore-wings of the Mantis *Pseudocreobotra wahlbergi*, on the hind-wings of the Eyed Hawk-moth (*Smerinthus ocellatus*), and on the anterior segments of Lepidopterous larvæ such as *Leucorampha* and *Chærocampa* (Sphingidæ) and *Prepona* (Nymphalidæ).

In his admirable chapters on mammals and birds in *The Meaning of Animal Colour and Adornment*, Hingston has discussed the significance of the real vertebrate eye as an instrument of intimidation. When we consider the almost bewildering variety of natural objects whose appearance is simulated by different animals, for purposes of protection—by concealment, by warning, by bluff, or by disguise—it is not surprising to find that the eye, of all possible patterns, should have been especially singled out for caricature on the masks worn in Nature's carnival of make-belief. In the first place, in its *pattern* and its *colour* it exhibits those combinations both of form and of hue which we have seen, on grounds discussed previously, make for the maximum of visibility. At its best this configuration is the advertisement *par excellence*. And in the second place, this pattern is, in actual fact, that found in the eyes of many vertebrates, and one which seems to occur typically in predaceous or well-protected forms, such as the cats among mammalia, and owls, diurnal birds of prey, and parrots among birds.

Of the various intimidating ' eyes ' of insects perhaps none are more remarkable than those carried beneath the hind wings of certain Brazilian butterflies belonging to the genus *Caligo*. Here, as may be seen by reference to the photograph on Plate 48, the appearance reaches a high degree of perfection. These large and handsome butterflies resemble moths in their crepuscular habits, feeding and flying through the forest at dusk. No one who has seen the insect, with its wonderful gleaming ocelli, can fail to be impressed both by their beauty and by their general deceptive resemblance to the eye of some large vertebrate such as an owl, and it seems reasonable—in view of analogous instances and observations—to conclude that the two staring eye-spots would be mistaken in the gloom by insectivorous birds and mammals for something on no account to be meddled with.

Possibly into the same category fall certain Fulgorid bugs of the genus *Laternaria*, also from tropical South America. These have the anterior part of the head produced into a large hollow structure which bears a marked superficial resemblance to the head of an Alligator—a similarity which is reflected in the name ' Jacarenam-boya ' (Alligator-Snake), by which the creature is known to the Indians. The resemblance extends to a number of independent details, including the nasal prominence in front, a large false eye behind, bearing a white mark which simulates light reflected from a real eye, and false teeth which are present not merely in colour but in relief. The supposed terrifying function of this remarkable mask—an example of which is figured on Plate 47—has been discussed in detail by Poulton (511). Cases such as this lead up to, and intergrade with, cases of true mimicry, which will be considered in a later section.

From what has been said above, it will be clear that the several classes of cases dealt with possess in common certain characteristic features—being *conspicuous in appearance*, *localized in distribution*, and *directional in function*. Now to these characters we must add a fourth feature which is typical at any rate of the majority of such cases: we are dealing here with something more than mere conspicuousness. It is true that the phenomena are based upon local advertisements or targets which appeal to the eyes of enemies, or of prey: but there is an additional element—the element of *deception*. These target marks and brightly coloured parts, these conspicuous individuals and conspicuous actions and the like operate by misleading, misdirecting, confusing, or bluffing enemies or prey. Sometimes they seem to reveal something that is not present; sometimes they seem to conceal something that is present; sometimes they disguise an animal's identity; sometimes they camouflage its posture; sometimes they cover its whereabouts.

Translated into terms of modern road traffic, we should have to picture a world in which signposts were apt to point away from the places which they indicated; in which pictures representing real roads were painted on walls, with traffic guiding lines leading into them; in which there were vehicles whose front end appeared to be at the back; in which others, like fire-engines and post-office vans, rushed conspicuously along the streets and kept suddenly stopping, and at the same time immediately becoming invisible to other road-users; in which signs of ' No Road ' were displayed in places where the road was open; and in which cleverly camouflaged pit-fall traps were dug in the street, with traffic police beckoning vehicles towards them.

Such conditions, did they exist, can hardly be conceived of as increasing road safety! And in nature, comparable deceptive phenomena undoubtedly make for ' errors of judgement '—mistaken directions, mistaken identities, mistaken attitudes—errors for which either a predator, or its prey, pays the penalty of hunger or of capture. We see then that deception forms an essential element in the adaptive coloration of many animals; and that the code on nature's highway is not ' Safety First ' but ' Survival of the Fittest '.

ALLURING AND MIMETIC RESEMBLANCES

6. ALLURING COLORATION

> Their throat is an open sepulchre: with their tongues they have used deceit: the poison of asps is under their lips.
>
> ROMANS III. 13

UNDER the heading of 'Special Protective and Aggressive Resemblance' we considered the case of animals which find security or sustenance in the deceptive likeness to natural objects of various kinds not intrinsically conspicuous. This was followed by an account of colour characters which are conspicuous, but restricted to part of an animal, and hence directional in function.

We now come to a class of coloration which at once advertises and disguises the animal as a whole. Such animals sail under false colours, and by so doing may deceive enemies or prey as to their identity—suggesting something repulsive to the former or attractive to the latter.

Bogus advertisements of this kind therefore have two main uses. They may serve to attract or ambush unsuspecting prey, or to mislead enemies as to the nature of their prey.

I. ADVENTITIOUS ALLUREMENT

Many spiders haunt the petals of flowers and there await the arrival of insect visitors. Species in which this habit is fixed generally harmonize more or less closely with the floral advertisement of which they form an inconspicuous part, and whose attractiveness they turn to their own ends.

The association thus formed between flower and arthropod is curious. Both members of the partnership are inherently conspicuous objects in nature; yet when *in situ* the spider is concealed both from its enemies and from its prey, while the latter are lured at once to the table and to the grave.

Thomisus citreus is a creamy-white species whose abdomen resembles in shape and colour the unopened flower-buds of the Wayfaring tree *Viburnum lantana*, and whose food consists of insects visiting the flowers among which it takes its stand (646). Such cases are by no means uncommon. We have already mentioned the flower-harmonizing spiders of the genus *Misumena*. On Luzon, in Manila, Mortensen came across a white spider with yellow legs, stationed in a white flower with yellow stamina, where, he states, it was very hard to distinguish (417).

Strictly speaking such spiders cannot be said to display alluring colours. For they do not provide the bait: they borrow it. And so the arrangement must be regarded rather as an adventitious allurement. Into the same category fall examples like the small green and white mantis found by Alcock (2) in the large white and green flowers of *Pancratium*, at Minnicoy: ' So exactly matched were the colours of the insect and the flower ', he writes, ' that had I not happened to shake the creature out of its ambush, where it was lying in wait like a spider for its prey, I should never have noticed it.'

II. SPECIAL ALLURING COLORATION

Such cases lead up to those where the function of the resemblance is alluring; where, in other words, the decoy is provided by the animal itself, rather than by an extraneous object in which the animal is concealed.

Annandale (7) gives a vivid account of the alluring appearance of a flower-like mantis *Hymenopus bicornis* from Malaya—a rare and remarkable creature, whose form, colour, attitude, and association with the ' Straits Rhododendron ' *Melastoma polyanthum* together provide one of the most convincing and wonderful examples of this habit yet known. In its nymphal state the insect is coloured pale pink and pearl white. ' The whole surface of the trunk and that of the flattened expansions of the femur of the posterior limbs had that semi-opalescent, semi-crystalline appearance that is caused in flower-petals by a purely structural arrangement of liquid globules or empty cells.' The petals of *M. polyanthum*, on which the mantis was found, are also mauve-pink; and the leaves are of the shade of green represented by a disruptive band traversing the insect's thorax.

On the morning after capture, the mantis was placed in the open near a large branch of the Rhododendron. ' It deliberately walked towards the branch, swaying its whole body from side to side as it progressed, and commenced to climb one of the twigs. This twig, however, bore only green buds and unripe fruit. When the Mantis reached the tip of the twig and found no flowers, it remained still for a few seconds, and then turned and descended with the same staggering gait. It proceeded to climb another twig. This also bore no flowers. The Mantis descended from it and mounted a third twig, which was topped by a large bunch of full-blown blossoms. To these it clung by means of the claws of the two posterior pairs of limbs. For a few minutes it remained perfectly still, and then began swaying its body from side to side, as it had done while walking.

' Almost as soon as the Mantis had settled itself on the inflorescence, a small, dark, dipterous insect, of a kind very commonly seen on the flowers of this species of *Melastoma*, alighted on one of its hinder legs. It was soon joined by others, apparently of the same species as itself. They settled quite indiscriminately on the petals and on the body and limbs of the Mantis. It was then that the significance of the black spot at the tip of the abdomen became apparent, for at the distance of a few feet it was impossible to distinguish it, except by its symmetrical position, from one of these small Diptera. The Mantis made no attempt either to drive off or to capture the small flies, for its motions seemed to attract rather than to repel them. After a short time a larger Dipteron, as big as a common house-fly, alighted on the inflorescence within reach of the predatory limbs. Then the Mantis became active immediately; the fly was seized, torn in pieces and devoured, notwithstanding the presence of a large crowd of natives who had collected to watch what was happening.'

The above state of affairs would be sufficiently curious if it stood by itself. But it does not stand by itself. The gentle art of allurement, as practised by certain spiders, presents some features even more remarkable than those just described. The account by Forbes (180) of the appearance and habits of a spider, *Ornithoscatoides decipiens*, found by him in West Java, is of the greatest interest, and I will quote his own description of the circumstances of his discovery, and of the nature and effect of the deceptive device involved. 'I had been allured into a vain chase after one of those large, stately flitting butterflies (*Hestia*), through a thicket of prickly *Pandanus horridus*, to the detriment of my apparel and the loss of my temper, when on the bush that obstructed my farther pursuit I observed one of the Hesperidæ at rest on a leaf on a bird's dropping. . . . I approached with gentle steps but ready net to see if possible how the present species was engaged. It permitted me to get quite close, and even to seize it between my fingers; to my surprise, however, part of the body remained behind . . . adhering, as I thought, to the excreta. . . . I looked closely at, and finally touched with the tip of my finger, the excreta to find if it were glutinous. To my delighted astonishment I found that my eyes had been most perfectly deceived, and that the excreta was a most artfully coloured spider lying on its back, with its feet crossed over and closely adpressed to its body.

'The appearance of the excreta rather recently left on a leaf by a bird or a lizard is well known. Its central and denser portion is of a pure white chalk-like colour, streaked here and there with black, and surrounded by a thin border of the dried-up more fluid part, which, as the leaf is rarely horizontal, often runs for a little way toward the margin. This spider, which belongs to the family Thomisidæ, possessing rather tuberculated, thick, and prominent abdomened bodies, is of a general white colour; the underside, which is the one exposed, is pure chalk-white, while the lower portions of its first and second pairs of legs and the spot on the head and on the abdomen are jet black.

'This species does not weave a web of the ordinary kind, but constructs on the surface of some prominent dark green leaf only an irregularly shaped film of the finest texture, drawn out towards the sloping margin of the leaf into a narrow streak, with only a slightly thickened termination. The spider then takes its place on its back on the irregular patch I have described, holding itself in position by means of several strong spines on the upper sides of the thighs of its anterior pair of legs thrust under the film, and crosses its legs over its thorax. Thus resting with its white abdomen and black legs as the central and dark portions of the excreta, surrounded by its thin web-film representing the marginal watery portion become dry, even to some of it trickling off and arrested in a thickened extremity such as an evaporated drop would leave, it waits with confidence for its prey—a living bait so artfully contrived as to deceive a pair of human eyes even intently examining it.'

The same naturalist subsequently came across a second specimen of this remarkable spider, and was again taken in by the extraordinary resemblance. He says (179): 'On June 25th, 1881, in the forest near the village of Lampar, on the banks of the Moesi river in Sumatra, while my "boys" were procuring for me some botanical specimens from a high tree, I was rather dreamily looking on the shrubs before me, when I became conscious of my eyes resting on a bird-excreta-marked leaf. How strange, I thought, it is, that I have never got another specimen of that curious Spider I found in Java which simulated a patch just like this! I plucked the leaf by the petiole while so cogitating, and looked at it half listlessly for some moments, mentally remarking how closely that other spider had copied nature, when, to my delighted surprise, I discovered I had actually secured a second specimen, but the imitation was so exquisite that I really did not perceive how matters stood for some moments. The Spider never moved while I was

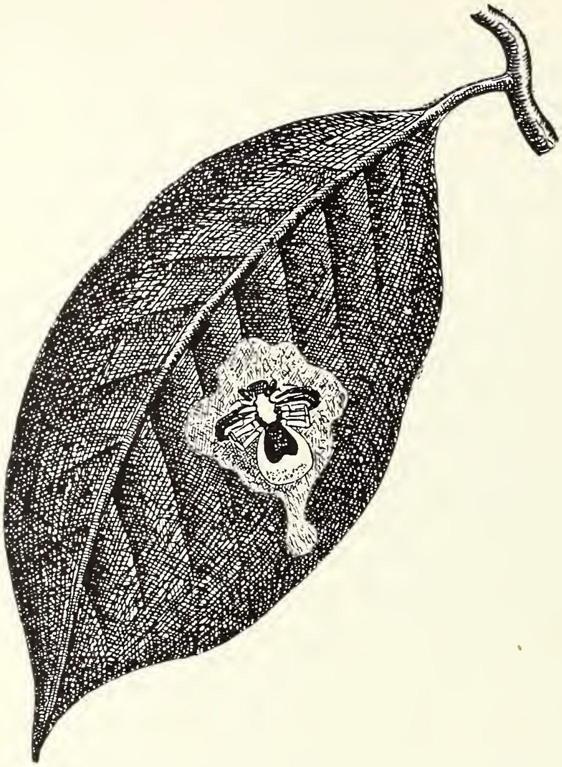

FIG. 82.—*Ornithoscatoides decipiens*: spider and web resembling a bird's dropping. (*Redrawn after* FORBES)

plucking or twirling the leaf, and it was only when I placed the tip of my little finger on it, that I observed that it was a Spider, when it, without any displacement of itself, flashed its falces into my flesh. . . .' (179). It was significant that here again the spider was seated in the middle of a small irregular web mat, which with a narrow streak laid down towards its sloping margin, represented accurately the more fluid part of the dropping even to the run-off portion with the thickened knob (which was not accidental, as it occurred in both cases), like the residue which semi-fluid substances ending in a drop leave on evaporation.

This example is of great interest. It shows how form, coloration, attitude, and habits combine to create the illusion: how, moreover, the spider supplements its own appearance by an addition in perfect harmony with the object simulated. An important feature in the deceptive appearance is the irregular shape of the web-mat on which the spider stations itself, and which perfects the disguise by making the apparent dropping *asymmetrical*—a point of some consequence, for resemblances of this particular kind, however detailed and elaborate in all other respects, tend to appear less plausible when they exhibit a marked symmetry of form.

Another closely related spider, *Phrynarachne Rothschildæ*—of somewhat similar habits and appearance—has been found by Rothschild (484) in Ceylon.

7. MIMICRY: THE ATTRIBUTES OF MIMICS

The possibilities of existence run so deeply into the extravagant that there is scarcely any conception too extraordinary for Nature to realize.

AGASSIZ

The phenomena of mimicry form an important and extremely interesting, if somewhat controversial, aspect of our subject, and comprise some of the most astonishing manifestations of animal coloration. The theory that the mimicking species are benefited by a superficially deceptive resemblance to a model which is either dangerous or distasteful to their natural enemies, or to one which is not feared or avoided by their prey, rests ultimately upon the validity of the theory of warning coloration—since the animals resembled are themselves typically aposematic. This is a type of coloration which we have already considered in detail from various biological aspects, so that the present subject need not be treated at length. In the following pages I shall bring forward certain facts which, directly or indirectly, throw light upon the nature and adaptive significance of these resemblances.

I. THE RELATION BETWEEN CRYPTIC AND MIMETIC RESEMBLANCE

The theory of mimicry has frequently been criticized as though it represented an attempt to explain an isolated, peculiar class of phenomena—championed and made much of by imaginative or over-enthusiastic arm-chair naturalists who take delight in discovering 'mimetic' resemblances in their cabinet specimens. Too often, moreover, the subject has been treated from the limited standpoint of a single order of insects, the Lepidoptera, in which group the phenomena were first recognized and described. Indeed, it is somewhat unfortunate that, historically, a conception which embraces so wide a field of animal life should in its early days have been confined almost exclusively to this one group.

Many years ago Poulton wrote: 'I cannot but think that this limitation of the survey to one small part of the field over which the resemblances commonly occur is, in large part, the cause of the rejection of Natural Selection and the substitution of alternate suggestions. There is something attractive and plausible in the idea that the strong mutual resemblances within a group of butterflies of different genera and Sub-Families, inhabiting a single locality, are due to the direct action of peculiar local physical or chemical influences; but the suggestion loses all its attractiveness when it is applied to the resemblances between a spider and an ant, or a moth and a wasp' (500).

Every one conversant with the facts available to-day realizes that the phenomena of mimicry are in no sense isolated or peculiar. On the contrary, they fall into place with, and form part of, that vast body of facts which embraces the whole sphere of adaptive appearance—whether exhibited in the guise of concealing, revealing, or deceiving coloration; whether serving the purpose of protection or predation, of warning or bluff, of ambush or allurement. To approach mimicry, as has been done recently by Professor Shull in his book *Evolution*, without taking into consideration the extent of the ground it covers, and its relation to the whole field of adaptive coloration, is to reveal an unfamiliarity with, or a contempt for, the subject quite foreign to the scientific spirit.

Sir Edward Poulton has consistently laid stress upon the fundamental unity of mimetic and other types of adaptive resemblance. In 1898 he described the relation between protective resemblance and protective mimicry as follows: 'In the former an animal resembles some object which is of no interest to its enemy, and in so doing is concealed; in the latter an animal resembles an object which is well known and avoided by its enemy, and in so doing becomes conspicuous' (500).

The relationship is beautifully demonstrated in a somewhat unexpected quarter, and from a rather different aspect, by the adaptive coloration of birds' eggs, which display the two functional extremes of general cryptic resemblance and aggressive mimetic resemblance—as seen in the eggs of many wading birds and cuckoos, which simulate, respectively, their general surroundings, and the eggs of the foster-birds in whose nests they are deposited. In both cases the resemblance tends to prevent their destruction—in the former, by potential enemies; in the latter, by unwilling fosterers.

Moreover, whether we examine the phenomena of adaptive coloration in terms of the object resembled, or of the function of the resemblance, every gradation from cryptic to mimetic coloration may be traced in different groups of animals. Among fishes, for example, we find species resembling such natural objects as gravel, sea-weed, leaves, cœlenterates, and sea-snakes. Or seen from a different angle, the colour-schemes may serve for protection, as in *Bothus* or *Cottus*; for ambush, as in *Raja* or *Astroscopus*; for stealthy approach, as in *Lepidosteus* or *Monocirrhus*; for alluring, as in *Lophius* or *Lasiognathus*; for warning, as in *Trachinus vipera*; or for false warning, as in *Solea vulgaris*.

Or where shall we say that mimicry begins and concealment ends in such an illuminating functional series as spiders present? Many are cryptic and resemble bark, or lichen, or blades of grass. Others are cryptic and resemble parts of flowers in which they lurk; but here the colour-scheme takes on a new shade of meaning—that of ambush. Some, again, resemble a bird's dropping —a type of disguise which must certainly be regarded as alluring. Another simulates the head of a dead ant, and so becomes in a sense mimetic. Many more resemble the whole of a living ant, and attain to true protective or aggressive mimicry. While yet others are themselves aposematic and well protected and so become potential models for mimicry.

II. THE RELATION BETWEEN BATESIAN AND MÜLLERIAN MIMICRY

In Batesian mimicry a relatively scarce, palatable, and unprotected species resembles an abundant, relatively unpalatable or well-protected species, and so becomes disguised. In Müllerian mimicry, on the other hand, a number of different species, all possessing aposematic attributes and appearance, resemble one another, and so become more easily recognized. Thus mimetic resemblance leads in a Batesian group to the *deception of enemies*—a function well expressed by Poulton's term Pseudaposematic, or False Warning Colours : in a Müllerian group, on the contrary, it leads to the *education of enemies*—due to the simplification resulting from Synaposematic, or Common Warning Colours. In the first, the mimic lives on the unpalatable reputation of its model ; and *the enemy is tricked by a sham warning* : in the second, the mimic shares the repellent nature of its model ; and *the enemy is taught by a real warning.*

Two further differences may be noted. Firstly, since Batesian mimicry is based upon deception, its success depends upon its comparative rarity—in other words, the mimics must be much less numerous than their models. Otherwise the results of experimental tasting would encourage an enemy to renewed attacks, since a large proportion of individuals wearing a particular conspicuous livery would be found edible. Viewed in this light the mimic is parasitic upon the unwholesome reputation of its model—for its presence *weakens the deterrent result of experimental attack.* Müllerian resemblances involve no such limitations on the proportion between models and mimics. For their success depends upon the increased power of a combined warning. All members of the association are aposematic, and the adoption of a common advertisement simplifies recognition, and *confirms the disagreeable results of experimental attack.*

The second point relates to the accuracy of the resemblance, which, as pointed out by Fisher (173), must in Batesian Mimicry be as detailed as possible, since its essential factor is disguise : the mimic must be *mistaken* for the model. With Müllerian mimicry, on the other hand, it is only necessary to call attention to disagreeable attributes shared by a number of different species : for this purpose it is sufficient for the coloration of the mimicking species to *suggest* the model.

Although in theory two distinct principles are embodied in Pseudaposematic and Synaposematic resemblance, in nature the two classes of phenomena are neither sharply defined nor easily diagnosed. It must be remembered, as already shown, that the terms ' distasteful ' and ' edible ' and ' protected ' are only relative, and never absolute in their application to animals—varying for different predators, or for the same predator at different times. And as pointed out by Poulton, recent investigations have tended more and more to remove examples of mimetic resemblance from the Batesian to the Müllerian category ; and in this connexion Carpenter writes : ' Pseudaposematic species are to be sought among comparatively scarce members of non-mimetic groups, whilst the wholesale likeness of one group to another is more probably due to Synaposematism ' (87).

III. THE GEOGRAPHICAL RELATIONS BETWEEN MODEL AND MIMIC

Assuming mimetic resemblances—whether synaposematic or pseudaposematic—to be protective, they can only take effect when their bearers share, and are exposed to attack in, the same locality. And it is a significant fact that over and over again we find that forms related by mimicry do inhabit the same geographical areas, and the same particular environments.

This is a point capable of wide demonstration, but I will give a single example—afforded by certain Oriental butterflies of the genus *Prioneris* which appear to mimic others of the genus *Delias*. In his paper on ‘ The Geographical Factor in Mimicry ’ Dixey (149) has traced a remarkable correlation between the pairs which resemble each other and the areas in South and Eastern Asia and the neighbouring islands where they occur. He states that there is not a single known member of the genus *Prioneris* which does not resemble a species of *Delias*. And everywhere the pairs which simulate each other inhabit the same area. In the Himalayas, Burma and farther India, *P. clemanthe* and *P. thestylis* resemble, respectively, *D. agostina* and *D. belladonna*. In Southern India and Ceylon *P. sita* and *D. eucharis* form a pair, whose resemblance is described by Wallace as ‘ perfect ’. *P. hypsipyle* and *D. egialea* show virtually the same pattern in Sumatra, as do *P. autothisbe* and *D. crithoe* in Java ; while in Borneo *P. cornelia* copies *D. indistincta*.

IV. THE TOPOGRAPHICAL RELATIONS BETWEEN MODEL AND MIMIC

The extraordinary parallelism exhibited by species of the above genera serves to illustrate another point, namely, the general coincidence, not merely in geographical distribution, but in the precise habitat, and habits, of mimetic species. For instance, Dixey refers to an observation by Fruhstorfer, ‘ that the *Prioneris* always flies in company with the *Delias*, and rests just like the latter with closed wings on the red flowers of the Lantana ’.

Similarly in Brazil, and elsewhere, ant-like spiders and ant-like Membracid bugs are found in association with the ants they resemble. Similarly Syrphid flies, such as *Volucella* and *Criorrhina*, mimic the bumble-bees (*Bombus*) whose nests they enter ; Drone flies of the genus *Eristalis* are often seen feeding at flowers in company with workers of the Hive-bee whose appearance they closely counterfeit ; and the same appears to be true of mimetic species generally.

Mimicry among Vertebrates is not common, but where it occurs the same principle obtains. We have already referred to the Weaver Fish (*Trachinus vipera*), whose intensely black *dorsal* fin—the only part visible when the fish lies buried in the sand, and the only part of the fish which is conspicuously coloured —is erected and spread out like a flag on provocation, apparently as a warning to intruders. The Common Sole (*Solea vulgaris*) has on the right or upper *pectoral* fin a large deep-black patch. When in danger, the fish erects and spreads this fin vertically, so that it bears a general resemblance to the danger signal formed by the dorsal fin of the Weever: and it has been suggested by Masterman (399) that this is a case of mimicry.

This view is supported by the following classes of evidence: (1) The geographical distribution of *Solea vulgaris* and its closest allies and of *T. vipera* and *T. draco* are almost identical. (2) The Sole and the Weevers agree in their sand-loving and sand-hiding habits. (3) Both inhabit the same grounds, young Soles with *T. vipera* in sandy bays in-shore, adults with *T. draco* in deeper water. (4) When disturbed both types hold the black fin erect in the same menacing manner—that of the Sole being displayed at right angles to the normal position for Pleuronectidæ. (5) The pectoral fins of other Pleuronectidæ lack the black colour and are not held erect under similar circumstances.

V. MIMICS DEPART WIDELY FROM THEIR CONGENERS IN APPEARANCE

One inevitable result of mimetic relations between distantly connected organisms is the departure of the mimic from the usual appearance of the group to which it belongs; and the assumption of alien characters suggestive of a widely separated class or order. For example, various Asilid flies bear a strong resemblance to Xylocopid bees, and thus come to differ markedly from closely related but non-mimetic species—the latter being slender and naked bodied, with narrow transparent wings; the former being broad-bodied and hairy, with pigmented wings.

This principle of divergence from the typical appearance of the group, and assumption of alien characters which are essentially of a superficial or visible kind, is fundamental to our subject. The same assumption of foreign characters is seen in the transparent wings of moths mimicking Hymenoptera; and conversely, in the case of Hymenopterous insects mimicking Lycid beetles, when the normally colourless wings become coloured orange and black like the elytra of their model.

VI. MIMICS DEPART WIDELY FROM THEIR CONGENERS IN BEHAVIOUR

An important body of evidence bearing upon the meaning of mimetic resemblances is found in the fact that they are brought about not merely by modified appearance but by modified *activity*. Mimics do not merely look like their models. They behave like them. Although they cannot perceive and know the things they ought to do, nevertheless by their reactions and instincts they faithfully fulfil the same. This is one reason why cabinet specimens may reveal little similarity between mimetic species whose resemblance in the field is so close as completely to hoodwink experienced entomologists.

(1) **Time of Activity**—A point of some significance to be noted in this connexion concerns the time of day when mimetic species are on the wing. We have seen elsewhere that mimics may be profoundly modified in form, so as to present an appearance diverging markedly from their nearest congeners. This structural divergence from the typical form is frequently accompanied by an ecological divergence from typical habits. This is well seen, for instance, in

the case of Lepidoptera. The majority of moths are crepuscular or nocturnal. But it is well known that species like the Lunar Hornet (*Trochilium crabroniformis*) fly not at night, but by day, when their models are active. The same remarks apply in general to moths whose models are day-flying butterflies. This is the case, for example, with the moth *Epicopeia polydora*, of Assam, which closely resembles the unpalatable butterfly *Papilio bootes*; and with various Indian species of *Amesia* and *Callamesia* which mimic the characteristically distasteful blue butterflies belonging to the genus *Euplœa.*

(2) **Special Activity**—Similarity of behaviour as between model and mimic is a theme about which much has been written by students of natural history —more especially by those with experience of nature in the tropics. Not only do mimics move, run, and fly, or perform other activities in such a fashion as to increase their likeness to their models—and, as we have noted, in so doing they adopt a type of behaviour quite alien to that of their non-mimetic congeners. But often this very behaviour may represent the essential feature on which the resemblance depends—a resemblance which cannot consequently be appreciated or criticized except in reference to wild specimens observed in the field. For this reason alone the study of cabinet material, unless combined with field experience, is liable to produce a very inadequate picture of mimetic phenomena.

Seitz points out that the likeness of the Brazilian grasshopper *Scaphura nigra* to the fossorial wasp *Pepsis sapphirus* is not at all striking when the insect is at rest: ' but both of them have the very curious habit of running short distances with expanded wings '. A Syntomid moth belonging to the genus *Macrocneme* which mimics the same model was observed by Seitz to carry its legs hanging downward, after the fashion of the wasp, when on the wing.

A well-known type of mimetic activity is presented by the British Longicorn beetle *Clytus arietis*—a banded yellow and black insect, whose alert, jerky, wasp-like gait strongly suggests the appearance of its model. Similarly the Indian Longicorn *Glenea pulchella* has been described by Andrewes as mimicking an ichneumon fly. He writes: ' When the beetle is in the hand it seems impossible to take it for anything but what it is. When it settles it curves the ends of its antennæ out and keeps them quivering just like those of an ichneumon ' (in Poulton, 503*a*).

Similarly in the case of mimetic spiders, the ant-like gait has been described by many writers. As an example I will quote the following passage by Hingston. Referring to the Indian ant-mimic *Myrmarachne*, he states: ' Their habits are as ant-like as their structure. The worker ants, as a rule, move quietly through the foliage in a steady searching kind of way. When alarmed, however, they rush about excitedly. The mimic also simulates these motions exactly. Its ordinary progression is steady and even. But the moment it is disturbed its behaviour changes. Then it assumes the bustle of the workers, simulates their rapid jerky gait, perhaps darts for safety underneath a leaf or escapes by a sudden spring. . . . Another habit of *Camponotus* ants is to erect the abdomen at right angles to the body and walk about with it thrust into the air. And this same peculiar attitude is sometimes assumed by the mimicking spider' (260).

We may also refer here, in passing, to a striking habit of Hymenopterous mimics in relation to the chief mode of defence in their models, namely, stinging. Hingston has described several cases of insects, belonging to widely different orders, which when captured behave as though they were going to sting (266). Forest dragonflies (*Microstigma maculatum*) 'bend the abdomen underneath the body and scrape its tip against the finger in a determined and menacing manner'. A moth belonging to the genus *Phægoptera* behaved in a similar manner, curling the yellow tip of its abdomen downwards as if about to sting. A Staphylinid beetle, probably a species of *Xanthopygus*, was observed to erect the bright red pointed end of its abdomen, its tip 'being all the time protruded and withdrawn'.

Carpenter has described pretences of the same type in *Dirphya*, a Longicorn mimic of a Braconid wasp. He states that when handled, it 'curved the tip of its abdomen in such a way as to suggest it was about to sting, and actually protruded a flexible white viscus which it moved about just like a sting. The Hymenopteroid appearance of the beetle with its false sting was so very striking that, although reason told me it was a beetle, instinct was so strong that misgivings almost prevented me handling it, and I feel certain that the great majority of people would have dropped the beetle in a panic.' Thus do harmless species intimidate their enemies not merely by resembling well-armed species, but by seeming to possess and use the very method of defence which renders their models dangerous.

VII. THE RESEMBLANCES BETWEEN MODEL AND MIMIC ARE NOT DUE TO SIMILARITIES OF LIFE-HISTORY

The suggestion has been made by critics of mimicry that the resemblances in question may be due to some common environmental factor, such as food, temperature, or humidity, which is supposed to affect both model and mimic alike. At first sight this view seems to have its attractions. For it is true that, as already mentioned, models and mimics do in general share the same geographical and ecological environment. Moreover, sometimes the resemblances occur within more or less nearly related genera or families.

But the so-called 'Theory of External Causes' entirely fails to explain the most fundamental aspects of mimetic phenomena. It takes no account of the essential kinship between mimicry and other types of adaptive coloration; nor of the superficial nature of the visual characters exhibited by mimics; nor of their independence of affinity, anatomy, and life-history. These points, except the last, are discussed in other parts of the present section, and it will be pertinent to add here a few words on the light which life-histories have to shed upon our subject.

The fact that similar results have been produced *in spite of* rather than *because of* environmental conditions may be illustrated by the following examples of Batesian mimicry. Several cases are known of Diptera mimicking Hymenoptera with which they are closely associated in nature. Various Syrphid flies of the genus *Volucella* closely resemble the bees, bumble-bees, or wasps in whose nests they lay their eggs. The adult insects fly in the same surroundings, and their larvæ live in the same nests. At first sight, therefore, such resemblances might be considered as due to common environmental factors. However, closer investigation of the insects' habits and interrelations render such an explanation most improbable; for the larval feeding habits introduce a different factor in each case: the Dipterous maggots live as scavengers on waste substances and nest-debris; but the Hymenopterous grubs upon a vegetable diet of honey and pollen. Carpenter brings forward a similar relationship between certain Asilid flies and Xylocopid bees. Here, again, the adult insects fly in the same locality and the larvæ occur together in the same tree-trunk: but in this case the food 'for the bee grub is honey and pollen, for the fly larva the bee grub itself' (87).

A similar argument applies to the great Müllerian assemblage of insects having as adults Lycoid coloration and habits. Lycid beetles, with their typical orange and black coloration, are resembled both in pattern and colour by a wide range of insects belonging to every order whose body-form yields a suitable background for a Lycoid appearance—Coleoptera, Hymenoptera, Diptera, and Lepidoptera. But the various members of this assemblage exhibit vast differences as larvæ both in their food and habitat. They may be vegetarians, feeding on dead wood, or on leaves or flowers; or carnivores, living as active predators or as internal parasites. They may live fully exposed in the open, or buried underground; within dead wood, or within the bodies of their hosts. Yet in spite of these fundamental ecological differences, the adult insects agree in the one singular characteristic of having a Lycoid appearance.

If mimetic resemblances were due to some general environmental factor affecting alike model and mimic, is it conceivable that this factor should operate between widely distinct organisms, while not affecting closely related species from the same environment? Moreover, as Nicholson points out: 'Actually we find that in many cases closely related mimics resemble a series of unrelated models which differ from one another greatly in appearance, and which have only one factor in common, that they are all found in the same environment.' We have also to bear in mind the fact that mimetic species do not resemble any kind of model indiscriminately. On the contrary, the models are limited to a few well-defined groups—they are typically aposematic in appearance and attributes.

VIII. MIMETIC RESEMBLANCES ARE INDEPENDENT OF AFFINITY

From what has already been said, it will, of course, be appreciated that mimetic resemblances cannot satisfactorily be explained in terms of affinity between model and mimic. Such an argument, which may seem plausible when applied to mimicry within the limited field of a sub-order, fails to have any meaning as applied to mimetic phenomena as a whole.

It is axiomatic that the similar visual effects under consideration are produced often enough in remotely related animals. Mimics of Hymenoptera are drawn not only from several different orders of insects, but from a totally distinct class of arthropods. Or among vertebrates, we find certain species of Serpent-Eels, of the family Ophichthyidæ, exhibiting a conspicuous banded colour-scheme similar to that worn by various venomous snakes of the family Hydrophidæ ; although further observations on the habits and ecological relationship of these animals are needed, it seems reasonable to suppose that we have here a genuine case of Batesian mimicry, as between a fish and a reptile. Even more remote is the relationship between a Sphingid caterpillar and the snake which its threatening attitude calls to mind.

The significant point is that such animals have become superficially or symbolically alike in appearance, in spite of, rather than because of, their position in the scale of creation. And it may be emphasized once again that mimetic phenomena run closely parallel with special cryptic resemblances. When we see one moth bearing a wonderful similarity to a scale of bark, another to the dropping of a bird, and another to an aposematic butterfly ; when in each case the likeness is achieved by a combined modification of pigment and pattern, attitude and behaviour ; is it to be suggested that the first two are the result of adaptation, the last of affinity ? Or are we to regard them all as expressions of a fundamental principle, embracing not only the facts of adaptive coloration but of all adaptive features whatsoever—which, in whatever guise or group they may be regarded, seem always to reveal the same supreme indifference to limitations imposed by ancestry ?

IX. MIMETIC RESEMBLANCES ARE INDEPENDENT OF ANATOMY

The almost complete independence of structure revealed in the technique of mimetic resemblance presents the same problem from a somewhat different aspect. This point is, of course, capable of wide demonstration, but I shall confine myself here to a few examples. The first relates to the superficial similarity borne by certain butterflies, described and figured by Dixey (149), in New Guinea. It will be remembered that when a butterfly alights with its wings closed over its back, the fore-pair normally drop back between the hind-pair, so that only the apical and anterior parts are then exposed. Now when in this attitude, the species in question—a Nymphaline *Mynes doryca*, and a Pierine *Huphina abnormis*—present virtually the same colour-scheme, being black, with a red streak and a red spot both situated near the margins where the fore-wings meet the hind. In *M. doryca* the streak occurs on the anterior margin of the hind-wing and the spot at the base of the exposed part of the fore-wing. In *H. abnormis* the same general result is obtained in precisely the opposite manner, for here the streak runs along the edge of the fore-wing, while the spot is near the border of the hind.

The second example is one brought forward by Poulton (518). In this case the similarity is between a Uraniid moth, *Alcidis agathyrsus*, and its mimic, the butterfly *Papilio laglaizei*. These insects, which also inhabit New Guinea, fly together in the same surroundings, and wear a strikingly similar pattern both upon the upper and under wing surfaces. On the model, however, the underside of the abdomen bears a vivid orange patch which in the resting attitude becomes a conspicuous warning mark, 'when the insects hang with drooping wings and the underside of the body is uppermost'. In the mimic, this orange patch is absent from the abdomen; but it occurs on the parts of the hind-wings which cover the abdomen, and which thus represent a precisely similar warning sign in an entirely different manner.

The same principle is beautifully demonstrated by a Bornean Longicorn, *Glenea iresine*, whose model is a blue Hymenopteron named *Hylotoma pruisona*. Shelford (569) has described how the resemblance is brought about. The elytra of the beetle exhibit three zones of colour, their middle third being brown, shading anteriorly into blue and posteriorly into greyish-white. The appearance of *Hylotoma* with its wings laid back is thus produced—the posterior part of its thorax being represented by the blue anterior third of the beetle's elytra; the abdomen with the superimposed wings by the brown middle zone; the tips of the wings, which in the model project beyond the end of the abdomen, by the posterior greyish-white portion.

Before leaving this aspect of the subject, it will be pertinent to point out once again that in the phenomena of procryptic coloration we have innumerable examples of the same principle—particular appearances being produced in spite of (one might almost say in defiance of) fundamental differences in structure. Everywhere we see the same story: the superficial nature of the appearance; and the independent manner of its production. We are compelled by such facts to believe that these characters have evolved in relation to the visual perceptions of other animals; that their end is an appeal to the eye. Appearance—whether cryptic, sematic, or mimetic—is something to which nature attaches importance; but the methods by which the result is achieved is unimportant—as Fisher says: 'Every property of the behaviour of matter, however odd and extraneous it may seem, seems to have been pounced upon as soon as it happened to produce a desirable effect' (173).

X. SIMILAR APPEARANCES MAY BE PRODUCED BY THE MOST WIDELY DIFFERENT METHODS

Even within the limits of a single order, mimetic resemblances may be produced by the most diverse methods. Poulton has illuminated this point brilliantly in reference to a large convergent group of Tropical American Lepidoptera, whose members—belonging to several sub-families and to many genera—possess a common characteristic feature in the transparency of their wings (500). But the similarity is purely superficial. And it is due, as Poulton has shown, to a variety of different causes.

In the Ithomiine genera *Methona* and *Thyridia*, the scales—which are normally of two alternating kinds, narrow and broad respectively—have been greatly *modified in shape*, being reduced to fine hairs, simple in the one type and Y-shaped in the other. In the Danaine genus *Ituna*, the scales retain their size and dark pigment, but are *reduced in numbers*. In the Pierine genus *Dismorphia* the scales retain their normal shape but are *reduced in size*.

Moths belonging to the group have attained transparency by two methods —which differ both from each other and from those employed by the butterflies. In the Castniid *Castnia* the scales are not reduced in size, but are *modified in arrangement*, being set up on edge, so that the light passes freely between them. In the Pericopine genus *Anthomyza* the scales are normal both in size and arrangement, but are *themselves transparent*.

Nor does this complete the list of devices employed. Various other moths belonging to a different mimicry association, bear a superficial similarity to stinging Hymenoptera such as honey-bees, bumble-bees, and wasps. For such mimics, as for those considered above, transparent wings are a primary requisite. This quality is achieved in moths belonging to the genera *Hemaris* (Sphingidæ) and *Trochilium* (Sesiidæ) by the *loose attachment* of the scales, which soon fall off and leave the wing hyaline and naked, except along the veins and margins.

It appears, therefore, that within the single order of Lepidoptera the special appearance of transparency has been produced by modifications along at least six different lines. Wing scales are the carriers of colour throughout the whole group, and where the absence of such colour is necessary its elimination has been achieved by structural or optical devices affecting these scales—which, as we have seen, may be modified in shape or arrangement, reduced in number or size, or rendered transparent or else easily shed.

Again, similar colours are often produced in quite distinct ways. We have already alluded to this point in the occurrence of green in general cryptic resemblance. Now in the sphere of mimicry, the same principle operates. It is essentially the make-up, and not its method, that matters. For example, in the large genus of Swallow-tail Butterflies (*Papilio*)—one group of which comprises distasteful species which act as models for many species, including those belonging to two other groups of *Papilio*—Ford (181*b*) finds that white and yellow colours are produced in two entirely different ways. The first group of white and yellow pigments, known as ‘ pterins ’, are synthesized by the insects themselves, and are chemically allied to uric acid. The second group, known as ‘ anthoxanthins ’, are derived from the larval food-plant.

Again, the red pigment in the form *romulus* of *Papilio polytes* is chemically distinct from that present in its model *P. hector* (181*b*). Facts such as these, like many others discussed in the present section, render untenable Punnett's attempt to explain the resemblances between model and mimic by assuming that they are due to parallel mutations (531).

Finally, we may note in passing that while mimetic effects in general (as indeed those whose function is cryptic) are typically arrived at by the most diverse means, even in related animals ; it is also true, conversely, that similar superficial results may be produced by similar means in distantly related groups. A striking example of this principle, described below under the heading ‘ Visual

Constriction of the Body ', is presented by the common use of a special optical device by insects belonging to several orders. Such facts can only mean one thing: that these visible effects are directed against the eye of a precipitant enemy.

XI. MIMETIC RESEMBLANCES ONLY AFFECT VISIBLE CHARACTERS

The natural art of mimicry and the theatrical art of make-up have in common one fundamental principle. When a white actor plays a negro's part he does not blacken his whole body. He blackens only the parts visible to his audience. For a similar reason a lazy boy may wash his face, while neglecting his feet. Now it is a highly significant fact that mimetic resemblances in nature involve *only those structures* (and habits) *which can be seen.* The effects are essentially external—such as can appeal directly to the eye. They do not extend beyond, to parts of the body which are hidden and therefore unable to contribute to a deceptive appearance. A single example must suffice to illustrate this point.

Abispa ephippium, a common Eumenid wasp of Australia, is mimicked by several insects of different orders, including flies, moths, and beetles. Among these mimics are two Cerambycid beetles, *Tragocerus formosus* and *Hesthesis ferrugineus.* Both display dorsally the model's coloration of orange boldly banded with black. But each does so in an entirely different fashion. In *T. formosus*, the wasp-like colour-scheme has been developed on the elytra, which are long and cover the abdomen. In *H. ferrugineus*, whose elytra are reduced to scale-like rudiments, the mimetic pattern is reproduced upon the uncovered abdomen, which is of course fully exposed in flight.

Now in *T. formosus* the wing-covers are not only long enough to cover the abdomen in the resting insect, but they are fused together, so that they still remain firmly fixed over the abdomen during flight—free movement of the wings being permitted by an arched excavation in the side of each elytron just above their point of origin. And in this species the upper surface of the abdomen (in striking contrast to that of *H. ferrugineus*) has remained un-wasp-like, being pale in colour and patternless.

A gruesome parallel from man is the making of dress-clothes for corpses, of which only the ventral half is complete. Better-known examples are the backless waistcoats worn with evening dress, and the waiters' dickey, which only resembles a shirt in the limited front area exposed to view.

XII. MIMETIC RESEMBLANCES INVOLVE MANY INDEPENDENT MODIFICATIONS

The general truth just mentioned—that mimetic resemblances do not go beyond the point of usefulness—appears the more suggestive when seen in the light of a complementary fact, namely, that the visible results produced are due not to one, but to a combination of several modifications, involving those of form, colour, pattern, posture, and movement, while the change in any one of these may be itself of a highly complex nature. As Fisher (173) says: ' Mimetic resemblances bear the hallmark of *adaptation* in the multiplicity of the simultaneous modifications to which they are due.'

Their very complexity discredits chance, or a direct environmental effect as the true explanation. This line of argument has been stressed by Nicholson (440) when he points out, for example, that very long antennæ are common in brachycerous flies which mimic wasps—the elongation being effected in different ways, even with closely related species—but that ' antennæ which even approach the length of those common amongst dipterous wasp-mimics are excessively rare amongst non-mimetic flies '. Yet in the mimics concerned, we find elongation of antennæ combined with a number of other wasp-like characters involving many modifications both of colour and contour, of attitude and activity.

XIII. MODIFICATION OF CONTOUR IN MIMICS OF HYMENOPTERA

All over the world Hymenopterous insects of different kinds have become the centre of mimetic associations whose more defenceless members include creatures so widely separated as beetles, grasshoppers, mantids, flies, moths, bugs, and spiders.

In the course of their evolutionary history, all such mimics have had to meet a number of demands involving striking divergence from their congeners in matters of appearance and behaviour. One of the main problems (which we shall here single out for study) has been the somewhat difficult question of reducing the ' figure '. For while their ancestors are robust or stout-bodied, the Hymenopterous fashion which they must follow dictates a slender, constricted waist-line as one of its chief attributes, whose achievement must have made almost unbelievable demands upon their powers of slimming. To put the matter in more zoological language, the resemblance necessitates profound structural or optical modification.

The ingenious and often elaborate devices used in the attainment of a wasp-like or ant-like contour are of peculiar interest, because they beautifully illustrate a number of principles which, as already indicated, are fundamental: (1) The same general effect has been achieved by a remarkable range and variety in technique and artistry. (2) It is in general entirely superficial, and in contradiction of underlying details of structure. (3) Similar visual results have been developed independently by widely dissimilar groups of animals, and among species having utterly different modes of life-history; and sometimes, moreover, they are produced by precisely analogous methods in widely separated orders. (4) The mimics depart widely from their congeners in both appearance and habits, which often closely simulate those of their models.

(1) **Actual Constriction of the Body**—Speaking in a superficial way, the shape of a spider differs mainly from that of an ant in that the former has only one constriction of the body (between the cephalothorax and abdomen), while the latter has two (between head and thorax, and between thorax and abdomen). Thus the mimetic spider starts with an initial disadvantage—it is a waist short. Now among spiders which resemble and live with ants, certain species have developed an additional constriction: but this modification may occur in one of two distinct regions of the body. In *Myrmarachne*, a mimic of the Indian black

ant *Camponotus compressus*, the cephalothorax is divided into two parts by a narrow waist (260). In *Synemosyna smithi*, a mimic of the Cuban *Pseudomyrma elongata*, it is the abdomen which bears a slight constriction (435). Dr. G. Salt has drawn my attention to the interesting fact that a bug, *Pamphantus mimeticus*, which belongs to the same mimicry association in Cuba, has achieved the ant-like appearance in two very different ways—as a nymph, and as an adult. The wingless nymph has a thin waist. But in the adult insect, which is, of course, handicapped as an ant-mimic by its broad hemielytra, the difficulty has been overcome by a purely pictorial effect, pale markings on the wings simulating a narrowing of the body in a corresponding position.

(2) **Concealment of the Body behind a Mask**—Yet more remarkable is the often-cited case of *Heteronotus trinodosus*, a Central American Membracid bug, in which the pronotum is immensely enlarged, being similar in form to the body of an ant, and extending backwards so as completely to cover, like a shield, the otherwise unaltered body. Nor is this the end of the story. Evidence of an instinct which seems to serve the same end has been obtained by Bristowe in Brazil (61) and by Hingston in Guiana (265). Both these observers describe a spider, itself un-ant-like, which is in the habit of running about in a jerky ant-like manner, and carrying over its back the empty and dried skeleton of a real ant considerably larger than itself, held in such a way as completely to hide the bearer from view. The appearance produced, as Hingston states, is that of an ant carrying a dead comrade.

This curious habit forms another link in the chain of phenomena which culminate in the case described by Poulton (497) of a Membracid bug, also from Guiana, whose resemblance to a Cooshie Ant (*Œcodoma cephalotis*) carrying its jagged segment of a leaf over its back is remarkable. ‘The leaf is represented by the thin flattened body of the insect, which in its dorsal part is so compressed laterally that it is no thicker than a leaf and terminates in a sharp jagged edge’, suggesting the roughly gnawed edge of a leaf fragment, beneath which the brown head and legs of the bug are just visible, as they would be in the case of the ant seen with its burden.

(3) **Visual Constriction of the Body**—Very different, and of great interest, are the methods by which the same end has been achieved in the case of certain stoutly built grasshoppers, beetles and other insects. Now these ant mimics have produced the necessary slender waist by optical illusion rather than by structural modification; and their appearance presents an illuminating lesson in applied camouflage.

In 1883 Brunner von Wattenwyl described from the Sudan a Tettigoniid grasshopper, *Myrmecophana fallax*, which has the narrow waist and swollen abdomen of an ant vigorously superimposed in black pigment upon its own stout and un-ant-like form—the remainder of its body being by contrast light in colour and therefore liable to escape notice when seen against a light background (506). Marshall found a Tettigoniid of the same genus in company with ants on a small bushy vetch, in Rhodesia (395). This insect had the superfluous parts of the body coloured green—and thus obliterated against the leaves. Here, then, we have nicely illustrated a special application of the principle of differential blending.

Shelford observed a similar disguise in certain Longicorn beetles of the genera *Scytasis* and *Oberea*, from Borneo, coloured precisely like their models, the red and black Braconids. They were marked boldly with a patch of white pubescence on the *sides* of the first and second abdominal segments, so as to give the impression of a wasp-like waist when seen in profile (569). Shelford draws attention to the further interesting fact that the thin waist of the Braconid model is hidden, when seen from above, by the laid-back wings. Consequently this obviates the necessity for dorsal white patches on the mimic—such as are present in the African *Myrmecophana fallax*, whose model is an ant with a waist plainly visible whether in a dorsal or a profile view (see Fig. 83).

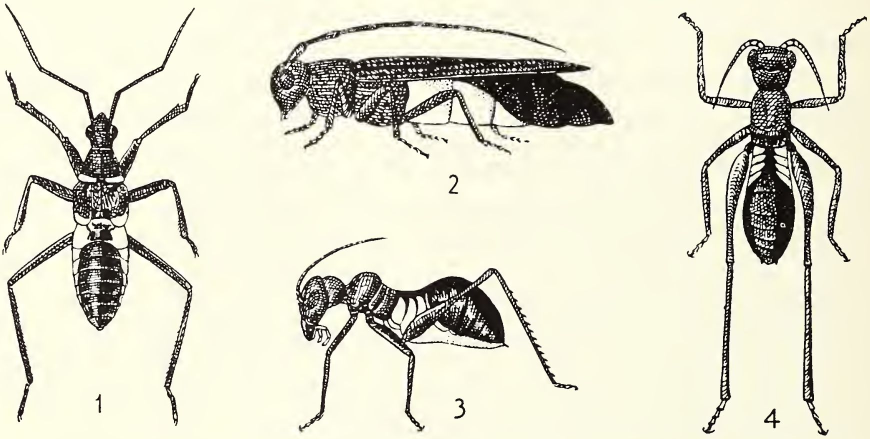

FIG. 83.—Mimicry of ants and wasps by stout-bodied insects, achieved by camouflage of the waist-line: 1 *Nabis lativentris*; 2 *Oberea brevicollis* (*after* SHELFORD); 3 and 4 *Myrmecophana fallax* (*after* BRUNNER VON WATTENWYL)

Poulton mentions the further instance of an Asilid fly, *Promachus iopterus*, from Pará, which likewise wears white patches on the sides of the basal abdominal segments, thus leaving the silhouette of a slender black stalk like that of its Hymenopterous model (506). Finally, the British Reduviid bug *Nabis lativentris* bears in its immature stages an ant-like appearance produced in precisely the same manner.

Here, then, we have a highly remarkable and specialized device—the production of a waspish waist by a special process of optical slimming—which has been evolved and utilized independently in insects belong to four distinct orders, namely, Orthoptera, Coleoptera, Diptera, and Hemiptera. These modifications present an extraordinary example of adaptive convergence in unrelated insects—modifications which are hardly to be accounted for except in terms of deceptive appearance.

XIV. MIMETIC MODIFICATIONS OF THE ANTENNÆ

The view that mimetic resemblances of various kinds have developed essentially in relation to, and are directed towards, the powers of visual perception in other animals—or, in other words, that their function is the deception of enemies—may be beautifully illustrated by tracing the part played by a particular organ in bringing about the desired appearance. For example, among various groups of insects, the antennæ form a fairly conspicuous and characteristic feature, and it is most instructive to notice how these appendages may be modified for the perfection of disguises.

In cases of special protective resemblance, much may depend upon the coloration and carriage of the antennæ. I have already referred to the case of three grasshoppers belonging to the family Acridiidæ—namely, *Acrida turrita*, *Omura congrua*, and *Eremocharis insignis*—which resemble respectively a grass-stem, a stick, and a stone. In each the form and attitude of these organs are adapted to the particular resemblance, being blade-like in the first, twig-like in the second, and concealed in the third, whose disguise they might otherwise betray. It is instructive to compare with the last the adaptive attitude employed habitually by many bark-like moths, such as the Scarce Tissue (*Eucosmia certata*) and the Willow Beauty (*Boarmia gemmaria*), which in the resting attitude tuck the antennæ back out of sight beneath the outstretched fore-wings.

(1) **Actual or Apparent Shortening of the Antennæ**—More remarkable, however, are the antennal arrangements in cases of true mimicry, where modifications of structure and colour, of attitude and movement, all combine to produce the desired result.

A number of insects with long antennæ have models whose antennæ are short, and it is instructive to notice the ways in which the reduction, or the appearance of reduction, in length has been achieved. The Brazilian long-horned grasshopper *Scaphura nigra*, which mimics the fossorial wasp *Pepsis sapphirus*, has the basal third of the antennæ thickened, strongly ringed, and banded distally with yellow, while the remaining two-thirds suddenly thin away to the usual hair-like fineness typical of Tettigoniid antennæ, so that at a little distance the antennæ appear to be short and yellow-tipped like those of the wasp—the basal segments alone doing duty for the entire organ of the model (507).

A similar optical device is reproduced in a different order of insects by certain Longicorn beetles such as *Doliops curculionoides* and *D. geometrica*, which resemble weevils whose antennæ are short and end in a knob. Here the resemblance is effected by a dilation of the third joint, which represents the terminal knob, while the remaining distal joints are concealed by their excessive fineness. Another Longicorn, *Estigmenida variabilis*, which closely resembles the Hispid beetle *Estigmena chinensis*, has the distal third of its antenna concealed in the same manner, but the apparent terminal knob is suggested in this case not by a special dilation but by hairs at the end of the stout basal part (500). Yet another device is seen in certain Longicorn mimics of Lycid beetles which have their typically long antennæ actually, rather than apparently, reduced in length, so as to approximate to those of their model, though the numerous joints are still present (87).

(2) **The Result Obtained by Lengthening Short Antennæ**—Certain mimics of Hymenoptera, namely, flies and spiders, have to contend with a difficulty precisely the opposite; for their antennæ, instead of being too long, are either too short (in the former) or altogether absent (in the latter).

In many Dipterous wasp-mimics the antennæ are greatly lengthened and thus rendered conspicuous and wasp-like. Typically, the antennæ of flies belonging to the sub-order Brachycera are very short and only visible on close inspection. But, as Nicholson has pointed out, although in this group long antennæ are quite exceptional, yet they are usually present in the mimetic species. He has shown, moreover, that the elongation has been produced by a number of entirely different structural modifications in different mimics, sometimes even when these are closely related. For instance, in the Syrphid *Cerioides breviscapa* all three antennal segments are elongated; in a related species, *C. variabilis*, the antennæ are borne on the end of an elongated frontal prominence, which increases their apparent length; in the Stratiomyid *Elissoma lauta* elongation is confined to the terminal segment; in the Bombylid *Systropus* sp. elongation occurs mainly in the basal segment (440).

(3) **Substitution of Antennæ by other Organs**—An alternative arrangement, serving the same end, has been evolved by mimics which are known to use the first pair of legs as substitutes for the deficient or missing members. Various mimetic Diptera, whose own antennæ are inconspicuous, have the habit of running on the surface of leaves and waving in the air the anterior pair of legs, which thus roughly simulate the antennæ of their model (87).

A beautiful example of this remarkable arrangement is described by Mrs. Brindley from British Guiana, where she found a fly belonging to the genus *Calobata*, together with two Coreid bugs and a cockroach, mimicking 'large Ichneumonids with conspicuous white-tipped antennæ which vibrate rapidly as the insects run over the foliage in search of prey'. The bug and cockroach have white-tipped antennæ. But in the fly their place in the make-up is taken by the anterior feet, which are white, and 'in the resting position gently waved to and fro' (232).

This habit is very marked in different ant-like spiders. For example, *Myrmecotypus cubanus* is described by Myers and Salt (435) as having a gait indistinguishable from that of its model, the first pair of legs being engaged 'in palpating the substratum in a manner at once suggestive of the movements of an ant's antennæ'. In such cases, so close is the similarity *in life* between mimic and model that the expert eye of the entomologist is liable to be deceived even after close examination of his catch.

Referring to a species of *Myrmarachne* which he observed at Fyzabad in central India, as a mimic of the large black ant *Camponotus compressus*, Hingston states: 'The most interesting feature in the resemblance is the way the spider simulates the antennæ. In ants the antennæ are conspicuous organs, thrust out in front and kept continually in motion. The mimic employs its front pair of legs in order to simulate the antennæ of its model. It does not use them for ordinary progression. They are thrust forward, bent into a right angle—in fact, made to occupy a position similar to that of the ant's antennæ. Moreover, their tips are kept continually in motion, a striking feature, for it is not just an aimless movement, but rather that methodical swaying motion so characteristic of *Camponotus* ants. I defy any one, when watching this mimic and particularly observing these false antennæ, not to be amazed at this wonderful resemblance between the mimicking spider and the ant' (260).

Finally, we may refer in this place once again to the singular deceptive device found in the so-called 'double-ended' butterflies belonging to such genera as *Thecla* and *Ialmenus*, in which the anal angle of the hind-wing carries an eye-spot and 'tail'. Not only does this arrangement produce the illusion of a head at the opposite end of the body to the true head, but the trick is improved upon by movements of the wings in the resting insect, which causes the slender tail-like processes to cross one another and tremble after the fashion of the real antennæ.

XV. THE EFFECTIVENESS OF MIMICRY

The literature of the subject abounds with instances of naturalists being deceived—even after years of field experience—by mimetic resemblances. Whether the natural enemies of the mimics are as easily taken in is a matter requiring further investigation and one offering a very promising field for research. There is, however, considerable evidence pointing to the conclusion that different animals are in fact likewise deceived (79, 134, 496, 609).

(1) **The Value of Mimicry in Nature**—The following experiment by Swynnerton throws light upon the protective value of mimicry and upon a predator's reactions in relation to mimetic coloration. At Chirinda, in Rhodesia, there are four species of birds whose similar coloration (which is black above and beneath) renders identification in the field somewhat difficult—namely, two Drongos (*Dicrurus afer* and *D. ludwigi*), a Flycatcher (*Bradyornis ater*), and a Cuckoo-Shrike (*Campephaga nigra*). According to Swynnerton's observations there is reason to regard the last two species as mimics of the first two, whose flesh is unpalatable. A Tit (*Parus niger*) from the same region differs from these birds in having some conspicuous white markings above, but like the others it is black beneath. Swynnerton offered his cat, which had developed an intense dislike for Drongos, a Drongo, Black Flycatcher, male Cuckoo-Shrike, and Tit, in that order, and *belly upwards*. They were all ignored. The birds were then turned over, in the same order. The cat still refused the first three. But when Swynnerton turned over the Tit, thus displaying the white dorsal markings, the animal at once came forward and tested it (608).

The mimicry problem has recently been approached experimentally by Darlington (134), from whose work the following account is taken. The models in the present case are Lycid beetles belonging to the genus *Thonalmus*. Two of the three Cuban species known to occur at Soledad, namely, *T. suavis* and

T. aulicus, are extremely conspicuous insects, almost identical in appearance. The head, thorax, and basal part of the elytra are red or orange in colour, the rest of the elytra being blue. Both the ventral surface of the abdomen, and its dorsal surface, which is exposed during flight, are bright red or orange. The beetles occur in bushy and overgrown places near the borders of woods, or in secondary growth. In spring and summer they are abundant and among the most conspicuous insects of their habitat; they are semi-gregarious; they are diurnal, generally resting or crawling exposed on the outer twigs of shrubs, and often fly in sunlight.

From a study of their conditions of life, Darlington concluded that their most formidable potential enemies were about a dozen species of birds; two Iguanid lizards of the genus *Anolis*; a few dragonflies, Asilid flies, and Reduviid bugs; and spiders. Among these the lizards were probably the most important insectivorous animals in the habitat. For his experiments Darlington selected *Anolis sagrei*, a very common species whose habitat coincides with that of *Thonalmus*. These lizards are diurnal: and they feed upon living insects which they hunt by sight.

In captivity the lizards consistently refused to eat *Thonalmus* over periods of several days, even when left without other food; while they freely took other cryptically coloured beetles as large as or even larger than the Lycids. I quote his own description of a further test of the beetles' flavour: 'To clinch the matter, on 21 August, an experiment was tried with a male lizard which had become somewhat accustomed to handling. First the lizard was held down by hand and a small, green, Geometrid-like larva was placed in its mouth, but not pushed down its throat. The lizard was then carefully released. It waited motionless for a few seconds and then swallowed the larva. The lizard was recaptured and a *Thonalmus* placed in its mouth. The beetle was shaken out at once by an energetic side-to-side motion of the lizard's head. Afterwards the lizard ran its blunt tongue over its lips as if cleansing them. About five minutes later another small larva was given and swallowed; then two more Lycids were emphatically rejected.'

Living in the same environment with *Thonalmus* are a number of beetles belonging to several families (Cantharidæ, Elateridæ, Œdemeridæ and Cerambycidæ) which in a superficial way resemble the Lycids more or less closely. In the Œdemerid *Copidita thonalmus*, and the Cerambycids *Calocosmus venustus*, *Trichrous divisus* and *T. pilipennis*, the general colour-scheme is almost identical, in *Calocosmus* and *Trichrous* even to the red under and upper surfaces of the abdomen.

Under experimental conditions various beetles (which we may term respectively models, mimics, and non-mimics) were offered to the lizards. In the first test, which covered a period of six days, not one of the four models (*Thonalmus aulicus*) and four mimics (two *Heterops dimidiata* and two *Trichrous pilipennis*) was eaten, while every one of ten non-mimetic species (five *Elaphidion guttiventre*, one *E. nanum*, one *Leptostylus incrassatus*, one *Eupogonius pilosulus*, one *Ataxia* *spinicauda* and one *Cyllene crinicornis*) was accepted. In the second experiment, occupying about a week, in which three mimetic and five non-mimetic species (but no models) were available to the lizards, the mimics were again rejected and four out of five non-mimics eaten.

(2) **Applied Aspects of Mimicry**—It is interesting to find that different primitive peoples have from antiquity adopted mimetic tactics for purposes of the chase, and strong confirmation of the theory is found in the successful application of mimetic principles for hunting, not to mention their more recent uses in the arts of bird photography and of war.

Disguises of one kind or another have been used to facilitate approach to their quarry by hunting tribes in all parts of the world. The African Bushmen, when taking the field against Elephant, Hippopotamus, or Rhinoceros, used to appear with the head and hide of a Hartebeest over their shoulders. What is especially interesting from our point of view is the statement by Stow that whilst advancing towards their quarry through the long grass, they would carefully mimic all the actions of the animal they wished to represent (592). Other disguises included the head and wings of a Vulture or the striped hide of the Zebra.

Sometimes they appeared in the guise of an Ostrich—a method employed when hunting Ostrich or Quagga. In this case a long pliant stick was used to keep the head erect, and this also enabled them to give it its natural movement as they walked. Stow writes: 'Most of them were very expert in imitating the actions of the living bird. When they sighted a herd of quaggas which they wished to attack, they did not move directly towards them, but leisurely made a circuit about them, gradually approaching nearer and nearer. Whilst doing so the mock bird would appear to feed and pick at the various bushes as it went along, and rub its head ever and anon upon its feathers, now standing to gaze, now moving stealthily towards the game, until at length the apparently friendly Ostrich appeared, as it was wont in its wild state, to be feeding among them.

'Singling out his victim, the hunter let fly his fatal shaft, and immediately continued feeding; the wounded animal sprang forward for a short distance, the others made a few startled paces, but seeing nothing to alarm them and only the apparently friendly ostrich quietly feeding, they also resumed tranquillity, thus enabling the dexterous huntsman to mark a second, if he felt so inclined' (592).

In these tactics we have something very reminiscent of the ant-like spiders which move about on the outside of the colony, with jerky ant-like gait, carrying the front pair of legs high off the ground to simulate the antennæ of their prey. It is also particularly interesting to find precisely the same device as that described above practised by aboriginal tribes in South East Australia. In this case it is the emptied skin of the Emu which provides the disguise used when hunting this bird, and here again the head is held erect with a stick. Basedow (22) describes how very cleverly the Emu's strut is imitated, the men carefully approaching with their spears firmly held between two toes and thus drawn along with them through the long grass. Availing themselves of the fact that Bison when in the herd together have little dread of the wolf, Indians of North America used to disguise themselves beneath a wolf-skin when hunting.

The importance of acting the part in a realistic manner is well illustrated by the methods employed by Esquimaux seal-hunters. A detailed account of the method adopted has been given by Vilhjálmur Stefánsson (586). When approaching seals on top of the Arctic spring ice, it is necessary (and only this is necessary) for the hunter to convince his quarry that he is a brother seal. To do so he must *act* as though he were a seal. ' The seal knows, exactly as the seal hunter knows, that no seal in this world will sleep continuously for as much as four minutes at a time. If you lie still for that long, he will know you are no seal and down he will slide into the water in the twinkling of an eye. When the seal, therefore, has been watching you carefully for twenty or thirty seconds, you must raise your head twelve to fifteen inches above the ice, look around in seal-fashion, so that your eyes will sweep the whole circle of the horizon, and drop your head again upon the ice. By the time he has seen you repeat this process two or three times in the space of five or six minutes, he will be convinced that you are a seal, and all his worries will be gone.'

Such instances which indicate the value of mimetic resemblance could, of course, be multiplied. We need only add here that disguises of some kind are frequently essential to the bird photographer, who, like the hunter possessed only of primitive weapons, must get to close quarters undetected, or rather unrecognized. In the early days of bird photography a number of workers adopted methods analogous to those described. Richard Kearton, for example, obtained very successful results with his camera concealed in the head of a stuffed ox. And in the Great War the same principle of aggressive mimicry offered great scope to men with sufficient imagination and initiative to apply it. An outstanding case was that of Rear-Admiral Gordon Campbell, in the evolution of the mystery ships adapted to deal with the submarine menace (78). These decoy vessels, looking like innocent merchant ships, but fitted internally as men-of-war, cruised on the trade routes hoping to attract the attention of an enemy submarine. On being attacked as an easy prey, part of the crew—the ' panic party '—would go through the motions of abandoning ship. Meanwhile hidden gun crews stood by their ingeniously concealed guns, waiting to open fire as soon as the submarine came to the surface and presented a vulnerable target.

8. BREEDING PARASITISM AND MIMICRY IN CUCKOOS

Sumer is icumen in,
Lhude sing cuccu !
Groweth sed, and bloweth med,
And springth the wude nu—
Sing cuccu !
ANON

Breeding parasitism in cuckoos has led to a type of mimicry which shows many remarkable features. The parasitic habit is, of course, here restricted to the nesting period ; and the resemblances between the eggs, or occasionally the young, of cuckoos, and those of the birds called upon to act as foster parents, are related to the necessity of hoodwinking an unwilling host.

In the account which follows I have drawn freely from two important memoirs : one by E. C. Stuart Baker (12) dealing mainly with Oriental cuckoos ; the other by F. C. R. Jourdain (295), whose survey of the subject should be referred to for fuller information than can be given here.

I. *CUCULUS CANORUS* : THE RELATIONSHIP BETWEEN PARASITE AND FOSTERER

It will help to clarify the subject if we begin by referring briefly to the main accepted facts in the breeding economy of the European Cuckoo (*Cuculus canorus*), a bird with the widest range of all cuckoos—being distributed ' practically throughout Europe and Asia as well as through much of Africa '.

The following points have been established : (1) Each female cuckoo has a special, restricted breeding territory, within which she lays. (2) The individual males also occupy definite breeding territory, which, since the species is polyandrous, does not coincide with that of the females. (3) Each female lays eggs of only one type throughout life. (4) As a rule, each female is parasitic on, and adheres to, a single species of fosterer. (5) In most if not in all observed cases, the eggs have been laid in the nests, and not inserted with the bill. (6) One egg is removed from the fosterer's nest at the time of laying. (7) Laying takes place on alternate days, and the number of eggs laid by one female may reach twenty-six—if a succession of suitable fosterers' nests is available. (8) There is evidence that in order to create opportunities for oviposition a cuckoo will destroy nests with young. (9) The egg tends to resemble, more or less closely, the eggs of the host species, though the British bird shows many exceptions in this respect. (10) When hatched, the young parasite ejects his foster brothers from the nest. Further points—such as the relationship between cuckoo and fosterer in different localities, and the selective action exercised by foster parents in rejecting unsuitable eggs—particularly concern us at present, and will now be considered.

II. THE FACTORS UPON WHICH EGG-MIMICRY DEPENDS

(1) **Segregation of Cuckoo Strains**—In our British Cuckoo the question of egg coloration is complicated by local conditions, and the degree of resemblance between eggs of parasite and host varies widely, according to the locality and to the fosterer employed. In the South of England Cuckoos commonly victimize several species, such as the Pied Wagtail (*Motacilla alba yarrellii*), Hedge-Sparrow (*Prunella modularis occidentalis*), Robin (*Erithacus rubecula melophilus*) and Reed-Warbler (*Acrocephalus scirpaceus*). These foster birds are found breeding close together. And they lay widely dissimilar eggs. Now assuming, as seems highly probable, that the male as well as the female transmits the characters upon which coloration of the egg depends, it is evident that under such conditions strains of Cuckoos laying one type of egg cannot be kept pure. And it is suggested by Jourdain that interbreeding between Wagtail, Robin or Hedge-Sparrow strains has lowered the standard of assimilation.

Confirmation of this view is obtained by a comparison with eggs from localities where a single foster species is pressed into service over a wide area. Thus mimetic resemblance is highly developed in the moorlands and hilly districts of northern England and in Scotland, where over extensive wastes of moor and rough pasture the Cuckoos normally parasitize a single host, the Meadow Pipit (*Anthus pratensis*); and moderately so locally in the southern counties, among Cuckoos which lay in the nests of Reed-Warblers and tend to keep to the restricted breeding haunts of their victims. Such conditions impose limits on interbreeding between different strains of cuckoos, and thus provide a degree of isolation necessary for the stabilization of one kind of egg.

But the effects of segregation are seen more clearly in certain parts of the Continent, where extensive districts provide only one or two regular fosterers. For example, in the densely wooded districts of Southern Finland the Redstart (*Phœnicurus phœnicurus*) is the normal fosterer and the Whinchat (*Saxicola rubetra*) is an occasional victim. Both these birds lay blue eggs, and it is significant that here ' practically the only type of Cuckoo's egg which has survived the ordeal of selection is the blue egg '. In a series of 40–50 eggs taken by Wasenius at Helsingfors, all but about four were blue.

Remarkable mimetic developments are known from other parts of Europe. Several of these show an advance on the plain blue egg, involving adaptations of ground coloration, surface markings, and pattern. Among the most perfect are imitations of the Great Reed-Warbler (*Acrocephalus arundinaceus arundinaceus*) in Hungary; the Orphean Warbler (*Sylvia hortensis*) in Spain; and the Brambling (*Fringilla montifringilla*) in Lapland.

Cuculus canorus telephonus, a closely allied Asiatic form of the European Cuckoo, shows advanced stages of egg-mimicry, its eggs closely resembling, in different localities, those of its habitual hosts—species of *Lanius*, *Enicurus*, *Trochalopterum*, *Larvivora*, *Emberiza*, and others.

Many other cuckoos are known to parasitize a particular host species or group of species with the utmost regularity over a wide area or throughout their entire range. For example, Stuart Baker states that the Koel (*Eudynamis scolopaceus*) practically never lays in any nest except in that of a true Crow. The only exceptions out of many thousands of records are a few deposited in the nests of Magpies and one from a Myna's nest. Similarly the Common Hawk-Cuckoo (*Hierococcyx varius*) and the Pied Crested Cuckoo (*Clamator jacobinus*) lay a hundred eggs in nests of their normal fosters—species of *Argya* and *Turdoides* —to every one laid in another bird's nest.

(2) **Selective Elimination by Fosterers**—Selective elimination by the fosterer of unsuitable eggs takes place when the degree of resemblance fails to satisfy her. When this happens, the attentions of the Cuckoo are frustrated in one of the following ways : (1) The nest may be deserted after the cuckoo's egg has been laid. (2) The cuckoo's egg may be ejected. (3) It may be broken in the nest, or eaten. (4) The fosterer may construct a new nest above the old one, building the cuckoo's egg into the foundations so as to prevent incubation.

As a remarkable example of the last method, we may cite the case of a three-storied Reed-Warbler's nest found in 1893 by the Rev. J. R. Hale. Beneath the four fresh warbler's eggs which it contained a cuckoo's egg was discovered built into the floor, with a fifth Reed-Warbler's egg near by ; and beneath these again another cuckoo's egg with a seventh egg of the rightful tenant—evidently a very critical bird.

The available evidence for selective elimination of the parasite's egg is discussed in Jourdain's paper. His main conclusions are : 'Firstly, the proportion of rejections by the fosterer either by desertion or rejection varies enormously. In some species the percentage falls to as low as 5 per cent. or less, while in others it rises to nearly 80 per cent., and perhaps in some cases almost to 100 per cent. Secondly, these rates are not necessarily connected with the closeness of the mimicry or the reverse. If the parasite is to hold its own it must reach a certain level to satisfy the discrimination of the host, but that level may be a low one or a high one, and varies according to the fosterer in question.'

' It is very significant ', writes Poulton (515), ' that the percentage of rejections is by far the highest with the rare fosterers. Here the Cuckoo is apparently seeking to establish itself on some new species and drastic selection is going on. Thus the proportion of failures is extremely high with the Wren—a very unsuitable fosterer, it would seem, and yet one which the Cuckoo is making persistent efforts to adopt. The failures are also very numerous with the Wood-Warbler, while with the Chiffchaff they apparently reach 100 per cent., although the records are few. The regular fosterers give very different results. With these the period of drastic selection is over, an equilibrium has been reached, and rejections are only important as the means by which the standard is kept up.'

III. THE DEGREE OF MIMETIC RESEMBLANCE ACHIEVED

(1) **Coloration of Eggs**—The degree of resemblance required to satisfy different fosterers varies enormously; hence also the final result attained after selection has ceased to operate. The Hedge-Sparrow is notorious for its lack of discrimination in this respect, or, as Jourdain puts it, for its 'lack of colour perception'. Habitually this bird accepts and broods cuckoos' eggs where the contrast with its own blue eggs is most striking. The same is true of the Bulbul (*Pycnonotus*), a common African fosterer, whose reputation as the 'fool' of the South African Passeres has been confirmed experimentally by Swynnerton.

In other cases a remarkable degree of assimilation has been enforced by selective destruction of the less mimetic eggs. The Koel (*Eudynamis scolopaceus*) lays its eggs in the nests of various crows in India, Ceylon, Burma, and Assam, and regularly hoodwinks these birds—which are generally regarded as the most astute members of their order—with an egg which they cannot distinguish from their own.

The blue eggs of *Clamator jacobinus*, the Pied Crested Cuckoo, and of *Hierococcyx varius*, the Common Hawk-Cuckoo, two common Indian species, come even nearer to those of the fosterer, with which they agree so closely not only in colour, but in size and shape, that 'often human eyesight is not acute enough to distinguish between the two' (12).

The attainment of mimetic results is not so simple a matter as might at first sight appear. It involves modification both of ground pigments and of shell markings. Most non-parasitic cuckoos, in which no selective agency has been at work, lay white eggs. In the higher types of mimicry we find eggs in which the primary colour deposits of blue are overlaid by a profuse blotching of brown pigment, as in *Eudynamis scolopaceus* and *Clamator glandarius*, whose young are reared by crows; or in which the blue ground colour is suppressed and replaced by a later surface deposit of red pigment, as in one type of egg laid by *Cuculus poliocephalus* in nests of *Cettia cantans* in Japan.

Perhaps most wonderful is the approximation of eggs laid by *Cuculus canorus telephonus* in the nests of buntings such as *Emberiza cioides ciopsis* in Japan. Except for size, these eggs have attained all the peculiarities of their models and show perfect imitation of the interlacing lines or 'scribbling' characteristic of the buntings. 'The network of irregular streaks and spots, especially towards the large end, is reproduced with marvellous exactitude in the Cuckoo's egg; and were it not for the fact that a whole series of the eggs is in existence, taken from the fosterers' nests, and that microscopic examination by R. Schlegel and others confirms their identification, we should be strongly inclined to doubt their authenticity (295).

(2) **Size of Eggs**—There is, however, as in the present case, a frequent disparity in size between the eggs of parasite and host. Indeed, it appears that size plays a far less important part than colour and pattern in the evolution of a mimetic make-up which will ensure deception. This seems to be true not only

in the present connexion, but of mimicry in the widest sense—as applied, for instance, to insects, and as exemplified in marked degree in the inequality of size between certain snake-like Sphingid larvæ or the Homopterous bug *Laternaria*, and the dangerous reptiles whose appearance their coloration or threatening attitudes suggest.

Special interest attaches to this comparison between cuckoo and insect, because, as pointed out by Poulton (515), in egg-mimicry divergence in size cannot be mistaken by the observer as an effect of distance, since both model and mimic are seen side by side—under the very conditions which make deception most difficult. It would be valuable to have experimental evidence confirming the inference from these facts, that birds can distinguish discrepancies of coloration more readily than disparity in size.

Yet it is to be noted that some degree of adaptation towards the size of the model has been achieved. Careful measurements by Latter of a large series of cuckoos' eggs showed a definite though slight approximation in size to the eggs of the fostering species (330).

Much more obvious and important, however, is the very low relative size of all *C. canorus* eggs (276*a*), and, on the other hand, the lack of reduction of egg-size in those Cuckoo-species which parasitize birds of their own size. A beautiful example of reduction in egg-size is furnished by the Large Hawk-Cuckoo (*Hierococcyx sparveroides*), which lays two types of egg. One of these, dark olive-brown in colour, is foisted upon the Great Spider-Hunter (*Arachnothera magna*), whose eggs are similar. The other, bright pale blue, is deposited in the nests of Laughing Thrushes, of the family Timeliidæ, which lay blue eggs. Now the Spider-Hunter's eggs are much smaller than those of the Laughing Thrushes, and correlated with this difference the brown eggs of the cuckoo are smaller than the blue—though still noticeably larger than those of the Spider-Hunter (12).

(3) **Modification of Nestling**—Everybody knows that the bird which hatches from the cuckoo's egg very soon grows into a creature totally different in appearance from young of the foster parent. ' Nothing ', writes Jourdain, ' more unlike the nestling of most of the ordinary fosterers can well be imagined than the great brown bird with huge orange gape and stumpy tail which sits on the crushed remains of what was once a nest and keeps up its penetrating food call, which, by the way, is quite unlike the ordinary notes of their young.' Nevertheless rejections at this stage are almost unknown. Indeed, other birds besides the real fosterer have been seen to respond to the young parasite's noisy and importunate demands for food !

At this stage, it would appear, the need for deception is at an end. But other genera reveal a very different state of affairs. The Great Spotted Cuckoo (*Clamator glandarius*) is parasitic on the Magpie (*Pica pica melanotus*) in parts of Spain, and in other countries on the Hooded Crow (*Corvus cornix*). On hatching, the impostor makes no attempt to expel his foster brothers. On the contrary, all live peaceably together in the nest. Now the nestling cuckoo has a dark crown, utterly different from the light ashy-grey crown of the adult, but closely approximating to the colour of the young Magpies with which it is brought up.

In *Clamator jacobinus*, a parasite of *Argya*, the relation between adult and juvenile coloration is reversed. Here the former has a green-glossed black crown, but the nestling is considerably lighter, with a brownish head which approaches the yet lighter plumage of its foster brothers. In both these cases it is the crown —namely, that part which is especially *exposed to view* as the young crowd together in the nest—whose coloration has been modified; in the one case becoming darker, in the other lighter, in its approach to the appearance of the Cuckoo's nest-fellows. In the Koel (*Eudynamis scolopaceus*), parasitic in India on *Corvus splendens splendens*, the young are at first black-headed like the young crows; but after leaving the nest they moult into a brown plumage like that of the adult female.

The explanation of this state of affairs, suggested by Jourdain, is 'that the Crows and Pies, with their superior intelligence, have enforced, by a process of selection, a certain degree of mimicry on the part of the young parasite in addition to extremely close resemblance in the egg; while the smaller Passeres, with their lower brain power, respond to the stimulus of the widely-opened mouth and the insistent hunger cry instinctively'.

IV. THE RELATIONS BETWEEN CUCKOO-MIMICRY AND INSECT-MIMICRY

From what has been said above it will be clear that we have in the coloration of cuckoos' eggs phenomena closely parallel to mimetic resemblances in other groups. We see the same principles at work in the very different fields of Ornithology and Entomology. Both mimetic eggs and mimetic insects exhibit profound modifications which in advanced stages involve colour and pattern, shape and size, habits and instinct. I have already referred to other parallel features: the greater importance of coloration than size in deceiving the eye; the different degrees of resemblance necessary to hoodwink different enemies; and the superficial nature of the modifications, which only affect parts ordinarily visible—as in the nestling of *Clamator glandarius*, whose crown has been influenced by selection, but whose throat has been neglected—so that while the latter resembles that of its parents, the former imitates that of its mess-mates.

(1) **Convergence: non-Mimetic Resemblance between Mimics**—*Clamator jacobinus* and *Hierococcyx varius* are the two most common cuckoos in India. Both deposit their eggs in the nests of various species of *Argya* and *Turdoides*, two of the most abundant and widely distributed genera of birds in their habitat. And both, like the foster species, lay deep blue eggs which according to Stuart Baker are so closely alike that it is almost impossible to distinguish them except by the colour of the yolk, and by size, though in this last respect they constantly overlap.

This resemblance between the eggs of cuckoos belonging to different genera is a striking example of convergence within the field of mimicry. Among mimetic arthropods it finds a parallel in the superficial similarity of unrelated animals such as flies, beetles, bugs, grasshoppers, and spiders, to a common model like the ant.

Such resemblances are, of course, entirely different in origin and function from cases of Müllerian mimicry, where the similarity between mimics is of biological significance. The present cases are rather akin to the common cryptic coloration of oceanic or lichenicolous animals : they are *incidental*, rather than functional ; convergent, but not mimetic—being the result of independent adaptation to similar ends.

(2) **Divergence : Polymorphism and Geographical Distribution**—The converse relationship—which also finds a parallel among insects, and in a general sense under the conception of adaptive radiation—is seen in the divergence within a species, whose members lay eggs resembling different models in different localities. We have already seen that certain strains of *Cuculus* are consistent in laying the same type of egg and in calling upon the same fosterer, or group of fosterers, to rear their young.

But this state of affairs is not possible with species of cuckoo which have a wider geographical or ecological range than any one suitable fosterer. Such species frequently exhibit divergent or polymorphic evolution, laying eggs of two or more distinct forms in different localities—as happens in the case of the European Cuckoo. The results are often very remarkable, and I shall here refer briefly to three instances described by Stuart Baker.

Eudynamis scolopaceus lays in the nests of different species or sub-species of crows throughout its breeding range, and the eggs of both cuckoo and fosterer tend to vary in the same way in different areas. Thus the eggs of both are dark in Siam and Assam, paler in the dry areas of Northern India, paler still in the Sind desert, while in Ceylon the eggs of both are either dark, or of a special reddish type, in different parts of the island. Poulton has drawn attention to the interesting fact that the relationships of butterfly mimics follow the same laws, and he cites the closely parallel case of *Papilio cynorta* ' with its three females, in W. Africa, Uganda and Abyssinia, resembling respectively two sub-species of an Acræine and one of a Danaine model ' (515).

More striking is the divergence of colour shown by eggs of *Cuculus poliocephalus*. This cuckoo ranges from the Western Himalayas through the mountains of China to Japan. In the western area small warblers of the genera *Phylloscopus* and *Acanthopneuste* are called upon to act as foster parents, and with these birds a white egg is laid. Her favourite species, *Acanthopneuste occipitalis* and *A. magnirostris*, themselves lay white eggs, and in other cases the fosterers' eggs are white and sparsely spotted. In Japan she selects as fosterer the equally common *Cettia cantans*, which lays ' a remarkably beautiful deep terra-cotta or chocolate-pink egg '. In these nests her own egg is similarly coloured, though larger. *Cettia* does not occur in India, and here the red type of egg is deposited with other fosterers belonging to the genus *Horornis*, all of which lay dark chocolate-coloured eggs.

Finally we come to *Hierococcyx sparveroides*, whose habit of laying olive-tinted eggs in nests of the Great Spider-Hunter, and blue eggs in those of the Laughing Thrushes, has already been mentioned. Here we have to notice a very interesting point. The blue type is laid by this cuckoo throughout its entire range from the North-West Himalayas to Assam. The brown type, on the other hand, is restricted to Assam, for it is only here in the whole range of the species that the Spider-hunters are sufficiently plentiful to ensure an adequate supply of nests. In Assam, therefore, the blue-egg laying and the olive-egg laying clans of cuckoo occur together and in about equal numbers. And Stuart Baker tells us that in spite of this no intermediate form of egg occurs, ' nor do we ever find a blue egg in a Spider-Hunter's nest or a brown egg in that of a Laughing Thrush '.

To this wonderful example of dimorphism Poulton finds a close parallel among butterflies in the Oriental *Papilio polytes*, ' with one female form mimicking *P. aristolochiæ* over a wide range, and also a second form mimicking *P. hector* in a relatively small part of the range where the two models exist side by side ' (515).

The whole question of polymorphism opens up a number of interesting problems in the field of genetics and selection, which lie outside the scope of this work. I must, however, touch upon one or two matters which seem to illuminate the parallelism just referred to. The phenomena of mimetic polymorphism in insects have been studied in recent years by Fisher (172*a*, 173) and Ford (181*a*, 181*b*), to whom the reader must refer for fuller information.

Polymorphism—namely, the occurrence in one locality of two or more forms of a species in stable equilibrium—always involves a balance of selective agencies, which maintain the forms in definite proportions (172*a*). For, as Fisher has pointed out, in the absence of opposing selective agencies, an advantageous character will spread gradually through the whole population.

Now the special conditions necessary for a balanced selection are present in the case of Batesian mimicry. If the numbers of the less-protected mimic rise in relation to those of the more protected model, the degree of protection will decline, and will eventually be converted into a disadvantage when the coloration becomes associated by predators with something palatable more often than with something repellent. There is therefore an optimum proportion between the numbers of model and mimic, and this limits the spread of the latter.

When, however, a mimetic species is dimorphic or polymorphic, different forms copy different models, and the advantage derived from mimicry will be extended. With insects, this advantage lies in the increased number of models available to the mimetic species : with Cuckoos' eggs, in the increased number of fosterers available to the parasitic bird.

Finally, as Dr. Julian Huxley has pointed out to me, balanced polymorphism may be fruitfully contrasted with another type of balance, seen in seasonal polymorphism, which has been mentioned early in this book. Here the diversity of form is determined by different intensities of selection at different times—warning coloration alternating with cryptic coloration as the available numbers of prey fluctuate with the seasons, from abundance to scarcity.

CONCLUSION

CONCLUSION

Who can utter the mighty acts of the Lord ? who can show forth all his praise ?
PSALM CVI. 2

THE force of the facts and arguments used in this work is cumulative in effect. Taken singly as isolated phenomena, they may appear to be insignificant. Taken together, and considered in relation to one another, and to kindred phenomena in other fields, they present a body of evidence which makes it appear that adaptive coloration is one of the chief attributes of the higher animals, and has been, indeed, one of the main achievements of organic evolution. In these concluding pages I shall endeavour to bring together several lines of thought which the work has invoked, and to relate the facts of adaptive coloration to general principles of which they are an outward expression.

I. ADAPTIVE COLORATION AND OPTICAL PRINCIPLES

Illuminated objects are rendered visible to the eye, and recognizable to the mind behind the eye, when they differ in various ways from their surroundings. These visual clues, by means of which we are able to judge the size and shape, colour and texture, position and nature of a solid body, are fundamentally of four kinds—depending upon questions of hue and tone, of light and shade, of surface and contour, and of cast shadow. Now we have seen, what is a very singular fact, and one appearing the more remarkable the more closely it is pondered, that in the case of cryptic animals, which are in actual fact difficult and at times almost impossible to recognize in the field, this end has been achieved by arrangements of pigment and pattern which, for optical reasons, are those best adapted to deal with the visual properties of matter. In other words, we find such animals have their colour differences obliterated by colour resemblance ; light and shade neutralized by countershading ; continuity of surface and outline disguised by disruptive patterns ; discontinuity of surfaces masked by coincident patterns ; and shadows concealed by a number of different devices, both structural and habitual.

Turning to the field of conspicuous characters : in general it will be noted here that the colours used are bright and saturated—conspicuous combinations of black, red, orange, white, or yellow ; and the patterns used are bold and simple —frequently in the form of broad bands or stripes, spots or ocelli : such combinations, in fact, as appear best suited for purposes of advertisement.

In particular it will be remembered that a circular target-like mark, when suitably coloured and displayed, constitutes the ideal advertisement, the essence of conspicuousness. The eyes of many animals tend to present such a pattern, and accordingly in various cryptic vertebrates belonging to groups the most remotely related—snakes, frogs, turtles, fishes, birds, and mammals, as well as in certain insects—they are camouflaged, as we have shown, by disruptive patterns specially adapted to that end. But where a premium is placed upon the opposite principle of advertisement, rather than effacement—whether for courtship, warning, or threat, for recognition or deflection—it is a singular fact that this, of all configurations, is the very one which has frequently been adopted.

Not only so, but these target-like ocelli may, and do, occur upon almost any kind of animal of sufficient size, including frogs and fishes of many families, birds, butterflies, moths and their larvæ, mantids, beetles, grasshoppers, crustaceans and cephalopods; they are painted in all kinds of media upon a base of scales or skin, chitin or feathers; and on a variety of structures—fins and flanks in fishes; tail or wings in birds; elytra, tegmina, or wings of insects or upon the segments of the body, as in various caterpillars.

Then there are the phenomena of mimetic and special resemblance. It is unnecessary to repeat here what has been said already in the relevant sections, where the points which I have attempted to express above are again abundantly illustrated. The essential principle, that appearance is the thing aimed at, is indicated by many independent lines of evidence. We have seen, for instance, that particular visual effects are achieved by a wide range of totally different optical, structural, and habitual contrivances in different animals; that the resemblances are achieved without regard to inherent differences of structure, to divergence of relationship, or to dissimilar life-histories: while their superficial nature is such as to suggest unmistakably that they are to be interpreted as an appeal to the eye; that they have evolved in relation to the visual perception of natural enemies (or more rarely of prey); and that their end is deception.

II. ADAPTIVE COLORATION AND VISUAL PERCEPTION

The black, yellow, and cow-red colour-scheme worn by a Heliconiid butterfly is as out of place in a museum cabinet as a railway poster would be in the primeval forests of Brazil. Such things are directed towards a seeing public: they are meant to attract the attention of potential enemies in the first case; of prospective travellers in the second. When divorced from their proper environment each becomes impotent and meaningless. But in the affairs of animals and of men, such visual stimuli are not devoid of meaning—for advertisement pays, just as in other circumstances concealment or deception pays.

Recent studies of visual perception lend support to the view that characters serving as visual stimuli have evolved parallel with the highly specialized sensory equipment against which they are directed. Not only is this correlation between appearance and perception true in a general way, but also, it seems, in a special way. Not only, for instance, is the evolution of floral advertisements—with all their elaborate alluring qualities, olfactory, gustatory and structural—unthinkable except in terms of an organism able to perceive and respond to them; but the particular optical properties of the structures displayed have a correlative in the particular receptive properties of the organisms which they are destined to attract.

Thus, as we have already indicated, light at the red end of the visible spectrum is an efficient stimulant to diurnal birds; and bird-flowers are typically orange-red, vermilion or scarlet. The same correlation is more precisely illustrated by the striking results obtained by Dr. Hertz in her training-experiments with bees (246, 247). Bees are blind to red, but have a range of vision extending far into the ultra-violet. Yellow and blue appear coloured to the bee, as to man. On the other hand, Hertz has demonstrated that white surfaces may appear very differently to the bee, according to their reflection, or absorption, of ultra-violet rays. White objects which reflect a fair proportion of ultra-violet light, and which therefore emit the bee's whole visible spectrum, appear neutral, and unattractive; but white surfaces which absorb ultra-violet light appear blue-green, and attractive, to the bee. Now in Europe the flowers visited by bees fall into three main colour-groups, being orange-yellow, blue-violet, and white or pale-tinted respectively. Those in the first two groups reflect light which acts as an efficient advertisement to the bee. More significant, however, is the fact that flower-petals of the last group reflect comparatively little ultra-violet, and therefore they too appear brightly coloured and attractive to the bee.

And what is true of colour appears to be equally true of pattern. When visibility from a distance is required, as in characters subserving the function of warning, threat, or recognition, coarse, bold, and simple patterns have been developed. On the other hand, characters which are directed against vision at close range, and serving for concealment by day, tend—especially in the case of specific disguises—to be detailed and delicate. The extraordinary degree of perfection attained by many insects and other animals in their special resemblance to bark, lichen, leaves, excrement, and other objects—achieved by the combined effect of pigment, pattern, and posture—almost presupposes in birds (their most common natural enemies) those exceptional powers of visual acuity and form-perception which on other grounds we know them to possess.

In the field of sound we find once again this intricate relationship between a transmitter and a receiver of particular stimuli. It is only necessary to recall here the evolution of soundless flight in owls, or the rustling machinery of rattlesnakes—each of which is related in a particular way to the hearing of enemies. The fact is, that all such characters—the long-range stimuli on the one hand, and the sensory equipment for their reception on the other—may be regarded as special manifestations of the age-long armament race in which animals (like men) are involved. The gradual perfection and specialization of visual disguises or displays, and of eyes which penetrate or appreciate them, find a close parallel in the increasingly complex equipment of modern warfare. For here, as in nature, new contrivances for aggression or protection have called forth new counter-measures in defence and offence—advances in the silencing of machinery compelling improvements in sound location ; developments in photographic materials and technique rendering more necessary corresponding progress in ground camouflage and the art of visual deception.

III. PATTERN AND ANATOMY

In the course of this work I have repeatedly stressed the apparent independence of underlying anatomy exhibited by systems of adaptive coloration. On the one hand, we have seen that related animals which resemble one another in their morphology but differ widely in their ecology (as do, for instance, members of the Felidæ among mammals, and of the Sphingidæ among moths) are dressed in suits whose coloration varies in relation to the appearance of their haunts and habits, but not at all to the details of their structure. We have seen, moreover, that special patterns which for optical reasons are suitable for particular purposes—such as the disruption of surface or the obliteration of contour—are of a kind which totally disregard the underlying details of structure upon which they are displayed.

Nowhere is this more beautifully illustrated than in the arrangements of colour which I have described under the heading of coincident patterns. Such patterns, it will be remembered, cut right across different organs or parts of the body, so that underlying anatomical features become entirely subordinate to the illusionary appearance superimposed upon them. We have also to bear in mind that such patterns are of a type in close harmony with the environment, so that it is often difficult to say which is the more remarkable—the disagreement of the dress with the morphological foundation upon which it is worn ; or its agreement with the ecological background against which it is seen.

Unconformity between structure and pattern is, of course, equally typical of mimetic colour-schemes, which resemble press propaganda in a totalitarian state, in that inconvenient truths are ruthlessly suppressed, and a false semblance of truth is made to override everything likely to interfere with the desired result. An opposite aspect of the relationship between anatomy and coloration is presented by such phenomena as flash colours, and characters exhibited in display but normally concealed. Here we find the nicest agreement between the disposition of conspicuous patches and the shape of the structures upon which they are at one time exhibited, and by which at another they are eclipsed : just as a politician may exaggerate some aspect of truth when it happens to suit his particular purpose.

In short, where structure hinders the effect, its details are disregarded : where it enhances the effect, its aid is enlisted, and different morphological elements are invoked and used, rather than contradicted and overriden. The essence of the matter is this : everything, where adaptive coloration is concerned, becomes subservient to outward appearance. The modifications are superficial ; the result is visible : the technique is not at all important ; the effect is all-important.

IV. PATTERN AND AFFINITY

When we analyse the distribution of colour-schemes within a group of animals, rather than their disposition on the body of an individual, a similar principle of latitude finds expression. Just as in the individual particular elements of a coincident pattern bridge the structural gaps between separate and independent parts of the body, transgressing the limits of anatomy so as to present a consistent appearance irrespective of deep-seated differences; in like manner among different animals, particular types of coloration totally disregard differences of origin, bridging the systematic gulf fixed between distantly related groups in a manner which shows outwardly complete independence of mere zoological status. These remarks do not apply to one or to a few classes of coloration, but generally, to the whole field of adaptive coloration in its most varied manifestations—as we have repeatedly seen in the foregoing pages.

For instance, warning colours and the associated attributes of aposematic animals are not the prerogative of a particular group. On the contrary, they crop up over and over again in class after class, and order after order. The same is true of conspicuous colours normally hidden but displayed as a second line of defence; of all the various grades of general cryptic resemblance, obliterative shading, disruptive coloration, and shadow elimination; of adventitious concealment and adventitious advertisement; of deflective and directive markings; and of special resemblances, and mimetic and alluring colour-schemes.

Or, to view the subject from a complementary aspect—that is to say, as an expression of divergent rather than convergent adaptation—we find that just as disruptive designs and mimetic patterns serve optically to break up what is, in fact, a continuous surface, thus utterly misrepresenting unity of structure and splitting up a related whole into what seem to be dissimilar parts; so in particular groups of animals we find the widest range of colour-schemes, and put to the most varied uses, within what is actually a natural group—so that in the matter of appearance the most closely related animals may come to diverge very markedly from one another, and in the extreme cases of mimicry and special resemblance seem, superficially, to have affinities with an alien order, or even with members of the vegetable world. In a word, whatever their guise and function, all such systems of adaptive coloration outwardly defy the ties of blood relationship, and seem to throw off the bonds imposed by their systematic status.

V. COLORATION AND ADAPTATION

Now these aspects of the subject are in no sense peculiar to coloration phenomena. On the contrary, I have stressed them not merely for their inherent significance, but because, by analogy, they bring coloration into line with adaptive characters in general. For the same principles apply widely over almost the whole field of adaptation. This point will be made clear if we consider briefly the occurrence of some other device—for example, organs serving for attachment.

A feature typical of adaptive characters is the variety of functions which a particular device may serve. Adhesive organs, like adaptive colours, have been put to the most varied uses by different animals. They may provide transport by adhesion to a moving object—as with *Remora*; or they may prevent movement by fixture to a stationary one. They may serve to attach an animal within the body of its host, or to the bottom of a mountain torrent, or to the bark of a forest tree—which is the case with various flukes, fishes, and frogs. They may be used for purposes of aggression or protection; for holding a victim or a mate; for creeping or for leaping.

Again, just as in the sphere of coloration we find that a particular effect like concealment may be achieved by the application of one or more different optical principles—colour resemblance, countershading, contour obliteration, coincident coloration, and so forth; so here we find that a number of relevant physical properties have been seized upon and utilized—friction or cohesion, seizure or suction, hooking or glueing.

Then as with coloration phenomena, the evolution of these contrivances has involved the modification of all kinds of structures morphologically distinct—whether the palm of the hand (as in the Tree Coney *Dendrohyrax*), or the foot (as in the Limpet *Patella*); the ball of the thumb (as in the bat *Thyroptera*); the under surface of the digits (in geckos), or of their swollen tips (in many tree-frogs), or of the body (in hill-stream fishes like *Garra* and *Gastromyzon*), or of the tail (in the lizard *Lygodactylus*), or of the tibia or tarsus in different insects; or the dorsal fin (in *Echeneis*) or pelvic fins (in *Cyclopterus*).

Another fundamental point, already referred to repeatedly in connexion with aspects of coloration, is the complex nature of adaptive characters. Adhesive organs may be complicated both in broad anatomy and in histological detail, involving profound modifications of form and function simultaneously in a number of distinct parts and tissues.

Again, as is usual with adaptive devices of all kinds, we find the same independent evolution of appropriate organs in group after group of creatures so utterly unrelated, in the present instance, as lizards and leeches, bugs and bats, cephalopods and caterpillars, tadpoles and tapeworms. Frequently, moreover, the structures present the most remarkable examples of convergence, not only of general form and function, but of microscopical and mechanical detail, as may be traced in the adhesive apparatus of torrent-dwelling larval frogs, and fishes.

Or if we view the subject from the complementary aspect of divergent adaptation within a group, the analogy is equally close. Just as the different types of coloration which serve essentially for concealment, for advertisement, or for disguise—with the many finer shades of function within each—have been reproduced again and again within single groups of animals—for instance, by snakes and caterpillars, by grasshoppers and mantids, by beetles and birds: so in the evolution of limbs or of teeth, for example, members of the different vertebrate orders exhibit, as is well known, that remarkable range of divergence correlated with various modes of life—whether aquatic, terrestrial, or aerial; and with the various methods of feeding—whether carnivorous, insectivorous, or herbivorous—with numerous subordinate grades of both.

VI. ADAPTIVE COLORATION AND MODE OF LIFE

In a general manner of speaking the phenomena of adaptive coloration fall, as we have seen, into three main classes, according to the visible result achieved, namely, concealment, advertisement, and disguise. The biological function of such elusive, attractive, or deceptive features varies widely, according to circumstances. Through reduced visibility they may facilitate the capture of food or escape from the aggressor. Through increased conspicuousness they may serve as a warning to enemies. Through deceptive or mimetic effects they may mislead an observer as to an animal's whereabouts, attitude, or identity. Now if such colours have indeed the functions assigned to them, we should expect this to be borne out by the animal's mode of life.

As regards the first category, it is clear that protective coloration is essentially an attribute of creatures which rest motionless by day, generally among surroundings with which their dress harmonizes, and which venture forth at dusk to take their place in nature's night life ; or again, to such as brood over their eggs or young in exposed positions. To put the matter in another light, such colour-schemes seem to be correlated with the necessity for self-effacement during more or less prolonged periods of enforced stillness ; or, in the case of predators, for purposes of approach, ambush, or allurement. This correlation between cryptic resemblance and crepuscular habits on the one hand, and aggressive tactics on the other, is, of course, in no sense restricted to one or a few groups of animals, but is quite general among the most distantly related creatures.

Aposematic species, on the contrary, are typically active by day, and like entomophilous and ornithophilous flowers, exhibit themselves to the best advantage in nature. Frequently, moreover, such animals are gregarious ; sluggish in movement or slow in flight ; and advertise their presence by sounds and smells as well as by displays of colour. Mimetic forms are likewise generally diurnal, but what makes this fact so interesting is the knowledge that such habits are frequently in marked contrast to those of their own nocturnal congeners, and thus have involved profound modification of behaviour in the direction of a distantly related model—as seen, for instance, in various day-flying moths and bugs. It is also to be remembered that such mimics are on the wing not only at the same time, but in the same place, as their models.

VII. ADAPTIVE COLORATION AND SPECIAL BEHAVIOUR

When the three main types of coloration are considered in relation to the special attitudes and reactions of the species exhibiting them, we are faced with a further important class of phenomena. In the cryptic group elaborate instincts have been evolved which increase the difficulty of recognition. We may recall, for instance, the inverted countershading of animals which habitually rest upside-down; the adaptive orientation of bark-like moths; the special habits of animals which dress themselves with adventitious material; or of those which rest against a specially prepared background which resembles their own coloration. Here, too, we have to include the technique of temporary cryptic reactions involving special deceptive poses; and instinctive immobility and silence—as assumed in times of danger by many birds, lizards, insects, and other animals.

With the various categories of conspicuous coloration, we see kinds of activity in many respects the very reverse of those just mentioned. Here, for example, are special types of display, often combined with orientation, but of such a kind as to make their author as conspicuous, rather than as inconspicuous, as possible: and the use of adventitious material for advertisement rather than effacement. So, too, in times of stress, stillness is here replaced by warning movements; silence, by warning sounds; and reactions occur involving the show of deflective or directive markings.

The reactions of mimetic species are often similar, though, of course, in the case of Batesian mimics the displays and imitations are sheer bluff. Moreover, as we have seen, this play-acting is carried out in a most thorough and perfect fashion, as when, for example, a wasp-like beetle goes through all the pantomime of stinging with its stingless abdomen.

VIII. ADAPTIVE COLORATION AND PROTECTIVE ATTRIBUTES

Concealing coloration and special cryptic resemblances are features commonly associated with defencelessness, or with aggression. In other words, cryptic species are those which, for securing safety or finding food, especially need to be concealed. If this relationship between coloration and other means of defence or offence applied throughout a single large group of animals, it would be very suggestive. But it does not stand alone. It applies widely, as we have seen, in group after group of animals; and it is impossible to disregard the implication—that concealment is an outward and visible sign of an inward ecological need, and that its function is directly concerned with the problem of survival in a dangerous world—a world in which hunger and murder are commonplace, and one in which the most pressing business of life is the search for security and sustenance.

When we turn to animals wearing warning colours, the opposite is the case. Warning colours are exhibited by members of different groups possessing qualities which render them more or less unsatisfactory as prey to many, if not to most or all, of their potential enemies. In other words, just as animals which exhibit cryptic colour-schemes are those which for various ecological reasons especially need to be concealed; so aposematic forms are typically those which for opposite reasons require to be conspicuous.

Here the equipment for defence is dual, and consists of a passive psychological warning—intended to avert attack; and of second-line active physical measures—adapted to defeat attack when it comes. The bite of such animals is worse than their bark. The allæsthetic challenge may be visual, in the shape of conspicuous colours, bold patterns, and special displays; or auditory, or olfactory, in the form of threatening sounds and repugnant smells.

The weapons employed for active defence include poison, often associated with special structures such as fangs, stings, spines, or nematocysts for its injection into the body of a victim; irritating or repellent secretions, which in some instances may be projected at the predator; nauseous taste, rendering the animal unfit for food; a protective integument, in the form of dense exoskeleton or spinescence, which renders the body indigestible or inaccessible; and lastly, qualities such as tenacity of life, and powers of resisting injury and of regenerating lost parts. Batesian mimics and other bluffers, on the other hand, are typically defenceless. Here reliance is placed upon deception. These are the sheep in wolves' clothing.

IX. ADAPTIVE COLORATION AND SURVIVAL VALUE

In attempting to account for the various phenomena of cryptic, aposematic, and mimetic coloration, we have had to consider not only their nature, but their function. To what extent, if at all, are these visual effects of real value to the organism in which they are exhibited? When the theories of Protective Resemblance, Warning Coloration and Batesian and Müllerian Mimicry were first propounded, they were open to one very serious objection, namely, lack of evidence that the schemes of coloration actually serve the functions assigned to them. This criticism is no longer admissible. The last fifty years have seen an immense number of observations in the field, and the application of experimental methods to test the validity of these theories. I have already referred in some detail to research bearing upon this matter, which is, of course, of fundamental importance to our subject.

Whereas formerly, in the absence of precise data, different types of concealing coloration were assumed to be useful in the struggle for life; now, at any rate in many cases that have been critically examined, positive evidence is available, which points unmistakably to the biological value of visual concealment as a means of protection from predators which hunt by sight. It is only necessary to recall here the work of Poulton and Sanders (526), di Cesnola (91), Young (681), Sumner (599, 600, 601), Carrick (88), and Isely (283), not to mention miscellaneous observations by Frohawk (in Collenette, 104), Bingham (in Poulton, 506), Cheesman (94), and others, to substantiate this statement.

The evidence available to-day is no less clear in regard to warning coloration. Such evidence, direct and indirect, whether derived from comparative studies of natural groups, or from feeding experiments, from the observed behaviour of wild animals or from the records supplied by the food in their stomachs, indicates that different insectivorous and carnivorous predators discriminate in the choice of food; that they quickly learn to recognize and to avoid unpalatable prey; and that aposematic animals do in fact enjoy considerable immunity from attack. Furthermore, in a general way this is true over a wide range of possible prey and potential predators. In the present connexion we may mention the work of Lloyd Morgan (414), Marshall and Poulton (395), Beal (28, 29, 32), Pritchett (529), Pocock (478), Eltringham (161), Schæffer (557), Longstaff (354), Hale Carpenter (79), Poulton (516), Phillips (469), Kluijver (313), Morton Jones (290, 291), Cott (111, 112, 113, 116), and others, which combines, from various aspects, to form the strongest support for the theory of warning coloration.

With the palatable bluffers and defenceless mimics of specially protected species it is becoming increasingly certain that different predators are hoodwinked by various types of deceptive appearance. In other words, that special resemblances and mimetic characters and other illusory devices are to be regarded as products of the psychology of vision. While this branch of the subject is one much requiring further research on experimental lines, a good deal of support is given to an adaptive interpretation of illusory appearance, as, for instance, by the investigations of Marshall and Poulton (395), Pocock (482), Swynnerton (607, 608), Darlington (134) and others ; while the phenomena of breeding parasitism and mimicry in cuckoos' eggs furnish an instructive and fully investigated example from a somewhat specialized field.

X. ADAPTIVE COLORATION AND APPLIED COLORATION

The innumerable visible devices used in everyday life, both by the more and by the less civilized races of man, in peace-time and in war-time, in courtship and in commerce, are merely rediscovered arrangements and applications of colour that have already reached a high, and indeed often a far higher, degree of specialization and perfection, among our contemporaries of the animal world, where they are employed for one purpose or another in the intricate relationships between predator and prey ; between rival males, or the opposite sexes ; between parents and offspring, or between members of the group.

Here and there throughout this book I have drawn attention, in passing, to many such comparisons. The hunting disguises put on by primitive races as a means of approaching, ambushing or alluring game, and the sniping suits, concealed machine-gun posts, and booby traps of his more enlightened brothers, are almost identical in principle with similar methods adopted for purposes of aggression by wild animals ; just as protective disguises, whether depending upon the principles of special resemblance, adventitious coloration, or mimicry, have their counterpart in the photographer's hide and the gunner's observation post.

In his posters and street signs man has only repeated and recently developed methods of catching the eye which have been in use through the ages by members of the animal and vegetable worlds. His lighthouses throw a beam that has a counterpart in the intermittent flashes of the firefly. The policeman's white gloves have their parallel in the white stripes or spots of nocturnal skunks and carabids. The Automobile Association has adopted a system of coloration whose copyright belongs by priority to wasps and salamanders.

The mantis or the Sphingid larva, which at one moment rests inconspicuously

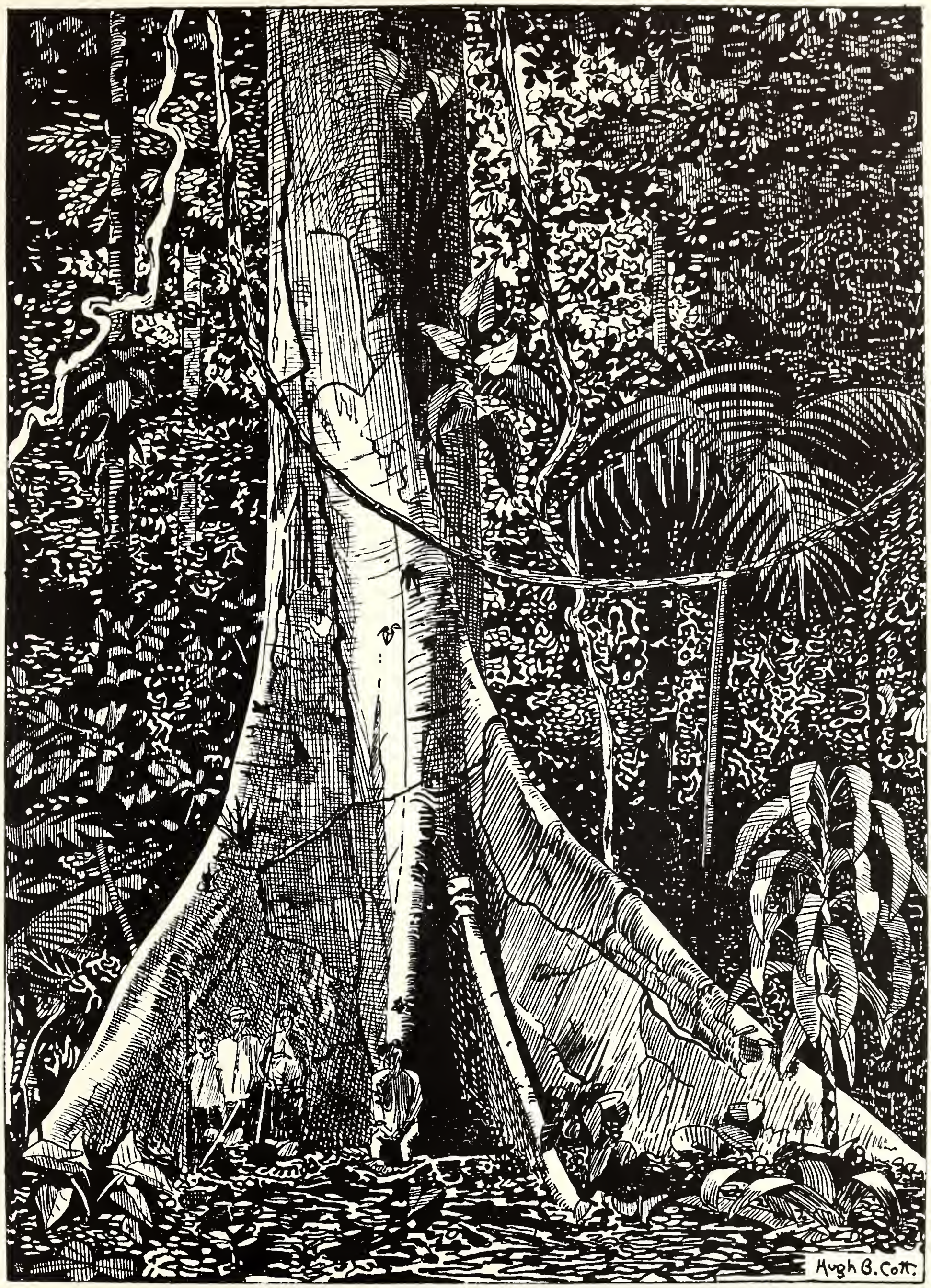

FIG. 84.—Tropical rain forest, Pará

safe among surroundings which it represents, and at another, when pressed by danger, undergoes a transformation into something rich and strange, at once glaringly conspicuous and apparently dangerous, is the natural correlative of the 'Go' and 'Stop' traffic signals. The hissing or growling or stridulating threats emitted by snakes, dogs, and crabs have their parallel in the motor-horn and air-raid siren as auditory warnings of danger. Strategic threats of force, as in the recent mobilization of the German Army, or of the British Navy, call to mind the baring of a Baboon's teeth or the lifting of a Lion's mane—symbolical gestures practised in one form or another by countless classes of wild animals.

In these days of unrest and uncertainty, it should not be necessary to stress the importance of this whole question of camouflage. In nature visual concealment and deception have proved one of the main means of obtaining those two essentials for life—security and sustenance. In everyday matters, opposite devices making for conspicuousness possess also a power—whether in the form of street signs or lip-stick—which is universally recognized: and on advertisement and cosmetics we are prepared as a nation to spend enormous sums annually. But camouflage, a product of the Great War, is still in its infancy—a child suffering from arrested development. Its importance and possibilities have yet to be fully appreciated in official quarters.

In a state of nature the unfit are eliminated speedily and ruthlessly; and a policy of 'muddling through' could not long survive. Instead, as a result of organic evolution, the wild animals have come to make full use of the relevant optical and psychical principles, and we find the most extraordinary efficiency and perfection in the deceptive devices adopted. Is it, then, too much to hope that the authorities concerned may be induced at long last to encourage scientifically the tardy growth of this infant, upon whose strength so much may one day well depend?

My reason for drawing attention here to these facts is that the analogy between natural and applied coloration appears to me to be sufficiently close to place our special subject in a somewhat new light—a light which sheds a beam of indirect evidence upon the functional side of animal coloration. An analogy must not be carried too far. The present one stops short at the point where we realize that while man-made contrivances have been invented, natural adaptations have been evolved. Nevertheless both are intimately related to the pressing needs for survival in this transitory life—whether those needs involve the capture of prey or the capture of markets; the frustration of a predatory animal or of an aggressive Power.

BIBLIOGRAPHY

1 ALCOCK, A. 1896. An Instance of the Natural Repellent Effect of 'Warning Colours'. *Journ. Asiat. Soc. Bengal,* LXV, pp. 539–40.

2 —— 1902. *A Naturalist in Indian Seas.* London, pp. xxiv + 328, 98 figs., 1 map.

3 ALLEN, G. M. 1920. An Insular Race of Cotton Rat from the Florida Keys. *Journ. Mamm.,* Baltimore, **1**, pp. 235–6.

4 ALLEN, HARRISON. 1887. On the Coloration of Mammals. *Science,* IX, p. 36.

5 ALLEN, J. A. 1874. On Geographical Variation in Color among North American Squirrels; with a List of the Species and Varieties of the American Squirridæ occurring North of Mexico. *Proc. Bost. Soc. Nat. Hist.,* XVI, pp. 276–94.

6 ANNANDALE, NELSON. 1897–1901. Notes on the Habits of Malayan Phasmidæ, and of a Flower-like Beetle Larva. *Proc. Roy. Phys. Soc. Edinburgh,* XIV, pp. 439–44.

7 —— 1900. Observations on the Habits and Natural Surroundings of Insects made during the 'Skeat Expedition' to the Malay Peninsula, 1899–1900. *Proc. Zool. Soc. London,* pp. 837–68, 2 figs.

8 —— 1905. Notes on some Oriental Geckos in the Indian Museum, Calcutta, with Descriptions of New Forms. *Ann. Mag. Nat. Hist.,* XV, (7), pp. 26–32.

9 ARROW, GILBERT J. 1927–8. Mimicry in Beetles. *Nat. Hist. Mag.* (British Museum), **1**, pp. 166–72, 3 figs.

10 ATKINSON, G. F. 1888. New Instances of Protective Resemblances in Spiders. *Amer. Nat.,* XXII, pp. 545–6.

11 BADOCK, H. D. 1917. Ant-like Spiders from Malaya, collected by the Annandale-Robinson Expedition, 1901–2. *Proc. Zool. Soc. London,* pp. 277–321, 12 figs.

12 BAKER, E. C. STUART. 1923. Cuckoos' Eggs and Evolution. *Proc. Zool. Soc. London,* pp. 277–94, 4 Pls.

13 —— 1931. The Game Birds of the Indian Empire. V. The Waders and other semi-sporting Birds. Part XV. *Journ. Bombay Nat. Hist. Soc.,* XXXV, 241–53, 1 Pl.

14 BALSS, H. 1927. Crustacea Decapoda in Kükenthal-Krumbach's Handbuch der Zoologie. 3, **1**, *Hälfte, Physiologie, Biologie,* pp. 925–77.

15 BANKS, E. 1925. Variation in the Colours of Palæarctic Birds in relation to the Conditions in which they live. *Proc. Zool. Soc. London,* pp. 311–22, 2 figs., 2 tables.

16 BANKS, NATHAN. 1892. Mimicry in Spiders. *Proc. Ent. Soc. Washington,* II, pp. 174–6.

17 —— 1908. Some Phases of Protective Resemblance in our Spiders. *Proc. Ent. Soc. Washington,* IX, pp. 2–9.

18 BANNERMAN, D. A. 1930–1951. *Birds of Tropical West Africa.* London, Vols. I–III.

19 BARBOUR, T. 1926. *Reptiles and Amphibians.* New York, pp. xvi + 125.

20 —— and LOVERIDGE, ARTHUR. 1928. A Comparative Study of the Herpetological Faunæ of the Uluguru and Usambara Mountains, with Descriptions of new Species. *Mem. Mus. Comp. Zool. Harvard College,* 1, (**2**), pp. 87–265.

21 BARRETT-HAMILTON, GERALD E. H. 1911. *A History of British Mammals.* Pts. VII, VIII, pp. 25–120.

21a BARROWS, WALTER BRADFORD. 1913. Concealing Action of the Bittern (*Botaurus lentiginosus*). *The Auk*, XXX, pp. 187–90.

22 BASEDOW, HERBERT. 1925. *The Australian Aboriginal.* Adelaide, pp. xx + 422.

23 BATES, H. W. 1862. Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidæ. *Trans. Linn. Soc., Zool.*, XXIII, pp. 495–566.

24 —— 1892. *The Naturalist on the River Amazons.* London, pp. lxxxix + 395, 1 Pl., 43 figs.

25 BATESON, W. 1889–90. Notes on the Senses and Habits of some Crustacea. *Journ. Mar. Biol. Assoc.*, I, pp. 211–14.

26 —— 1889–90. The Sense-organs and Perceptions of Fishes; with Remarks on the Supply of Bait. *Journ. Mar. Biol. Assoc.*, I, pp. 225–56, 1 Pl.

27 BAUER, VICTOR. 1910. Über das Farbensunter Scheidungsvermögen der Fische. *Arch. ges. Physiol.*, 133, pp. 7–26.

28 BEAL, F. E. L. 1907. Birds of California in Relation to the Fruit Industry. *U.S. Dept. Agric., Biol. Surv., Bull.*, **30**, pp. 1–100.

29 —— 1912. Food of our more important Flycatchers. *Ibid.*, **44**, pp. 1–67, 5 Pls.

30 —— 1915. Food of the Robins and Bluebirds of the United States. *Ibid.*, **171**, pp. 1–31.

31 —— 1915. Food Habits of the Thrushes of the United States. *Ibid.*, **280**, pp. 1–23, 2 figs.

32 —— 1918. Food Habits of the Swallows, a Family of valuable Native Birds. *Ibid.*, **619**, pp. 1–28.

33 BEDDARD, FRANK E. 1892. *Animal Coloration.* London, pp. viii + 288, 4 Pls., 36 figs.

34 BEEBE, W. 1908. Preliminary Report on an Investigation of the Seasonal Changes of Color in Birds. *Amer. Nat.*, XLII, pp. 34–56.

35 —— 1917. *Tropical Wild Life in British Guiana.* New York, pp. xx + 504.

36 —— 1925. Studies of a Tropical Jungle. *Zoologica, New York*, 1, **(6)**, pp. 1–193, 2 Pls., 17 figs.

37 —— 1928. *Beneath Tropic Seas. A Record of Diving among Coral Reefs of Haiti.* New York, pp. xiii + 234, with illustrations.

38 —— 1935. *Half Mile Down.* New York, pp. xix + 344, 8 Pls., 123 figs.

39 —— and M. B. 1910. *Our Search for a Wilderness.* New York, xix + 408, 160 figs.

40 BEHRE, ELLINOR H. 1933. Color Recognition and Color Changes in certain species of Fishes. *Copeia Ann Arbor, Mich.*, pp. 49–58.

41 BELCHER, CHARLES, and SMOOKER, G. D. 1936. Birds of the Colony of Trinidad and Tobago. Part III. *Ibis*, (13) 6, pp. 1–35.

42 BELJAJEFF, M. M. 1927. Ein Experiment über die Bedeutung der Schutzfärbung. *Biol. Zentralbl.*, **47**, pp. 107–13, 2 figs.

43 BELL, T. R. 1906. Observations on Indian Butterflies. *Ent. Month. Mag.*, **42**, pp. 121–8.

44 BELL, T. R. D., and SCOTT, F. B. 1937. The Fauna of British India. Moths V. *London.* pp. xviii + 537, 17 Pls., 14 figs.

45 BELT, T. 1874. *The Naturalist in Nicaragua.* London, pp. xvi + 403.

46 BENSON, SETH B. 1932. Three new Rodents from Lava Beds of Southern New Mexico. *Univ. Cal. Pub. Zool.*, **38**, pp. 335–44, 2 Pls.

47 —— 1933. Concealing Coloration among some Desert Rodents of the South-western United States. *Ibid.*, 40, **1**, pp. 1–70, 2 Pls., 8 figs.

48 BEQUAERT, J. 1922. The Predaceous Enemies of Ants. *Bull. Amer. Mus. Nat. Hist.*, XLV, pp. 271–331, 3 Pls.

49 —— 1930. Are Ants better protected against the Attacks of their Predeaceous Enemies than other Arthropods? *Zoologischer Anzeiger*, 88, **7/8**, pp. 163–76.

50 BERG, LEO S. 1926. *Nomogenesis or Evolution determined by Law.* London, xviii + 477, 33 figs.

51 BIERENS DE HAAN, J. A. 1925. Experiments on Vision in Monkeys. 1. The Colour-Sense of the Pig-tailed Macaque. *Journ. Comp. Psychol.*, 5, pp. 417–53.

52 —— 1926. Versuche über den Farbensinn und das Psychische Leben von *Octopus vulgaris*. *Zeits. f. vergl. Physiol.*, **4**, pp. 766–96, 2 figs.

53 —— und FRIMA, MARGARETA. 1930. Versuche über den Farbensinn der Lemuren. *Zeits. f. vergl. Physiol.*, **12**, pp. 603–31, 8 figs.

54 BINGHAM, HAROLD C. 1913. Size and Form Perception in *Gallus domesticus*. *Journ. Anim. Behav.*, III, pp. 65–113, 4 figs.

55 BLAKISTON, T., and ALEXANDER, T. 1884. Protection by Mimicry—A problem in Mathematical Zoology. *Nature*, **29**, pp. 405–6.

56 BLÄSSER, A. 1927. Die partielle relative Farbenblindheit der Hühner. *Zool. Jahrb. Ab. Alg. Zool.*, XLIII, pp. 69–120.

57 BORRADAILE, L. A. 1923. *The Animal and its Environment.* London, pp. vii + 399, 4 Pls., 426 figs.

58 BOULENGER, G. A. 1911. On a new Tree-Frog from Trinidad, living in the Society's Gardens. *Proc. Zool. Soc. London*, pp. 1082–3, 1 Pl.

59 BOZLER, EMIL. 1928. Ueber die Tätigkeit der einzelnen glatten Muskelfaser bei der Kontraktion. II. Mitteilung : Die Chromatophorenmuskeln der Cephalopoden. *Zeits. f. vergl. Physiol.*, **7**, 379–406, 7 figs.

60 BRIDGES, ELIZABETH. 1911. Experiments in 1909 and 1910 upon the Colour Relation between Lepidopterous Larvæ and Pupæ and their Surroundings. *Trans. Ent. Soc. London*, pp. 136–47.

61 BRISTOWE, W. S. 1924. Notes on the Habits of Insects and Spiders in Brazil. *Trans. Ent. Soc. London*, pp. 475–504.

62 BRONGERSMA, L. D. 1937. Herpetological Notes. XVI. On a small Collection of Amphibia from Central East Borneo. *Zoologische Mededeelingen*, XX, pp. 6–10, 1 Pl.

63 BRUNNER, A. FRASER-. 1933. A Revision of the Chætodont Fishes of the Subfamily Pomacanthinæ. *Proc. Zool. Soc. London*, pp. 543–99, 1 Pl., 29 figs.

64 BRUNNER VON WATTENWYL, C. 1897. *Betrachtungen über die Farbenpracht der Insekten.* Vienna, pp. 16, 9 Pls.

65 BRYANT, HAROLD C. 1911. The Horned Lizards of California and Nevada of the Genera *Phrynosoma* and *Anota*. *Univ. Cal. Pub. Zool.*, **9**, 1, pp. 1–84, 9 Pls., 6 figs.

66 BUDDENBROCK, W. VON. 1928. *Grundriss der vergleichenden Physiologie.* Berlin, pp. viii + 830, 3 Pls., 254 figs.

67 BUDGETT, J. S. 1899. Notes on the Batrachians of the Paraguayan Chaco, with Observations upon their Breeding Habits and Development, especially with regard to *Phyllomedusa hypochondrialis* Cope. *Quart. Journ. Micr. Sci.*, XLII, pp. 305–33, 5 Pls.

68 BULL, HERBERT O. 1935. Studies on Conditioned Responses in Fishes. Part III. Wave-length Discrimination in *Blennius pholis L. Journ. Mar. Biol. Ass.*, XX (n.s.), pp. 347–64.

69 BURGER, OTTO. 1903. Ueber das Zusammenleben von *Antholoba reticulata* Couth. und *Hepatus chilensis* M.E. *Biol. Zentralbl.*, XXIII, pp. 678–9.

70 BURT, W. H. 1932. McAtee on the effectiveness in Nature of the so-called Protective Adaptations in the Animal Kingdom, chiefly as illustrated by the Food Habits of Nearctic Birds. *Condor*, **34**, pp. 196–8.

71 BURTT, ERIC. 1938. Irritant Exudation from a Millipede. *Nature*, **142**, p. 796.

72 BUTLER, A. G. 1868. The Larva of *Abraxas grossulariata* distasteful to Frogs. *Ent. Month. Mag.*, V, pp. 131–2.

73 —— 1869. Remarks upon certain Caterpillars, etc., which are unpalatable to their Enemies. *Trans. Ent. Soc. London*, pp. 27–9.

74 BUTTEL-REEPEN, H. V. 1915. Haben die Bienen einen Farben- und Formensinn? *Die Naturwisschenschaften Berlin*, **3**, pp. 80–2.

75 —— 1916. Sind die Bienen wirklich Farbenblind? *Ibid.*, **4**, pp. 289–91.

76 BUXTON, P. A. 1923. *Animal Life in Deserts.* London, pp. xv + 176, 43 figs.

77 CAMBRIDGE, F. PICKARD. 1902. On the Spiders of the Genus *Latrodectus*, Walckenaer. *Proc. Zool. Soc. London*, pp. 247–61, 2 Pls.

78 CAMPBELL, GORDON. 1929. *My Mystery Ships.* London, pp. xx + 300, 9 Pls., 20 figs.

79 CARPENTER, G. D. HALE. 1921. Experiments on the Relative Edibility of Insects, with special reference to their Coloration. *Trans. Ent. Soc. London*, pp. 1–105.

80 —— 1929. Mimicry. *Nature*, **123**, pp. 661–3.

81 —— 1935. Attacks of Birds upon Butterflies. *Nature*, **135**, p. 194.

82 —— 1935. Mimikry. *Entomologischen Rundschau*, **2**, pp. 20–4; **3**, pp. 37–9; **4/5**, pp. 50–3.

83 —— 1937. Further Evidence that Birds do attack Butterflies. *Proc. Zool. Soc. London*, A, **3**, pp. 223–47, 2 Pls.

84 —— 1937. Mimicry, as viewed by Professor Shull. *Science*, **85**, 2206, pp. 356–9.

85 —— 1937. Lizards as Enemies of Butterflies. *Proc. Roy. Ent. Soc. London*, **12**, pp. 157–61, 2 Pls.

✓ 86 —— 1938. Audible Emission of Defensive Froth by Insects. With an Appendix on the Anatomical Structures concerned in a Moth by H. Eltringham. *Proc. Zool. Soc. London*, A, **108**, pp. 243–52, 1 Pl.

87 —— and FORD, E. B. 1933. *Mimicry.* London, pp. viii + 134.

88 CARRICK, ROBERT. 1936. Experiments to test the Efficiency of Protective Adaptations in Insects. *Trans. Roy. Ent. Soc. London*, **85**, pp. 131–9, 3 Pls.

89 CARTER, G. S. 1928. A Naturalist's Journey in South America. *Proc. Roy. Phil. Soc. Glasgow*, LVI, pp. 82–107, map.

89*a* —— 1929. Mimicry. *Nature*, **123** p. 713.

90 CAVE, W. A. 1908. Note on *Kallima philarchus*. *Spolia Zeylanica*, V, p. 142.

91 CESNOLA, A. P. DI. 1904. Preliminary Note on the Protective Value of Colour in *Mantis religiosa*. *Biometrika*, **3**, pp. 58–9, 2 figs.

92 CHAPMAN, ABEL. 1921. *Savage Sudan: its Wild Tribes, Big Game, and Bird Life.* London, xx + 452.

93 CHAPMAN, R. N. 1931. *Animal Ecology with special reference to Insects.* New York, pp. x + 464, 16 figs.

94 CHEESMAN, R. E. 1926. *In Unknown Arabia.* London, pp. xx + 447, 32 Pls., 3 maps.

95 CHOPARD, LUCIEN. 1938. La Biologie des Orthoptères. *Encyclopédie Entomologique*, A, XX, pp. 1–541, 4 Pls., 453 figs.

96 CLARKE, AUSTIN H. 1937. Secondary Binocular Vision in Birds. *Science, N.Y.*, LXXXVI, pp. 223–4.

97 CLARKE, G. L. 1936. Light Penetration in the Western North Atlantic and its Application to Biological Problems. *Rapp. Cons. Explor. Mer.. Copenh.*, **101/2/3**, pp. 3–14, 6 figs.

98 —— 1936. On the Depth at which Fish can see. *Ecology, Brooklyn*, **17**, pp. 452–6.

99 COATES, C. W. 1933. Behavior of a Pair of Leaf-fish, *Monocirrhus polyacanthus* Heckel. *Bull. N.Y. Zool. Soc.*, XXXVI, pp. 68–71, 3 figs.

100 COCKAYNE, E. A. 1911. Notes on Insect Enemies in the Tropics and their Influence on Mimicry. *Trans. Ent. Soc. London*, pp. 168–72.

101 COCKERELL, T. D. A. 1936. Evolution. *Science*, **84**, pp. 203–6.

102 COLE, LEON J. 1907. An Experimental Study of the Image-forming Powers of Various Types of Eyes. *Proc. Amer. Acad. Arts Sci. Boston*, XLII, pp. 333–417, 14 figs.

103 COLE, L. W. 1907. Concerning the Intelligence of Raccoons. *Journ. Comp. Neurol.*, 17, pp. 211–61.

104 COLLENETTE, C. L. 1935. Notes concerning Attacks by British Birds on Butterflies. *Proc. Zool. Soc. London*, pp. 201–17, 1 Pl.

105 COLLINGE, W. E. 1913. *The Food of some British Wild Birds : a Study in Economic Ornithology*. London, pp. viii + 109.

106 CORNES, J. J. S. 1937. Attitude and Concealing Coloration. *Nature*, **140**, p. 684, 1 fig.

107 COTT, HUGH B. 1926. Observations on the Life-Habits of some Batrachians and Reptiles from the Lower Amazon : and a Note on some Mammals from Marajó Island. *Proc. Zool. Soc. London*, pp. 1159–78, 6 Pls., text fig., and map.

108 —— 1929. Observations on the Natural History of the Land-Crab *Sesarma meinerti*, from Beira, with special reference to the Theory of Warning Colours. *Ibid.*, pp. 679–92, 1 Pl., 4 figs.

109 —— 1929. Observations on the Natural History of the Racing-Crab *Ocypoda ceratophthalma*, from Beira. *Ibid.*, pp. 755–65, 1 Pl., 1 fig.

110 —— 1932. Protective Adaptations of Animals. *Nature*, **130**, pp. 962–3.

111 —— 1932. On the Ecology of Tree-Frogs in the Lower Zambesi Valley, with special reference to Predatory Habits considered in relation to the Theory of Warning Colours and Mimicry. *Proc. Zool. Soc. London*, pp. 471–541, 2 Pls., 7 figs.

112 —— 1934. On the Ecology of *Hyla arborea* var. *meridionalis* in Gran Canaria, with special reference to Predatory Habits considered in relation to the Protective Adaptation of Insects. *Ibid.*, pp. 311–31.

113 —— 1935. Warning Colours and Mimicry : a Reply to Dr. McAtee. *Proc. Royal Ent. Soc. London*, pp. 109–19, 4 Pls.

114 —— 1935. The Nature and Function of Disruptive Coloration in Animals. *Rept. Brit. Assn. Adv. Sci.*, pp. 384–5.

115 —— 1936. Concealing Coloration in Nature. *Geog. Mag.*, London, III, **2**, pp. 73–88, 16 figs.

116 —— 1936. The Effectiveness of Protective Adaptations in the Hive-bee, illustrated by Experiments on the Feeding Reactions, Habit Formation, and Memory of the Common Toad (*Bufo bufo bufo*). *Proc. Zool. Soc. London*, pp. 111–33, 6 figs.

117 —— 1938. Adaptive Appearance and Interspecific Relationships. *Rept. Brit. Assn. Adv. Sci.*, pp. 440–1.

118 —— 1938. Camouflage in Nature and in War. *Royal Engineers Journal*, December, pp. 501–17, 16 figs.

119 COUES, ELLIOT. 1874. *Birds of the Northwest : a Handbook of the Ornithology of the Region drained by the Missouri River and its Tributaries.* Washington, pp. xi + 791.

120 COWDRY, E. V. 1911. The Colour Changes of *Octopus vulgaris*, Lmk. *Univ. Toronto Stud., Biol. Ser.* 10, pp. 1–53, 4 Pls.

121 CROSSLAND, CYRIL. 1911. Warning Coloration in a Nudibranch Mollusc and in a Chamæleon. *Proc. Zool. Soc. London*, pp. 1062–7.

122 CROZIER, W. J. 1916. On the Immunity Coloration of some Nudibranchs. *Proc. Nat. Acad. Sci., Washington*, II, pp. 672–5.

123 CUÉNOT, L. 1898. Les moyens de défense chez les animaux. *Bull. Soc. Zool. France*, XXIII, pp. 37–58.

124 —— 1921. *La Génèse des Espèces animales.* Paris, vii + 558.

125 —— 1925. *L'Adaptation.* Paris, pp. ix + 420, 82 figs.

126 —— 1927. Recherches sur la Valeur Protectrice de l'Homochromie chez quelques Animaux aquatiques. *Ann. de Sci. nat. Zoo.*, X, pp. 123–50.

127 CUNNINGHAM, D. D. 1903. *Some Indian Friends and Acquaintances.* London, pp. 284–5.

128 CUNNINGHAM, J. T. 1891. An Experiment concerning the Absence of Colour from on the Lower Sides of Flat-fishes. *Journ. Mar. Biol. Assoc.*, IV (n.s.),

129 —— 1897. Additional Evidence on the Influence of Light in producing Pigments on the Lower Sides of Flat-fishes. *Journ. Mar. Biol. Assoc. U.K.*, IV (n.s.), pp. 53–9, 3 figs.

130 DAHL, F. 1903. Ueber Täuschende Aehnlichkeit zwischen einer deutschen Springspinne (*Ballus depressus*), und einem am gleichen Orte vorkommenden Rüsselkäfer (*Strophosomus capitatus*). *SB. Ges. naturf. Berlin*, pp. 273–8.

131 —— 1905. Anpassungsfarben bei Krabbenspinnen. *Naturw. Wochenschr.*, IV (n.s.), pp. 597–9.

132 —— 1907. Versuche über den Farbensinn bei einer Meerkatze. *Zool. Jahrb., Jena, Abt. f. Syst.*, **25**, pp. 329–38.

133 DAKIN, W. J. 1921. Some Visual Organs and their Bearing upon Evolutionary Biology (An Inaugural Lecture). Liverpool, University Press, pp. 3–20.

134 DARLINGTON, P. J. 1938. Experiments on Mimicry in Cuba, with Suggestions for Future Study. *Trans. Roy. Ent. Soc. London*, **87**, pp. 681–95, 1 Pl.

135 DARWIN, CHARLES. 1890. *Journal of Researches into the Natural History and Geology of the Countries visited during the Voyage of H.M.S. 'Beagle' round the World.* London, pp. 615.

136 —— 1890. *The Descent of Man.* London, pp. xiv + 693, 78 figs.

137 DAVENPORT, C. 1908. Elimination of self-coloured Birds. *Nature*, **78**, p. 101.

138 DEAN, BASHFORD. 1908. Accidental Resemblances among Animals. A Chapter in Un-natural History. *Pop. Sci. Monthly*, LXXII, pp. 304–12, 10 figs.

139 DE VOSS, J. C., and GANSON, ROSE. 1915. Color Blindness in Cats. *Journ. Anim. Behav.*, **5**, pp. 115–39.

140 DEWAR, D., and FINN, F. 1909. *The Making of a Species.* London, pp. xix + 400.

141 DICE, LEE R. 1930. Mammal Distribution in the Alamogordo Region, New Mexico. *Occ. Pap., Mus. Zool. Univ. Michigan*, **213**, pp. 1–32, 3 Pls.

141a —— and BLOSSOM, PHILIP M. 1937. Studies of Mammalian Ecology in southwestern North America with special Attention to the Colors of Desert Mammals. *Carnegie Inst. Wash. Pub.*, No. 485, pp. iv + 129, 8 Pls., 8 figs.

142 Discussion, 1932 (1933). Protective Adaptations of Animals—especially Insects. *Proc. Ent. Soc. London*, VII, pp. 79–105 : also, 1934. Replies to Dr. W. L. McAtee's Rejoinder in *Proc. Roy. Ent. Soc. London*, VIII, pp. 113–26, to Papers on Protective Adaptations published by the Society (*loc. cit.*, VII : pp. 79–105).

143 DITMARS, R. L. 1907. *The Reptile Book.* London, xxxii + 472, 136 figs.

144 —— 1912. The Feeding Habits of Serpents. *Zoologica*, New York, I, pp. 197–238.

145 —— 1931. *Snakes of the World.* New York, pp. xi + 207, 84 Pls.

146 —— 1933. *Reptiles of the World.* London, pp. xx + 321, 89 Pls.

147 DIXEY, F. A. 1896. On the Relation of Mimetic Patterns to the Original Form. *Trans. Ent. Soc. London*, pp. 65–79, 3 Pls.

148 —— 1902. Notes on some Cases of Seasonal Dimorphism in Butterflies, with an Account of Experiments by Mr. Guy A. K. Marshall, F.Z.S. *Proc. Ent. Soc. London*, pp. xv–xviii.

149 —— 1919. The Geographical Factor in Mimicry. Presidential Address, Sect. D, *Rept. Brit. Assn. Adv. Sci.*, pp. 199–207, 1 Pl.

150 —— and LONGSTAFF, G. B. 1907. Entomological Observations and Captures during the Visit of the British Association to South Africa in 1905. *Trans. Ent. Soc. London*, pp. 309–81, 1 Pl.

151 DIXON, G. Y., and A. F. 1891. Report on the Marine Invertebrate Fauna near Dublin. *Proc. Roy. Irish Acad.*, Ser. 3, II, pp. 19–33.

152 DOFLEIN, F. 1908. Über Schutzanpassung durch Ähnlichkeit. *Biol. Centralbl.*, XXVIII, pp. 243–54.

153 DONALDSON, THOMAS. 1887. *The George Catlin Indian Gallery in the U.S. National Museum.* Washington, pp. vii + 939.

154 DONCASTER, L. 1906. Collective Inquiry as to progressive Melanism in Lepidoptera. *Ent. Rec. London*, **18**, pp. 165–254.

155 DRAKE, C. J. 1914. The Food of *Rana pipiens* Schreber. *Ohio Nat.*, XIV, (5), pp. 257–69.

156 DRUCE, HAMILTON H. 1902. On some new and little-known Butterflies of the Family Lycænidæ from the African, Australian and Oriental Regions. *Proc. Zool. Soc. London*, pp. 112–21.

157 DUNN, EMMETT R. 1935. The Survival Value of Specific Characters. *Copeia, Ann Arbor, Mich.*, pp. 85–98.

158 EIGENMANN, C. H., and ALLEN, W. R. 1921. A Leaf-mimicking Fish. *Biol. Bull. Wood's Hole Mass.*, **41**, pp. 301–5.

159 EIMER, T. 1881. Ueber neue und über schon bekannte auf Felsen isolirt lebende Varietäten. Besondere Beweise für höchste Farbenanpassung der Mauereidechsen. *Arch. Naturgesch.*, pp. 239–517, 3 Pls.

160 ELTON, CHARLES. 1927. *Animal Ecology.* London, pp. xxi + 207, 8 Pls., 13 figs.

161 ELTRINGHAM, H. 1909. An Account of some Experiments on the Edibility of certain Lepidopterous Larvæ. *Trans. Ent. Soc. London*, pp. 471–8.

162 —— 1910. *African Mimetic Butterflies.* Oxford, pp. 136, 10 Pls., 1 map.

163 —— 1916. On Specific and Mimetic Relationships in the Genus *Heliconius* L. *Trans. Ent. Soc. London*, pp. 101–48, 7 Pls.

164 —— 1919. Butterfly Vision. *Ibid.*, pp. 1–49, 5 Pls.

165 —— 1933. *The Senses of Insects.* London, pp. x + 120, 25 figs.

166 ENTZ, G. 1907. Die Farben der Tiere und die Mimikry. *Math. Nat. Ber. Ungarn*, **24**, pp. 171–201.

167 EVANS, A. H. 1909. Birds. *Cambridge Natural History*, IX, pp. xvi + 635, 144 figs.

168 EXNER, S. 1891. *Die Physiologie der facettierten Augen von Krebsen und Insekten.* Leipzig, viii + 206, 7 Pls., 23 figs.

169 FARREN, WILLIAM. 1908. The Crouching Habit of the Stone Curlew. *Brit. Birds*, I, pp. 301–8.

170 FAURE, J. C. 1932. The Phases of Locusts in South Africa. *Bull. Ent. Res. London*, **23**, pp. 293–405, 25 Pls., 1 map.

171 FINN, FRANK. Contributions to the Theory of Warning Colours and Mimicry.
No. I. Experiments with a Babbler (*Crateropus canorus*). 1895. *Journ. Asiat. Soc. Bengal*, LXIV, pp. 344–56.
No. II. Experiments with a Lizard (*Calotes versicolor*). 1896. *Ibid.*, LXV, pp. 42–8.
No. III. Experiments with a Tupaia and a Frog. 1897. *Ibid.*, LXVI, pp. 528–33.

172 —— 1902. Notes on the Painted Snipe (*Rostratula capensis*) and Pheasant-tailed Jacaná (*Hydrophasianus chirurgus*). *Proc. Zool. Soc. London*, pp. 261–4.

172a FISHER, R. A. 1927. On some Objections to Mimicry Theory; Statistical and Genetic. *Trans. Ent. Soc. London*, LXXV, pp. 269–78.

173 —— 1930. *The Genetical Theory of Natural Selection.* Oxford, pp. xiv + 272, 2 Pls., 11 figs.

174 FLATTELY, F. W., and WALTON, C. L. 1922. *The Biology of the Sea-shore.* London, xvi + 336, 16 Pls., 23 figs.

175 FLETCHER, B. M. 1909. Cases of Mimicry from Ceylon. *Proc. Ent. Soc. London*, pp. xxvi–viii.

176 FLETCHER, T. BAINBRIGGE. 1936. Stridulation in Insects. *Proc. Roy. Ent. Soc. London*, **11**, p. 68.

177 FLOWER, S. S. 1933. Notes on the recent Reptiles and Amphibians of Egypt, with a List of the Species recorded from that Kingdom. *Proc. Zool. Soc. London*, pp. 735–851, 1 fig. and map.

178 FOLSOM, J. W. 1923. *Entomology, with special reference to its Ecological Aspects.* London, pp. vii + 502, 5 Pls., 308 figs.

179 FORBES, HENRY O. 1883. On the Habits of *Thomisus decipiens*, a Spider from Sumatra. *Proc. Zool. Soc. London*, pp. 586–8, 1 Pl.

180 —— 1885. *A Naturalist's Wanderings in the Eastern Archipelago.* London, pp. xix + 536.

181 FORBES, S. A. 1878. The Food of Illinois Fishes. *Bull. Ill. St. Lab. Nat. Hist.*, **2**, pp. 71–86.

181*a* FORD, E. B. 1937. Problems of Heredity in the Lepidoptera. *Biol. Rev.*, Cambridge, XII, pp. 461–503.

181*b* —— 1938. The Genetic Basis of Adaptation. In *Evolution*, edited by G. R. de Beer, Oxford, pp. 43–55.

182 FOREL, A. 1908. *The Senses of Insects.* (Trans. Yearsley.) London, pp. xiv + 324, 2 Pls.

183 —— 1928. *The Social World of the Ants.* (Trans. Ogden.) London, Vol. II, Ch. V, pp. 287–92.

184 FOWLER, W. W. 1918. A combined Instance of Protective Resemblance and Mimicry in a Locust Larva. *Ent. Month. Mag.*, LIV, (iii–iv), p. 92.

185 FRANZ, VICTOR. 1910. Die japanischen Knochen fische der Sammlungen Haberer und Doflein. *München Abh. Ak. Wiss. Math.-phys. Kl.*, Supp. 1, Bd. 4, pp. 135, 11 Pls.

186 FRISCH, K. VON. 1912. Sind die Fische farben blind? *Zool. Jahrb. Jena Abt. f. allg. Zool.*, **33**, pp. 107–26.

187 —— 1913. Weitere Untersuchungen über den Farbensinn der Fische. *Ibid.*, **34**, pp. 43–68.

188 —— 1915. Der Farbensinn und Formensinn der Bienen. *Zool. Jahrb. Abt. Zool. Physiol.*, XXXV, pp. 1–182, 5 Pls., 13 figs.

189 —— 1923. Das Problem des tierischen Farbensinnes. *Naturwissenschaften*, Berlin, **11**, pp. 470–6.

190 —— 1925. Farbensinn der Fische und Duplizitätstheorie. *Zeits. f. vergl. Physiol.*, **2**, pp. 393–452, 2 Pls., 31 figs.

191 GABRITSCHEVSKY, E. 1927. Experiments on Color Changes and Regeneration in the Crab-spider, *Misumena vatia. Journ. Exp. Zool.*, **47**, pp. 251–67.

192 GADOW, H. 1902. Colour in Amphibia. *P.R. Inst. Brit.*, XVI, pp. 587–94.

193 —— 1903. Evolution of the Colour-pattern and orthogenetic Variation in certain Mexican Species of Lizards, with Adaptation to their Surroundings. *Proc. Roy. Soc. London*, **72**, pp. 109–25, 3 Pls., 7 figs.

194 —— 1911. Isotely and Coral Snakes. *Zool. Jahrb. Jena Abt. f. Syst.*, **31**, pp. 1–24, 1 Pl., 18 figs.

195 —— 1923. Amphibia and Reptiles. *Cambridge Natural History*, VII, pp. xiv + 668, 181 figs.

196 GAHAN, C. J. 1912. Exhibition of *Phromnia superba* Melich . . . taken by Dr. A. C. Parsons in Northern Nigeria. *Proc. Ent. Soc. London*, pp. lxxxviii–xc.

197 —— 1913. Mimicry in Coleoptera. *Proc. S. London Ent. Nat. Hist. Soc.*, 1912–14, pp. 28–38, 3 Pls.

198 GAMBLE, F. W. 1910. The Relation between Light and Pigment-Formation in *Crenilabrus* and *Hippolyte. Quart. Journ. Micr. Sci.*, **55**, pp. 541–84, 1 Pl.

199 —— and KEEBLE, F. W. 1900. *Hippolyte varians*: a Study in Colour-Change. *Ibid.*, **43**, pp. 589–698, 5 Pls.

200 GARMAN, H. 1901. The Food of the Toad. *Kentucky Agric. Exp. Sta., Bull.*, **91**, p. 66.

201 GARSTANG, WALTER. 1889–90. Report on the Nudibranchiate Mollusca of Plymouth Sound. *Journ. Mar. Biol. Assoc.*, I (n.s.), pp. 173–98.

202 GARSTANG, WALTER. 1889–90. A Complete List of the Opisthobranchiate Mollusca found at Plymouth ; with further Observations on their Morphology, Colours, and Natural History. *Ibid.*, pp. 399–457, 2 Pls.

203 —— 1890. Foreign Substances attached to Crabs. *Nature*, **41**, pp. 417, 490, 538.

204 GEROULD, JOHN H. 1916. Mimicry in Butterflies. *Amer. Nat.*, **50**, pp. 184–92.

205 —— 1921. Blue-green Caterpillars ; the Origin and Ecology of a Mutation in Hemolymph Color in *Colias* (*Eurymus*) *philodice*. *Journ. Exp. Zool.*, **34**, pp. 385–416,, 1 Pl., 1 fig.

206 GIARD, ALFRED. 1888. Le Laboratoire de Wimereux en 1888 : Recherches Fauniques. *Bull. Sci. de la France et de la Belgique*, Ser. III, ix–xii, pp. 499–503.

207 GIERSBERG, H. 1928. Über den Morphologischen und Physiologischen Farbwechsel der Stabheuschrscke *Dixippus*. *Zeits. f. vergl. Physiol.*, **7**, pp. 657–95, 10 figs.

208 GODDARD, T. RUSSELL. 1935. A Census of Short-eared Owls (*Asio f. flammeus*) at Newcastleton, Roxburghshire, 1934. *Journ. Anim. Ecol.*, 4, pp. 113–18.

209 GOELDI, EMIL A. 1896. On the Nesting of *Nyctibius jamaicensis* and *Sclerurus umbretta*. *Ibis*, Ser. 7, VII, pp. 299–309, 4 figs.

210 GOLDMAN, EDWARD A. 1910. Revision of the Wood Rats of the Genus *Neotoma*. *U.S. Dept. Agric., Bur. Biol. Surv., N. Amer. Fauna*, **31**, p. 124, 8 Pls., 14 figs.

211 GOSSE, P. H. 1859. On the Transfer of *Adamsia palliata* from Shell to Shell (and) Additional Notes on the above. *Zoologist*, 7, pp. 6580–4.

212 GOULD, L. J. 1892. Experiments in 1890 and 1891 on the Colour-relation between certain Lepidopterous Larvæ and their Surroundings, together with some other Observations on Lepidopterous Larvæ. *Trans. Ent. Soc. London*, pp. 215–46, 1 Pl.

213 GRAHAM, R. R. 1934. The Silent Flight of Owls. *Journ. Roy. Aero. Soc.*, **38**, pp. 837–43, 6 figs.

214 GREEN, E. E. 1904. Notes on some Ceylon Butterflies. *Spolia Zeylanica*, II, p. 76.

215 —— 1908. Mimicry in Insect Life, as exemplified by Ceylon Insects. *Ibid.*, V, pp. 87–94, 5 Pls.

216 —— 1912. On a Remarkable Mimetic Spider. *Ibid.*, VIII, pp. 92–3, 1 Pl.

217 GREGORY, J. W. 1896. *The Great Rift Valley*. London, pp. xxi + 422, 20 Pls., 23 figs., 2 maps.

218 GUDGER, E. W. 1928. Association between Sessile Colonial Hydroids and Fishes. *Ann. Mag. Nat. Hist.*, Ser. 10, Vol. 1, pp. 17–48, 2 Pls., 8 figs.

219 GURNEY, ROBERT. 1936. Notes on some Decapod Crustacea of Bermuda and their Larvæ. *Proc. Zool. Soc. London*, pp. 25–32, 5 Pls.

220 HAASE, E. 1893. Untersuchungen über die Mimicry auf Grundlage eines natürlichne Systems der Papilioniden. *Bibl. Zool.*, **8**, pp. 99–161.

221 HABER, V. R. 1926. The Food of the Carolina Tree Frog, *Hyla cinerea* Schneider. *Journ. Comp. Psychol.*, VI, pp. 189–220.

222 HADLEY, C. E. 1929. Color Changes in two Cuban Lizards. *Bull. Mus. Comp. Zool. Harvard*, LXIX, pp. 107–13.

223 HADWEN, S. 1929. Fly Attack and Animal Coloration. *Trans. 4th Int. Congr. Ent. Ithica* (1928), **2**, pp. 199–202, 2 figs.

224 HAGEN, H. A. 1882. On the Color and Pattern of Insects. *Proc. Amer. Acad. Arts Sc.*, XVII, pp. 234–67.

225 HAHN, ERNA. 1916. Über den Farbensinn der Tagvögel und die Zapfenölkugeln. *Zeitschr. wiss. Zool.*, CXVI, pp. 1–42, 7 figs.

226 HAMILTON, W. F., and COLEMAN, T. B. 1933. Trichromatic Vision in the Pigeon as illustrated by the Spectral Hue Discrimination Curve. *Journ. Comp. Psychol.*, XV, pp. 183–91, 3 figs.

227 HAMM, A. H. 1906. A Permanent Record of British Moths in their Natural Attitudes of Rest. *Trans. Ent. Soc. London*, pp. 483–5, 1 Pl.

228 HARGITT, C. W. 1912. Behavior and Color Changes of Tree Frogs. *Journ. Anim. Behav.*, 2, pp. 51–78.

229 HARPER, FRANCIS. 1932. A Voice from the Pines. *Journ. Amer. Mus. Nat. Hist.*, XXXII, **3**, pp. 280–8, 11 figs.

230 HARRISON, J. W. HESLOP. 1920. Genetical Studies in the Moths of the Geometrid Genus *Oporabia* (*Oporinia*) with a special Consideration of Melanism in the Lepidoptera. *Journ. Genetics*, IX, **3**, pp. 195–280, 13 figs.

231 HARVEY, E. NEWTON. 1919. The Nature of Animal Light. *Mon. Exp. Biol. Philadelphia*, pp. x + 182.

232 HAVILAND, MAUD D. 1926. *Forest, Steppe and Tundra.* Cambridge, pp. xii + 218, 8 Pls.

233 HEIKERTINGER, FRANZ. 1919. Die metöke Myrmekoidie. *Bio. Zentralbl. Leipzig*, XXXIX, pp. 65–102.

234 —— 1929. Ueber das Mimikryproblem und seine Schwesterprobleme. *Trans. 4th Int. Congr. Ent. Ithaca* (1928), **2**, pp. 821–31.

235 —— 1933. Kritisches zum Mimikryproblem: über Schmetterlingsmimikry. *5e Congr. int. Ent. Paris*, **2**, pp. 119–30, 3 Pls.

236 HENKE, K. 1931. Der Gesichtssinn der Wolfsspinnen. *Naturwissenschaften*, **19**, pp. 828–9.

237 HENNING, H. 1920. Optische Versuche an Vögeln und Schildkröten über die Bedentung der roten Olkugeln im Auge. *Arch. ges. Physiol.*, **178**, pp. 91–123.

238 HERDMAN, W. A. 1889. On the Structure and Function of the Dorsal Papillæ in Nudibranchiata. *Rept. Brit. Assn. Adv. Sci.*, pp. 630–3.

239 —— 1889. On the Electric Light as a means of attracting Marine Animals. *Ibid.*, pp. 633–5.

240 HERRE, A. W. C. T. 1936. Some Habits of *Amphiprion* in relation to Sea Anemones. *Copeia, Ann Arbor, Mich.*, pp. 167–8.

241 HERTER, K. 1929. Weitere Dressurversuche an Fischen. *Zeits. f. vergl. Physiol.*, **11**, pp. 730–48, 16 figs.

242 HERTZ, MATHILDE. 1928. Wahrnehmungspsychologische Untersuchungen am Eichelhäher. II. *Ibid.*, **7**, pp. 617–56, 38 figs.

243 —— 1931. Die Organisation des optischen Feldes bei der Biene. III. *Ibid.*, **14**, pp. 629–74, 27 figs.

244 —— 1934. Zur Physiologie des Formen- und Bewegunssehens. III. Figurale Unterscheidung und reziproke Dressuren bei der Biene. *Ibid.*, **21**, pp. 604–15, 2 figs.

245 —— 1937. Versuche über das Farbensystem der Bienen. *Naturwissenschaften*, Berlin, pp. 492–3.

246 —— 1937. Beitrag zum Farbensinn und Formensinn der Bienen. *Zeits. f. vergl. Physiol.*, **24**, pp. 413–21, 1 fig.

247 —— 1939. New Experiments on Colour Vision in Bees. *Journ. Exp. Biol.*, pp. 1–8, 2 figs.

248 —— and IMMS, A. D. 1937. On the Responses of the African Migratory Locust to different Types of Background. *Proc. Roy. Soc. London*, B, CXXII, **828**, pp. 281–97, 3 figs.

249 HESS, C. VON. 1911. Experimentelle Untersuchungen zur vergleichenden Physiologie des Gesichtssinnes. Untersuchung des Farbensinnes der Vögel nach dem Prinzip der Seebeck-Holmgren'schen Probe. *Arch. ges. Physiol.*, **142**, pp. 405–46.

250 —— 1912. Untersuchungen zur Frage nach dem Vorkommen von Farbensinn bei Fischen. *Zool. Jahrb., Jena Abt. f. allg. Zool.*, **31**, pp. 629–46.

251 —— 1912. Vergleichende Physiologie des Gesichtssinnes. *Jena*, Fischer, pp. vi + 299, 3 Pls.

252 HESS, C. VON. 1917. Der Farbensinn der Vögel und die Lehre von den Schmuckfarben. *Arch. ges. Physiol.*, **166**, pp. 381–426, 3 figs.

253 —— 1922. Farbenlehre. *Ergebnisse Physiologie*, **20**, pp. 1–107.

254 HEWER, H. R. 1926. Studies in Colour Changes in Fish. Parts II–IV. *Phil. Trans. Roy. Soc. London*, Ser. B, **215**, pp. 177–200.

255 —— 1931. Studies in Colour-changes in Fish.—Part V. The Colour-patterns in certain Flat-fish and their Relation to the Environment. *Journ. Linn. Soc., Zool.*, XXXVII, pp. 493–513.

256 HICKSON, S. J. 1891. Animal Life on a Coral Reef. *Nature*, **44**, pp. 90–1.

257 —— 1910. Colour in Animals. *Ann. Rep. and Trans. Manchester Micr. Soc.*, pp. 36–48.

258 HINDE, SIDNEY LANGFORD. 1902. The Protective Resemblance to Flowers borne by an African Homopterous Insect, *Flata nigrocincta*, Walker. *Trans. Ent. Soc. London*, pp. 695–8, 2 Pls.

259 HINELINE, GERTRUDE M. WHITE. 1927. Color Vision in the Mud-minnow. *Journ. Exp. Zool.*, **47**, pp. 85–94.

260 HINGSTON, R. W. G. 1927. Field Observations of Spider Mimics. *Proc. Zool. Soc. London*, pp. 841–58, 10 figs.

✓261 —— 1927. Protective Devices in Spiders' Snares, with a Description of seven New Species of Orb-weaving Spiders. *Proc. Zool. Soc. London*, pp. 259–93, 21 figs.

✓262 —— 1927. The Liquid-squirting Habit of Oriental Grasshoppers. *Trans. Ent. Soc. London*, LXXV, pp. 65–8, 1 Pl.

✓263 —— 1929. A Study in Insect Protection. *Journ. Bombay Nat. Hist. Soc.*, XXXIII, pp. 341–6, 2 Pls.

264 —— 1931. The Grasshopper (*Isopera pedunculata*) as a Mimic of the Black Ant (*C. compressus*). *Ibid.*, XXXIV, pp. 1095–6.

265 —— 1932. *A Naturalist in the Guiana Forest.* London, pp. xvi + 384, 16 Pls., 150 figs.

266 —— 1933. *The Meaning of Animal Colour and Adornment.* London, pp. 411, 40 figs.

267 HISAW, FREDERICK L. 1923. Feeding Habits of Moles. *Journ. Mamm.*, Baltimore, **4**, pp. 9–20.

268 HOGBEN, LANCELOT T. 1924. *Pigmentary Effector System.* London, xi + 152, 18 figs.

269 HOLMES, WILLIAM. The Colour Changes and Colour Patterns of *Sepia officinalis*, Linn. *Proc. Zool. Soc. London* (in the press).

270 HOPKINS, A. E. 1927. Experiments of Color Vision in Mice in relation to the Duplicity Theory. *Zeits. f. vergl. Physiol.*, **6**, pp. 299–344, 15 figs.

271 —— 1927. Vision and Retinal Structure in Mice. *Proc. Nat. Acad. Sci. Washington*, **13**, pp. 488–92.

272 HOUSSAY, F. 1912. *Forme, Puissance et Stabilité des Poissons.* Paris, pp. 372, 117 figs.

273 HOUSSAY, B. A., and UNGAR, J. 1925. Facteurs qui réglent la coloration de *Leptodactyllus ocellatus*. *Compt. rend. Soc. Biol. Paris*, XCIII, pp. 259–60.

274 HUBBARD, MARION E. 1903. Correlated Protective Devices in some California Salamanders. *Univ. Cal. Pub. Zool.*, 1, **4**, pp. 157–70, 1 Pl.

275 HUDSON, W. H. 1893. *Idle Days in Patagonia.* London, pp. viii + 256.

275*a* —— 1903. *The Naturalist in La Plata.* London, pp. ix + 394.

276 —— 1920. *The Birds of La Plata.* London, Vol. II, pp. ix + 240, 22 illustrations.

276*a* HUXLEY, JULIAN S. 1927. On the Relation between Egg-weight and Body-weight in Birds. *Journ. Linn. Soc., Zool.*, XXXVI, pp. 457–66, 5 Pls.

✓277 —— 1932. 'Protective' Adaptations of Animals. *Nature*, **130**, p. 203.

278 —— 1938. Threat and Warning Coloration in Birds, with a General Discussion of the Biological Functions of Colour. *Proc. 8th Int. Ornith. Congr. Oxford* (1934), pp. 430–55.

278a HUXLEY, JULIAN S. 1938. The Present Standing of the Theory of Sexual Selection. In *Evolution*, edited by G. R. de Beer, Oxford, pp. 11–42.

279 ILSE, DORA. 1932. Zur ‘ Formwahrnehmung ’ der Tagfalter. 1. Spontane Bevorzugung von Formmerkmalen durch Vanessen. *Zeits. f. vergl. Physiol.*, **17**, pp. 537–56, 8 figs.

280 IMMS, A. D. 1914. Observations on the Homopterous Insect *Phromnia* (*Flata*) *marginella* Oliv. in the Himalayas. *Mem. and Proc. Manchester Lit. and Phil. Soc.*, LVIII, **4**, pp. 1–10, 2 Pls.

281 —— 1931. *Recent Advances in Entomology*. London, pp. viii + 374, 84 figs.

282 ISELY, F. B. 1938. Experimental Study of the Survival Value of Acridian Protective Coloration. *Science*, **87**, pp. 40–1.

283 —— 1938. Survival Value of Acridian Protective Coloration. *Ecology*, **19**, **3**, pp. 370–89, 3 figs.

284 JACOBI, A. 1913. *Mimikry und verwandte Erscheinungen*. Braunschweig, pp. xi + 216, 31 figs.

285 JAMESON, H. LYSTER. 1898. On a probable Case of Protective Coloration in the House-Mouse (*Mus musculus*, Linn.). *Journ. Linn. Soc., Zool.*, XXVI, pp. 465–73, 1 Pl.

286 JANDA, V. 1936. Ueber den Farbwechsel transplantierter Hautstücke und künstlich verbundener Körperfragmente bei *Dixippus morosus* (Br. et Redt.). *Zool. Anz.*, CXV, pp. 177–85, 3 figs.

287 JOBLING, B. 1936. On the Stridulation of the Females of *Parnassius mnemosyne* L. *Proc. Roy. Ent. Soc. London*, **11**, pp. 66–8, 1 fig.

288 JOHNSON, C. E. 1921. The ‘ Hand-stand ’ Habit of the Spotted Skunk. *Journ. Mamm.*, Baltimore, **2**, pp. 87–9.

289 JOLY, N. 1871. Contribution à l’Histoire naturelle et à l’Anatomie de la Mouche-feuille des îles Seychelles *Phyllium crurifolium* (Audinet-Serville), *Mantis siccifolia* (Linn.). *Mém. Ac. Sc. Toulouse*, III, **7**, pp. 1–30, 4 Pls.

290 JONES, F. MORTON. 1932. Insect Coloration and the Relative Acceptability of Insects to Birds. *Trans. Ent. Soc. London*, LXXX, pp. 345–85, 11 Pls.

291 —— 1934. Further Experiments on Coloration and Relative Acceptability of Insects to Birds. *Trans. Roy. Ent. Soc. London*, LXXXII, pp. 443–53, 2 Pls.

292 —— 1937. Relative Acceptability and Poisonous Food-plants. *Proc. Roy. Ent. Soc. London*, 12, **4–6**, pp. 74–6.

293 JORDAN, D. S. 1925. *Fishes*. New York, pp. xv + 773, 18 Pls., 673 figs.

294 —— and EVERMANN, B. W. 1903. The Aquatic Resources of the Hawaiian Islands. 1. The Shore Fishes. *Bull. U.S. Fish. Comm.*, XXIII, **1**, pp. xxviii + 574, 138 Pls., 229 figs.

295 JOURDAIN, F. C. R. 1925. A Study on Parasitism in the Cuckoos. *Proc. Zool. Soc. London*, pp. 639–67, 5 Pls.

296 —— 1936. The so-called ‘ Injury-feigning ’ in Birds. *Ool. Rec. London*, **16**, pp. 25–37 ; 62–70.

✓297 JUDD, S. D. 1899. The Efficiency of some Protective Adaptations in securing Insects from Birds. *Amer. Nat.*, XXXIII, pp. 461–84.

298 —— 1900. The Food of Nestling Birds. *Yearbook, U.S. Dept. Agric.*, pp. 411–36, 5 Pls., 9 figs.

299 KANE, WILLIAM F. DE V. 1896. Observations on the Development of Melanism in *Camptogramma bilineata*. *Irish Nat.*, V, pp. 74–80.

300 KATZ, DAVID. 1937. *Animals and Men : Studies in Comparative Psychology*. London, pp. xi + 263, 37 figs.

301 —— and KATZ, ROSA. 1936. Some Problems concerning the Feeding Behaviour of Monkeys. *Proc. Zool. Soc. London*, pp. 579–82.

302 KATZ and REVESZ, G. 1909. Experimentelle-Psychologische untersuchungen mit hühnern. *Zeit. Psychol.*, **50**, p. 93.

303 KEEBLE, F. W., and GAMBLE, F. W. 1899. The Colour-Physiology of *Hippolyte varians*. *Proc. Roy. Soc. London*, **65**, pp. 461–8.

304 —— 1904. The Colour-Physiology of Higher Crustacea. *Phil. Trans. Roy. Soc.*, B, CXCVI, pp. 295–388.

305 KEELER, CHARLES A. 1893. *Evolution of the Colors of North American Land Birds.* San Francisco, pp. xii + 361, 18 Pls.

306 KERR, J. GRAHAM. 1924. An Experiment in Binocular Vision. *Trans. Ophth. Soc.*, XLIV, pp. 183–5.

307 —— 1926. *Evolution.* London, pp. x + 278, 2 Pls., 53 figs.

308 KERVILLE, H. GADEAU DE. 1907. Sur l'homochromie protectrice des femelles de *Misumena vatia* Clerck. *Bull. Soc. Ent. Fr.*, pp. 145–6.

309 KINGHORN, J. R. 1921. Some large non-venomous Snakes and their Food. *Austr. Mus. Mag. Sydney* 1 (2), pp. 53–5, 2 figs.

310 KINNAMAN, A. J. 1902. Mental Life of Two *Macacus rhesus* Monkeys in Captivity. *Amer. Journ. Psych.*, **13**, pp. 98–148 ; 173–218.

311 KIRBY, F. VAUGHAN. 1896. *In Haunts of Wild Game.* London, pp. xvi + 576.

312 KIRKLAND, A. H. 1897. The Habits, Food, and Economic Value of the American Toad, *Bufo lentiginosus americanus* le C. *Hatch. Exp. Sta. Mass. Agric. Coll., Bull.*, **46**, pp. 1–30.

313 KLUIJVER, I. H. N. 1933. Bijdrage tot de biologie en de ecologie van den Spreeuw (*Sturnus vulgaris vulgaris* L.) gerurende zijn voortplantingstijd. *Versl. Meded. Plantenyiekt. Wageningen*, **69**, pp. 1–145, 3 Pls., 5 figs.

314 KNIGHT, H. H. 1924. On the Nature of the Color Patterns in Heteroptera with Data on the Effects produced by Temperature and Humidity. *Ann. Ent. Soc. Amer.*, **17**, pp. 258–72, 1 Pl.

315 KNOLL, FRITZ. 1921. Insekten und Blumen. Experimentelle arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen Zwischen Pflanzen und Tieren. I. Zeitgemäsze ziele und Methoden für das Studium der Ökologischen Wechselbeziehungen. *Abhandl. d. zool.-bot. Ges. in Wien*, XII, pp. 1–16.

316 —— 1921. II. *Bombylius fuliginosus* und die Farbe der Blumen. *Ibid.*, pp. 17–119, 6 Pls., 23 figs.

317 —— 1922. III. Lichtsinn und Blumenbesuch des Falters von *Macroglossum stellatarum*. *Ibid.*, pp. 121–377, 3 Pls., 38 figs.

318 —— 1924–5. Lichtsinn und Blütenbesuch des Falters von *Deilephila livornica*. *Zeits. f. vergl. Physiol.*, **2**, pp. 329–80, 8 figs.

✓319 KNOWLTON, G. F., and JANES, M. J. 1932. Studies of the Food Habits of Utah Lizards. *Ohio Journ. Sci.*, XXXII, pp. 467–70, 1 fig.

320 KOLLER, G. 1928–29. Versuche über die inkretorischen Vorgänge beim Garneelenfarbwechsel. *Zeits. f. vergl. Physiol.*, **8**, pp. 601–12.

321 KOLOSVÁRY, GÁBOR. 1934. A Study of Color Vision in the Mouse (*Mus musculus* L.) and the Houslik (*Citellus citellus* L.). *Pedagogical Sem. and Journ. Gen. Psych.*, **44**, pp. 473–7.

322 KROPP, B. 1927. The Control of the Melanophores in the Frog. *Journ. Exp. Zool.*, XLIX, pp. 289–318.

323 —— 1929. The Melanophore Activator of the Eye. *Proc. Nat. Acad. Sci.*, XV, pp. 693–4.

324 KRÜGER, PAUL, and KERN, H. 1924. Die physikalische und physiologische Bedeutung des Pigmentes bei Amphibien und Reptilien. *Arch. ges. Physiol. Berlin*, CCII, pp. 119–38, 3 figs.

325 KÜHN, ALFRED. 1927. Über den Farbensinn der Bienen. *Zeits. f. vergl. Physiol.*, **5**, pp. 742–800, 33 figs.

326 LACK, D. 1933. Habitat Selection in Birds with special reference to the Effects of Afforestation on the Breckland Avifauna. *Journ. Anim. Ecol.*, **2**, pp. 239–62, 2 Pls.

327 LAMBORN, W. A. 1921. A Hypsid Moth inspected and neglected by Geckos. *Proc. Ent. Soc. London*, p. vii.

✓ 328 —— 1935. Further striking Evidence of the Distastefulness which accompanies the Aposematic Display of the African Acridian *Zonocerus elegans* Thun. *Proc. Roy. Ent. Soc. London*, X, p. 4.

329 LANG, H. 1923. Caudal and Pectoral Glands of African Elephant Shrews. *Journ. Mamm. Baltimore*, **4**, pp. 261–3.

330 LATTER, O. H. 1901. The Egg of *Cuculus canorus*. *Biometrika*, I, pp. 164–76.

✓ 331 LENG, C. W., and MUTCHLER, A. J. 1922. The Lycidæ, Lampyridæ, and Cantharidæ (Telephoridæ) of the West Indies. *Bull. Amer. Mus. Nat. Hist.*, **44**, pp. 413–99, 65 figs.

332 LILFORD, LORD. 1887. A few Words on European Bats. *Zoologist* (3), XI, pp. 61–7.

333 LINDEN, MARIA VON. 1900. Die ontogenetische Entwicklung der Zeichnung unserer einheimischen Molche. *Biol. Zentralbl.*, XX, pp. 144–67; 226–41, 25 figs.

334 LINSDALE, J. M. 1928. Variations in the Fox Sparrow (*Passerella iliaca*) with reference to Natural History and Osteology. *Univ. Cal. Pub. Zool.*, **30**, pp. 251–392, 5 Pls., 38 figs.

335 LIU, CHI-YING, and CHEN, KAN-FAN. 1932. Analysis of the Stomach Contents of two Species of Frogs (*Rana limnocharis* and *Rana nigromaculata*) in the Vicinity of Kashing with special Reference to Insects. *Yearbook, Bur. Ent. Hangchow*, **2**, pp. 183–91.

336 LONGLEY, W. H. 1914. Report upon Color of Fishes of the Tortugas Reefs. *Year Book*, **13**, Carnegie Inst., Washington, pp. 207–8.

337 —— 1915. Coloration of Tropical Reef Fishes. *Ibid.*, **14**, pp. 208–9.

338 —— 1916. Observations upon Tropical Fishes and Inferences from their Adaptive Coloration. *Proc. Nat. Acad. Sci.*, Washington, **2**, pp. 733–7.

339 —— 1916. The Significance of the Colors of Tropical Reef Fishes. *Year Book*, **15**, Carnegie Inst., Washington, pp. 209–12.

340 —— 1917. Studies upon the Biological Significance of Animal Coloration. 1. The Colors and Color Changes of West Indian Reef-Fishes. *Journ. Exp. Zoology*, pp. 533–99, 1 Pl.

341 —— 1917. Studies upon the Biological Significance of Animal Coloration. *Amer. Nat.*, **51**, pp. 257–85.

342 —— 1918. Marine Camoufleurs and their Camouflage: the present and prospective Significance of Facts regarding the Coloration of Tropical Fishes. *Smithsonian Report*, Washington, pp. 475–85, 5 Pls.

343 —— 1918. Haunts and Habits of Tropical Fishes. *Amer. Mus. Journ.*, XVIII, **2**, pp. 79–88, 10 figs.

344 —— 1918. Habits and Coloration of Hawaiian Brachyura and Fishes, with a Note on the Possibility of Submarine Color-photography. *Year Book*, **17**, Carnegie Inst., Washington, pp. 158–63.

345 —— 1919. Report of Additional Observations and Experiments upon Problems of Animal Coloration. *Ibid.*, **18**, pp. 201–2.

346 —— 1920. The Fishes of Samoa. *Ibid.*, **19**, pp. 195–6.

347 —— 1922. The Fishes of Tortugas and their Habits. *Ibid.*, **21**, pp. 171–3.

348 —— 1925. Observations upon the Powers of Discrimination and Association in the Grey Snapper, and upon the Coloration of the Eyes of Fishes. *Ibid.*, **24**, pp. 228–9.

349 —— 1926. Observations on Tortugas Fishes. *Ibid.*, **25**, pp. 241–2.

350 LONGLEY, W. H. 1927. Observations upon the Ecology of Tortugas Fishes, with Notes upon the Taxonomy of Species new or little known. *Ibid.*, **26**, pp. 222–4.

351 —— 1930. Observations upon Distribution and Behavior of Tortugas Fishes. *Ibid.*, **29**, pp. 337–8.

352 LONGSTAFF, GEORGE B. 1905. Notes on the Butterflies observed in a Tour through India and Ceylon, 1903–4. *Trans. Ent. Soc. London*, pp. 61–144.

353 —— 1906. Some Rest-Attitudes of Butterflies. *Ibid.*, pp. 97–118.

354 —— 1912. *Butterfly-hunting in many Lands.* London, pp. xx + 729, 16 Pls.

355 —— and POULTON, E. B. 1907. A few Notes on some African Chamæleons, etc. *Journ. Linn. Soc., Zool.*, XXX, pp. 45–8.

356 LORENZ, KONRAD Z. 1935. Der Kumpan in der Umwelt des Vögels. *Journ. f. Ornith.*, **83**, pp. 10–213; 289–413. (Translated.) The Companion in the Bird's World. *The Auk*, **54** (1937), pp. 245–73.

357 LOTMAR, R. 1933. Neue Untersuchungen über den Farbensinn der Bienen, mit besonderer Berücksichtigung des Ultra-violetts. *Zeits. f. vergl. Physiol.*, **19**, pp. 671–723, 51 figs.

358 LOVELL, JOHN H. 1910. The Color Sense of the Honey Bee: can Bees distinguish Colours? *Amer. Nat.*, **44**, pp. 673–92.

359 —— 1912. The Color Sense of the Honey Bee: the Pollination of Green Flowers. *Ibid.*, **46**, pp. 83–107.

360 LOVERIDGE, ARTHUR. 1920. Notes on East African Lizards collected 1915–1919, with Description of a new Genus and Species of Skink and new Subspecies of Gecko. *Proc. Zool. Soc. London*, pp. 131–67, 1 fig.

361 —— 1923. Notes on East African Snakes, collected 1918–1923. *Ibid.*, pp. 871–97.

362 —— 1923. Notes on East African Mammals. *Ibid.*, pp. 685–739.

363 —— 1923. Notes on East African Lizards collected 1920–1923, with the Description of two new Races of *Agama lionotus* Blgr. *Ibid.*, pp. 935–69.

364 —— 1923. Notes on East African Birds (chiefly Nesting-habits and Endo-parasites) collected 1920–1923. *Ibid.*, pp. 899–921.

365 —— 1928. Notes on East African Birds (chiefly Nesting-habits and Stomach-contents) collected in 1926. *Ibid.*, pp. 71–9.

366 —— 1933. Reports on the Scientific Results of an Expedition to the Southwestern Highlands of Tanganyika Territory. VII. Herpetology. *Bull. Mus. Comp. Zool. Harvard*, LXXIV, **7**, pp. 197–416, 3 Pls.

367 LOWE, PERCY R. 1911. *A Naturalist on Desert Islands.* London, pp. xii + 300.

368 LUCKIESH, M. 1915. *Color and its Applications.* London, pp. xii + 357, 4 Pls., 129 figs.

369 LUKJANOVA, V. S. 1936. The Physical Characteristics of the Mimicry of Fish. *C.R. Acad. Sci. Uass*, New Ser., 3, pp. 57–60, 3 figs.

370 LULL, R. S. 1917. *Organic Evolution.* New York, pp. xviii + 729.

371 LUNDSTROM, H. M., and BARD, P. 1932. Hypophysial Control of Cutaneous Pigmentation in an Elasmobranch Fish. *Biol. Bull., Woods Hole*, **62**, pp. 1–9, 4 Pls.

372 LYDEKKER, R. 1893. *The Royal Natural History, Mammals*, i, pp. xvi + 583.

373 —— CUNNINGHAM, J. T., BOULENGER, G. A., and THOMSON, J. A. 1912. *Reptiles, Amphibia, Fishes and Lower Chordata.* London, pp. xvi + 510.

374 LYNGE, H. 1909. Marine Lamellibranchiata. The Danish Expedition to Siam 1899–1900. *København Vid. Selsk. Skr.*, V, pp. 100–299, 5 Pls., 1 map.

375 MCATEE, W. L. 1908. Food Habits of the Grosbeaks. *U.S. Dept. Agric., Bur. Biol. Surv., Bull.*, **32**, pp. 1–92, 1 Pl.

376 —— 1912. The Experimental Method of testing the Efficiency of Warning and Cryptic Coloration in protecting Animals from their Enemies. *Proc. Acad. Nat. Sci. Philad.*, pp. 281–364.

✓377 MCATEE, W. L. 1932. Effectiveness in Nature of the so-called Protective Adaptations in the Animal Kingdom, chiefly as illustrated by the Food-habits of Nearctic Bird. *Smith. Misc. Coll., Washington*, 85, **7**, pp. 1–201.

✓378 —— 1932. ' Protective ' Adaptations of Animals. *Nature*, **130**, pp. 961–2.

✓379 —— 1933. Rejoinder to Papers on Protective Adaptations recently published by the Entomological Society of London. *Proc. Roy. Ent. Soc. London*, VIII, pp. 113–26.

380 McCOOK, HENRY C. 1888. Notes on the Relations of Structure and Function to Color Changes in Spiders. *Proc. Acad. Nat. Sci. Philad.*, pp. 172–6.

381 —— 1889–93. *American Spiders and their Spinning Work*, I, pp. 373, 354 figs.; II, pp. 480, 401 figs.; III, pp. 285, 30 Pls., 98 figs.

382 McDERMOTT, F. ALEX. 1910. A Note on the Light-emission of some American Lampyridæ. *Canad. Ent.*, **42**, pp. 357–63.

383 —— 1911. Some further Observations on the Light-emission of American Lampyridæ: the photogenic Function as a Mating Adaptation in the Photinini. *Ibid.*, **43**, pp. 399–406.

384 —— 1912. Observations on the Light-emission of American Lampyridæ. *Ibid.*, **44**, pp. 309–12.

385 —— 1912. The Light-emission of American Lampyridæ: Notes and Corrections. *Ibid.*, **44**, p. 73.

386 M'INTOSH, W. C. 1901. The Coloration of Marine Animals. *Ann. Mag. Nat. Hist.*, VII, pp. 221–40.

387 MACKENZIE, J. M. D. 1930. Means of Defence in Insects. *Journ. Bombay Nat. Hist. Soc.*, **33**, p. 1000.

✓388 McKEOWN, K. C. 1936. The Food of Australian Birds, with Reference to Protective Adaptations in Insects. *Emu*, **36**, pp. 21–30.

389 MACPHERSON, REV. H. A. 1886. The Habits of the Greater Horse-shoe Bat. *Naturalist*, November, pp. 337–9.

390 MANDERS, NEVILLE. 1911. An Investigation into the Validity of Müllerian and other Forms of Mimicry, with special reference to the Islands of Bourbon, Mauritius, and Ceylon. *Proc. Zool. Soc. London*, pp. 696–749.

391 —— 1912. The Study of Mimicry (Batesian and Müllerian) by Temperature Experiments on two Tropical Butterflies. *Trans. Ent. Soc. London*, pp. 445–69, 1 Pl.

392 MARPLES, GEORGE. 1933. Experiments on Colour Sense in Birds. *Brit. Birds*, XXVI, pp. 238–45.

393 MARSHALL, G. A. K. 1908. On Diaposematism, with reference to some Limitations of the Müllerian Hypothesis of Mimicry. *Trans. Ent. Soc. London*, pp. 93–142.

394 —— 1909. Birds as a Factor in the Production of Mimetic Resemblances among Butterflies. *Ibid.*, pp. 329–83.

395 —— and POULTON, E. B. 1902. Five Years' Observations and Experiments (1896–1901) on the Bionomics of South African Insects, chiefly directed to the Investigation of Mimicry and Warning Colours. *Ibid.*, pp. 287–584, 15 Pls.

396 MASON, CLYDE W. 1926. Structural Colours of Insects. *Journ. Phys. Chem.*, XXX, pp. 383–95.

397 —— and MAXWELL-LEFROY, H. 1912. The Food of Birds in India. *Mem. Dept. Agric. India, Ent. Ser.*, III, pp. 1–371.

398 MAST, S. O. 1916. Changes in Shape, Color, and Pattern in Fishes and their bearing on the Problems of Adaptation and Behavior, with special reference to the Flounders, *Paralichthys* and *Ancylopsetta*. *Bull. U.S. Bur. Fish.*, **34**, pp. 173–238.

399 MASTERMAN, A. T. 1908. On a possible case of Mimicry in the Common Sole. *Journ. Linn. Soc., Zool.*, XXX, pp. 239–44.

400 MATHEW, A. P. 1935. Transformational Deceptive Resemblance as seen in the Life-history of a Plant Bug (*Riptortus pedestris*), and of a Mantis (*Evantissa pulchra*). *Journ. Bombay Nat. Hist. Soc.*, XXXVII, pp. 803–13, 1 Pl.

401 MATHEWS, G. M. 1918–19. *The Birds of Australia.* London, VII, xii + 499.

402 MATTHES, E. 1924. Die Rolle des Gesichts-, Geruchs- und Erschütterungs-sinnes für den Nahrungserwerb von Triton. *Biol. Zentralbl.*, **44**, pp. 72–86.

403 MAYER, ALFRED G. 1896. The Development of the Wing Scales and their Pigment in Butterflies and Moths. *Bull. Mus. Comp. Zool. Harvard*, **29**, pp. 209–36, 7 Pls.

404 —— 1897. On the Color and Color-patterns of Moths and Butterflies. *Proc. Bost. Soc. Nat. Hist.*, **27**, pp. 243–330, 10 Pls.

405 MEADE WALDO, G. 1910. Protective Attitude of a Mantis from Borneo. *Proc. Ent. Soc. London*, pp. i–lii.

406 MEEK, A. 1929. Adaptation. *Nature*, **124**, p. 509.

407 MELDOLA, R. 1873. On a certain Class of Cases of Variable Protective Colouring in Insects. *Proc. Zool. Soc. London*, pp. 153–62.

408 MERRIAM, C. HART. 1890. Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona. *U.S. Dept. Agric., North American Fauna*, **3**, pp. 1–86, 1 Pl., 2 figs.

409 MERRIFIELD, F. 1892. The Effects of artificial Temperature on the Colouring of several Species of Lepidoptera, with an Account of some Experiments on the Effect of Light. *Trans. Ent. Soc. London*, pp. 33–44.

410 —— and POULTON, E. B. 1899. The Colour-relation between the Pupæ of *Papilio machaon*, *Pieris napi* and many other Species, and the Surroundings of the Larvæ preparing to pupate, etc. *Ibid.*, pp. 369–433.

411 METZGER, WOLFGANG. 1935. Gestaltgesetse im Dienste der Tarnung. *Natur u. Volk, Frankfurt a. M.*, **65**, pp. 600–18, 25 figs.

412 MEYER, P. F. 1930. Untersuchungen über die Aufnahme pflanzlicher Farbstoffe in den Korper von Lepidopteren-Larven. *Zeits. vergl. Physiol.*, **11**, pp. 173–209, 8 figs.

413 MITCHELL, P. CHALMERS. 1912. *The Childhood of Animals.* London, pp. xiv + 269, 12 Pls., 36 figs.

414 MORGAN, C. LLOYD. 1896. *Habit and Instinct.* London, pp. 351.

415 MORRIS, RANDOLPH C. 1921. Porcupine's Method of Attack. *Journ. Bombay Nat. Hist. Soc.*, XXVI, 1918–21, p. 1040.

416 MORTENSEN, TH. 1901. *Dansk Fiskeriforenings Medlemsblad*, pp. 134–6.

417 —— 1917. Observations on Protective Adaptations and Habits, mainly in Marine Animals. *Saertryk af Vidensk. Medd. fra Dansk naturhist. Foren.*, **69**, pp. 57–96.

418 MOSELEY, H. N. 1897. *Notes by a Naturalist on the 'Challenger'.* London, pp. xvi + 599, 3 Pls.

419 MOSS, REV. A. MILES. 1911. On the Sphingidæ of Peru. *Trans. Zool. Soc. London*, XX, pp. 73–118, 10 Pls.

420 —— 1920. Sphingidæ of Para, Brazil. *Novitates Zoologicæ*, XXVII, pp. 333–424.

421 MOSS, J. E. 1933. The Natural Control of the Cabbage Caterpillars, *Pieris* spp. *Journ. Anim. Ecol.*, **2**, pp. 210–31, 2 figs.

422 MOSTLER, GERHARD. 1934–35. Beobachtung zur Frage der Wespenmimikry. *Zeits. Morph. und Ökol.*, **29**, pp. 381–454.

423 MOTTRAM, J. C. 1914. *Controlled Natural Selection and Value Marking.* London, pp. ix + 130.

424 —— 1915. Some Observations on Pattern-Blending with reference to Obliterative Shading and Concealment of Outline. *Proc. Zool. Soc. London*, pp. 679–92, 5 figs.

425 MOTTRAM, J. C. 1915. The Distribution of Secondary Sexual Characters amongst Birds, with relation to their Liability to the Attack of Enemies. *Ibid.*, pp. 663–78.

426 —— 1916. An Experimental Determination of the Factors which cause Patterns to appear Conspicuous in Nature. *Ibid.*, pp. 383–419, 20 figs.

427 —— 1918. Some Observations on the Feeding-habits of Fish and Birds, with special reference to Warning Coloration and Mimicry. *Journ. Linn. Soc. Zool.*, **34**, pp. 47–60.

428 MÜHLMANN, HEINRICH. 1933–4. Im Modellversuch künstlich erzeute Mimikry und ihre Bedeutung für den ' Nachahmer '. *Zeits. Morph. und Ökol.*, **28**, pp. 259–96, 14 figs.

429 MUIR, ALEC, and BUTLER, A. L. 1925. The Nesting of *Nyctibius griseus* (Gmel.) in Trinidad. *Ibis*, Ser. 12, I, pp. 654–9, 6 Pls.

430 MÜLLER, FRITZ. 1879. (Trans. by Meldola.) *Ituna* and *Thyridia*; a remarkable Case of Mimicry in Butterflies. *Proc. Ent. Soc. London*, pp. xx–xxix.

431 MURRAY, J., and HJORT, J. 1912. *The Depths of the Ocean.* London, pp. xx + 821, 9 Pls., 4 maps, 575 figs.

432 MYERS, J. G. 1929. The Nesting-together of Birds, Wasps and Ants. *Proc. Ent. Soc. London*, **4**, pp. 80–8.

✓433 —— 1930. Observations on the Insect Food of the Coati. *Ibid.*, **5**, pp. 69–75.

434 —— 1935. Nesting Associations of Birds with Social Insects. *Trans. Roy. Ent. Soc. London*, LXXXIII, pp. 11–22, 1 Pl.

435 —— and SALT, G. 1926. The Phenomenon of Myrmecoidy, with new examples from Cuba. *Trans. Ent. Soc. London*, 74, pp. 427–36, 1 Pl., 1 fig.

436 NEEDHAM, J. G. The Summer Food of the Bull-frog (*Rana catesbiana* Shaw) at Saranac Inn. *New York State Mus. Bull.*, **86**, pp. 9–15.

437 NEWBIGIN, M. I. 1898. *Colour in Nature. A Study in Biology.* London, pp. xii + 344.

438 NEWMAN, H. H. 1925. *Evolution, Genetics and Eugenics.* Chicago, pp. xxx + 639, 99 figs.

439 NEWTON, ALFRED. 1896. *A Dictionary of Birds.* London, pp. xii + 1088.

440 NICHOLSON, A. J. 1927. A New Theory of Mimicry in Insects. *Austr. Zool. Sydney*, **5**, pp. 10–104, 14 Pls., 3 figs.

✓441 —— 1932. ' Protective ' Adaptations of Animals. *Nature*, **130**, p. 696.

442 NOBLE, G. K. 1918. The Amphibians collected by the American Museum Expedition to Nicaragua in 1916. *Bull. Amer. Mus. Nat. Hist.*, XXXVIII, pp. 311–47, 6 Pls.

443 —— 1921. Snakes that Inflate. *Nat. Hist. New York*, **21**, pp. 166–71.

444 —— 1924. Contributions to the Herpetology of the Belgian Congo based on the Collection of the American Museum Congo Expedition, 1909–1915. Part III. *Bull. Amer. Mus. Nat. Hist.*, XLIX, pp. 147–347.

445 —— 1931. *Biology of the Amphibia.* New York, pp. xiii + 577, 1 Pl., 174 figs.

446 NORMAN, J. R. 1931. *A History of Fishes.* London, pp. xv + 463, 9 Pls., 417 figs.

447 OGILVIE, F. M. 1920. *Field Observations on British Birds.* London, xvi + 226, 6 Pls., 14 figs., 3 maps.

448 OLDHAM, C. 1901. Observations on the Noctule. *Zoologist*, v, (**4**), pp. 51–9.

449 ONSLOW, H. 1923. On a Periodic Structure in many Insect Scales, and the cause of their Iridescent Colours. *Phil. Trans. Roy. Soc. London*, pp. 1–74, 3 Pls.

449*a* OSBORN, H. L. 1885. Mimicry among Marine Mollusca. *Science*, VI, pp. 9–10.

450 OSGOOD, W. H. 1909. Revision of the Mice of the American Genus *Peromyscus. U.S. Dept. Agric., North Amer. Fauna*, **28**, pp. 285.

451 PACKARD, ALPHEUS S. 1904. The Origin of the Markings of Organisms (Pœcilogenesis) due to the Physical rather than to the Biological Environment; with Criticisms of the Bates-Müller Hypotheses. *Proc. Amer. Phil. Soc.*, **43**, pp. 393–450.

452 PACKARD, ALPHEUS S. 1905. Change of Color and Protective Coloration in a Flower-Spider (*Misumena vatia* Thorell). *Journ. N.Y. Ent. Soc.*, XIII, pp. 85–96.

453 PALMER, WILLIAM. 1909. Instinctive Stillness in Birds. *The Auk*, **26**, pp. 23–36.

454 PANTEL, J., ET SINÉTY R. DE. 1918. Réactions chromatiques et non chromatiques de quelques Phasmides aux excitations dépendant de la lumière. *Bull. biol. Fr. Belg.*, LII, pp. 177–283, 2 Pls.

455 PARKER, G. H. 1930. Chromatophores. *Biol. Rev.*, Cambridge, V, pp. 59–90.

456 —— 1933. The Color Changes of Elasmobranch Fishes. *Proc. Nat. Acad. Sci. Washington*, 19, **12**, pp. 1038–9.

457 —— and PORTER, HELEN. 1934. The Control of the Dermal Melanophores in Elasmobranch Fishes. *Biol. Bull.*, LXVI, pp. 30–7, 1 fig.

458 —— and STARRATT, S. A. 1904. The effect of Heat on the Color Changes in the Skin of *Anolis carolinensis*. *Proc. Amer. Acad. arts and sci.*, **40**, pp. 457–66.

459 PARSONS, J. HERBERT. 1915. *An Introduction to the Study of Colour Vision.* London, viii + 308, 1 Pl., 75 figs.

460 PAWLOWSKY, E. N. 1914. Über den Bau der Giftdrüsen bei *Plotosus* und anderen Fischen. *Zool. Jahrb. Abt. f. Anat.*, **38**, pp. 427–42, 3 Pls.

461 PEARL, RAYMOND. 1911. Data on the relative Conspicuousness of Barred and Self-colored Fowls. *Amer. Nat.*, XLV, pp. 107–17, 4 figs.

462 PEARSE, A. S. 1911. The Influence of Different Color Environments on the Behavior of certain Arthropods. *Journ. Anim. Behav.*, **1**, pp. 79–110.

463 PECKHAM, E. G. 1889. Protective Resemblances in Spiders. *Occ. Pap. Nat. Hist. Soc. Wis.*, I, pp. 61–113, 4 Pls., 12 figs.

464 PECKHAM, G. W., and E. G. 1892. Ant-like Spiders of the Family Attidæ. *Occ. Pap. Nat. Hist. Soc. Wis.*, II, pp. 1–84, 6 Pls.

465 —— 1894. The Sense of Sight in Spiders, with some Observations on the Color Sense. *Trans. Wis. Acad. Sci.*, X, pp. 231–61.

466 PERCIVAL, A. BLAYNEY. 1924. *A Game Ranger's Note Book.* London, pp. xvii + 369, 32 Pls.

467 PERKINS, R. C. L. 1912. The Colour-groups of the Hawaiian Wasps, etc. *Trans. Ent. Soc. London*, pp. 677–701.

468 PETERS, JAMES L., and LOVERIDGE, ARTHUR. 1936. Scientific Results of an Expedition to Rain Forest Regions in Eastern Africa. IV. Birds. *Bull. Mus. Comp. Zool. Harvard*, LXXIX, *f*, pp. 129–205, 2 Pls.

469 PHILLIPS, W. W. A. 1931. The Food of the Ceylon Slender Loris (*Loris tardigradus*) in Captivity. *Spolia Zeylanica*, XVI, pp. 205–8, 1 Pl.

470 PICKENS, A. L. 1930. Favorite Colors of Humming Birds. *The Auk*, XLVII, pp. 346–52, 1 fig.

471 PIEPERS, C. 1903. Mimikry, Selektion und Darwinismus. *Leiden*, pp. 452.

472 PITMAN, C. R. S. 1921. Porcupine's Method of Attack. *Journ. Bombay Nat. Hist. Soc.*, XXVI, 1918–21, pp. 1034–40.

473 —— 1929. Experiments with Insect-food on the African Lemur *Perodicticus potto*, Lesson. *Proc. Ent. Soc. London*, IV, pp. 90–1.

474 PLATEAU, FÉLIX. 1892. La Ressemblance protectrice dans le Règne Animal. *Bull. de l'Acad. R. d. sci. de Belgique*, 3, **23**, pp. 89–135.

475 PLATH, O. E. 1923. The Bee-eating Proclivity of the Skunk. *Amer. Nat.*, **57**, pp. 570–4.

476 POCOCK, R. I. 1899. The Genus Pœcilotheria: its Habits, History and Species. *Ann. Mag. Nat. Hist.*, III (7), pp. 82–96.

477 —— 1906. Exhibition of, and Remarks upon, the 'rattle' of a Porcupine. *Proc. Zool. Soc. London*, pp. 902–3.

478 —— 1908. Warning Coloration in the Musteline Carnivora. *Ibid.*, pp. 944–59.

479 —— 1909. Mimicry in Spiders. *Journ. Linn. Soc., Zool.*, XXX, pp. 256–70, 1 Pl.

480 POCOCK, R. I. 1909. Description of a new Form of Ratel (*Mellivora*) from Sierra Leone, with Notes upon the described African Forms of this Genus. *Proc. Zool. Soc. London*, pp. 394–8, 1 Pl.

481 —— 1911. Some probable and possible Instances of Warning Characteristics amongst Insectivorous and Carnivorous Mammals. *Ann. Mag. Nat. Hist.*, **8**, pp. 750–7.

482 —— 1911. On the Palatability of some British Insects, with Notes on the Significance of Mimetic Resemblance. *Proc. Zool. Soc. London*, pp. 809–64. Notes upon some of the above described Experiments, by Prof. E. B. Poulton, pp. 864–8.

483 —— 1929. Tigers. *Journ. Bombay Nat. Hist. Soc.*, **33**, pp. 505–41, 13 Pls.

484 —— and ROTHSCHILD, N. C. 1903. On a new 'Bird's-dung' Spider from Ceylon. *Proc. Zool. Soc. London*, pp. 48–51, 1 Pl.

485 PORTER, JAMES P. 1904. A Preliminary Study of the Psychology of the English Sparrow. *Amer. Journ. Psych.*, XV, **3**, pp. 313–46, 8 figs.

486 —— 1906. Further Study of the English Sparrow and other Birds. *Ibid.*, XVII, **2**, pp. 248–71.

487 POTTS, F. A. 1914. Researches at Murray Island. *Year Book*, **13**, Carnegie Inst., Washington, pp. 208–10.

488 POULTON, E. B. 1884. Notes upon, or suggested by, the Colours, Markings, and Protective Attitudes of certain Lepidopterous Larvæ and Pupæ, and of a Phytophagous Hymenopterous larva. *Trans. Ent. Soc. London*, pp. 27–60, 1 Pl.

489 —— 1885. The Essential Nature of the Colouring of Phytophagous Larvæ (and their Pupæ); with an Account of some Experiments upon the Relation between the Colour of such Larvæ and that of their Food-plants. *Proc. Roy. Soc. London*, **38**, pp. 269–315.

490 —— 1885. Further Notes upon the Markings and Attitudes of Lepidopterous Larvæ, together with a complete Account of the Life-history of *Sphinx ligustri* and *Selenia illunaria* (larvæ). *Trans. Ent. Soc. London*, pp. 281–329, 1 Pl.

491 —— 1887. An Enquiry into the Cause and Extent of a Special Colour-relation between certain exposed Lepidopterous Pupæ and the Surfaces which immediately surround them. *Phil. Trans. Roy. Soc. London*, **178**, pp. 311–441, 1 Pl.

492 —— 1887. The Secretion of Pure Aqueous Formic Acid by Lepidopterous Larvæ for purposes of Defence. *Nature*, **36**, pp. 593–4.

493 —— 1887. Further Experiments upon the Protective Value of Colour and Markings in Insects. *Ibid.*, **36**, pp. 594–5.

494 —— 1887. The Experimental Proof of the Protective Value of Colour and Markings in Insects in reference to their Vertebrate Enemies. *Proc. Zool. Soc. London*, pp. 191–274.

495 —— 1888. Notes in 1887 upon Lepidopterous Larvæ, etc., including a Complete Account of the Life-History of the Larvæ of *Sphinx convolvuli* and *Aglia tau*. *Trans. Ent. Soc. London*, pp. 515–606, 3 Pls.

496 —— 1890. The Colours of Animals. *Int. Sci. Ser.*, LXVIII, London, pp. xiii + 360, 1 Pl., 66 figs.

497 —— 1891. On an Interesting Example of Protective Mimicry discovered by Mr. W. L. Sclater in British Guiana. *Proc. Zool. Soc. London*, pp. 462–4, 1 Pl.

498 —— 1892. Further Experiments upon the Colour-relation between certain Lepidopterous Larvæ, Pupæ, Cocoons and Imagines and their Surroundings. *Trans. Ent. Soc. London*, pp. 293–487, 2 Pls.

499 —— 1893. The Experimental Proof that the Colours of certain Lepidopterous Larvæ are largely due to modified Plant Pigments derived from Food. *Proc. Roy. Soc. London*, LIV, pp. 417–30, 2 Pls.

500 —— 1898. Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours. *Journ. Linn. Soc., Zool.*, XXVI, pp. 558–612, 5 Pls.

501 POULTON, E. B. 1898. Protective Mimicry and Common Warning Colours. *Nature*, **57**, p. 398.

502 —— 1903. Experiments in 1893, 1894, and 1896 upon the Colour-relation between Lepidopterous Larvæ and their Surroundings, and especially the effect of Lichen-covered Bark upon *Odontopera bidentata*, *Gastropacha quercifolia*, etc. *Trans. Ent. Soc. London*, pp. 311–74, 3 Pls.

503 —— 1904. The Bearing of the Study of Insects upon the Question, 'Are Acquired Characters Hereditary?' *Proc. Ent. Soc. London*, pp. civ–cxxxii.

503*a* —— 1904. Exhibition of a specimen of *Glenea pulchella* (Thoms.). *Proc. Ent. Soc. London*, pp. vi–vii.

504 —— 1906. A Note of the Cryptic Resemblance of two South American Insects, the Moth *Dracenta rusina* Druce and the Locustid *Plagioptera bicordata* Serv. *Trans. Ent. Soc. London*, pp. 533–9, 1 Pl.

505 —— 1907. Predaceous Insects and their Prey. *Ibid.*, pp. 323–409.

506 —— 1908. *Essays on Evolution* 1889–1907. Oxford, pp. xlviii + 479, 7 figs.

507 —— 1913. A Locustid and a Reduviid mimic of a Fossorial Aculeate in the S. Paulo district of Brazil. *Proc. Ent. Soc. London*, pp. l–liii.

508 —— 1919. Notes on the Locustid Ant-mimic *Myrmecophana* sp.? *fallax*. *Ibid.*, pp. xxxix–xl.

509 —— 1922. Experimental Evidence that Commensalism may be beneficial to Crustacea. *Proc. Zool. Soc. London*, pp. 897–8.

510 —— 1924. Modes of Protection in the Pupal Stage of Butterflies and Moths. *Trans. S.E. Union Sci. Soc.*, pp. 72–7.

511 —— 1924. The Terrifying Appearance of *Laternaria* (Fulgoridæ) founded on the most Prominent Features of the Alligator. *Proc. Ent. Soc. London*, pp. xliii–xlix, 1 Pl.

512 —— 1924. Dr. J. Bequaert's Memoir on the Predaceous Enemies of Ants. *Ibid.*, pp. lxviii–lxxi.

513 —— 1924. The Detailed Resemblance of an Indian Lepidopterous Larva to the Excrement of a Bird. A similar Result obtained in an entirely different way by a Malayan Spider. *Ibid.*, pp. xc–xciii.

514 —— 1926. Protective Resemblance borne by certain African Insects to the blackened Areas caused by Grass Fires. *III Int. Ent. Kongress, Zurich* (1925), II, pp. 433–51, 1 Pl.

515 —— 1926. The Evolution of the Colours and Patterns of Cuckoos' Eggs and its Relation to that of Insect Resemblances, such as Mimicry. *Proc. Ent. Soc. London*, pp. xcii–civ.

516 —— 1929. British Insectivorous Bats and their Prey. *Proc. Zool. Soc. London*, pp. 277–303.

517 —— 1929. Ants as Models for Mimicry. *Zool. Anz. Leipzig* (Wasmann Festband), pp. 79–86.

518 —— 1931. A Hundred Years of Evolution. Presidential Address, Section D, *Rept. Brit. Assn. Adv. Sci.*, pp. 71–95, 2 Pls.

519 —— 1931. The Gregarious Sleeping Habits of *Heliconius charithonia* L. *Proc. Ent. Soc. London*, VI, pp. 4–10, also pp. 68 and 71.

520 —— 1931. The Gregarious Sleeping Habits of a Heliconian and an Ithomiine Butterfly in Trinidad, observed by P. Lechmere Guppy. *Ibid.*, VI, pp. 68–9.

521 —— 1931. Two specially significant Examples of Insect Mimicry. *Trans. Ent. Soc. London*, **79**, pp. 395–8, 2 Pls.

522 —— 1932. 'Protective' Adaptations of Animals. *Nature*, **130**, pp. 202–3.

523 —— 1932. Feeding Experiments with Lepidoptera conducted by W. W. A. Phillips on a Ceylon Lemur. *Proc. Ent. Soc. London*, VII, pp. 32–5, 49–50.

524 —— 1932. Attempts to disprove the Theories of Warning Colours, Mimicry and Protective Resemblance in Insects. *Ve Congrès int. Ent., Paris*, pp. 33–44.

525 POULTON, E. B. 1934. The President's Address. *Proc. Roy. Ent. Soc. London*, pp. 157–72.

526 —— and SANDERS, CORA B. 1898. An Experimental Enquiry into the Struggle for Existence in certain Common Insects. *Rept. Brit. Assoc. Adv. Sci.*, pp. 906–9.

527 PRAEGER, WM. V. 1891. Protective Coloration in the Genus *Aegialitis*. *The Auk*, VIII, p. 236.

528 PRIEBATSCH, I. 1933. Der Einfluss des Lichtes auf Farbenwechsel und Phototaxis von *Dixippus* (*Carausius*) *morosus*. *Zeits. f. vergl. Physiol.*, XIX, pp. 453–88, 13 figs.

✓ 529 PRITCHETT, ANNIE E. 1903. Some Experiments in feeding Lizards with protectively coloured Insects. *Biol. Bull.*, V, pp. 271–87.

530 PUNNETT, R. C. 1911. Enemies of Butterflies in Ceylon. *Spolia Zeylanica*, VII, pp. 9–15.

531 —— 1915. *Mimicry in Butterflies*. Cambridge, pp. viii + 188, 16 Pls.

532 PYCRAFT, W. P. 1925. *Camouflage in Nature*. London, 2nd rev. ed., pp. xi + 280.

533 RABAUD, E. 1923. Recherches sur la variation chromatique et l'homochromie des Arthropodes terrestres. *Biol. Bull. Paris*, **57**, pp. 1–69.

534 RAU, P. 1933. Jungle Bees and Wasps of Barro Colorado Island (Panama). *Kirkwood, Mo., Phil. Rau.*, pp. 324, 1 Pl., 112 figs.

535 RAYLEIGH, LORD. 1930. Iridescent Colours in Nature from the Standpoint of Physical Optics. *Journ. Sci. Instruments*, VII, **2**, pp. 34–40.

536 —— 1930. The Iridescent Colours of Birds and Insects. *Proc. Roy. Soc.*, **128**, pp. 624–41, 2 Pls.

537 REGAN, C. TAIT. 1909. Exhibition of sketches of, and remarks upon, Colour-changes in some Fishes in New York Aquarium. *Proc. Zool. Soc. London*, pp. 130–2.

538 REIGHARD, J. 1908. An Experimental Field-Study of Warning Coloration in Coral-Reef Fishes. *Dept. Mar. Biol. Carn. Inst. Washington*, Papers from the Tortugas Laboratory, 2, 9, pp. 257–325, 5 Pls.

539 —— 1912. An Experimental Study of Color-discrimination, Association, and Memory in the Grey Snapper *Lutianus griseus* (Linnæus), and of Warning Coloration in Coral-Reef Fishes. *Proc. 7th Int. Zool. Cong. Cambs. Mass.*, pp. 154–5.

540 RÉVÉSZ, G. 1924. Experiments on Animal Space Perception. *Brit. Journ. Psych.*, XIV, pp. 387–414.

541 RICHARDSON, C. H. 1914. Some Comments on the Value of Warning Colours and Mimicry in Insects. *Psyche*, Boston, **21**, pp. 136–7.

542 RIDLEY, H. N. 1936. The Luminous Secretion of the Centipede *Geophilus electricus* (L.) as a Defence against the Attack of Beetles, etc. *Proc. Roy. Ent. Soc. London*, **11**, p. 48.

543 ROBSON, G. C., and RICHARDS, O. W. 1936. *The Variation of Animals in Nature*. London, pp. xvi + 425, 2 Pls., 30 figs.

544 ROONWAL, M. L. 1938. The Frightening Attitude of a Desert Mantid, *Eremiaphila braueri* Kr. (Orthoptera, Mantodea). *Proc. Roy. Ent. Soc. London*, **13**, pp. 71–2, 1 fig.

545 ROOSEVELT, THEODORE. 1910. *African Game Trails: an Account of the African Wanderings of an American Hunter-Naturalist*. London, pp. xvii + 534. Appendix E: Protective Coloration, pp. 491–512.

546 —— 1911. Revealing and Concealing Coloration in Birds and Mammals. *Bull. Amer. Mus. Nat. Hist.*, XXX, pp. 119–231.

547 —— 1914. *Through the Brazilian Wilderness*. London, pp. xiv + 374, 49 Pls., 2 maps.

548 RUSSELL, E. S. 1934. *The Behaviour of Animals*. London, pp. vi + 184, 6 Pls., 26 figs.

549 RUSSELL, E. S., and BULL, H. O. 1932. A selected Bibliography of Fish Behaviour. *Journ. du Conseil*, Copenhagen, VII, pp. 255–76.

550 SAND, A. 1935. The Comparative Physiology of Colour Response in Reptiles and Fishes. *Biol. Rev.*, Cambridge, X, pp. 361–82.

551 SANDERSON, IVAN T. 1936. The Amphibians of the Mamfe Division, Cameroons — II. Ecology of the Frogs. *Proc. Zool. Soc. London*, pp. 165–208, 1 Pl., 7 figs.

552 SARGENT, OSWALD H. 1918. Fragments of the Flower Biology of Westralian Plants. *Ann. Bot.*, XXXII, pp. 215–31.

553 SAUNDERS, A. A. 1937. Injury-feigning in a Wood Duck. *The Auk*, **54**, pp. 202–3.

554 SAVILLE-KENT, W. 1893. *The Great Barrier Reef of Australia ; its Products and Potentialities.* London, pp. xix + 387, 64 Pls.

555 —— 1897. *The Naturalist in Australia.* London, pp. xv + 302.

556 SAVORY, THEODORE H. 1928. *The Biology of Spiders.* London, pp. xx + 376.

557 SCHAEFFER, A. A. 1911. Habit Formation in Frogs. *Journ. Anim. Behav.*, I pp. 309–35.

558 SCHMIDT, K. P. 1919. Contributions to the Herpetology of the Belgian Congo based on the Collection of the American Museum Congo Expedition, 1909–1915. Part I. *Bull. Amer. Mus. Nat. Hist.*, XXXIX, pp. 385–624.

559 SCHNEIDER, G. 1906. Mitteilungen über interessante Mimikryfälle bei sumatranischen Spinnen. *Colmar. Mitt. nathist. Ges.*, VIII, pp. 213–18, 1 Pl.

560 SCHWANWITSCH, B. N. 1938. On the Stereoeffect of Cryptic Colour-patterns in Lepidoptera. *Comptes Rendus* (*Doklady*) *de l'Académie des Sciences de l'Urss*, XXI, **4**, pp. 179–82, 2 figs.

561 SEITZ, A. 1913. On the Sense of Vision in Insects. *Trans. 2nd Ent. Congr. Oxford*, **2**, pp. 198–204.

562 SELOUS, F. C. 1908. *African Nature Notes.* London, pp. xxx + 356.

563 SEMON, R. 1896. *Im australischen Busch und an den Kuste des Korallenmeeres.* Leipzig, pp. xvi + 569, 85 figs., 4 maps.

564 SEMPER, KARL. 1881. Animal Life. *Int. Sci. Ser.*, pp. xvi + 472, 106 figs.

565 SEVASTOPULO, D. G. 1936. The Prey of House Lizards (*Hemidactylus* sp.) in Calcutta. *Proc. Roy. Ent. Soc. London*, **11**, pp. 91–2.

566 SHAW, W. T. 1928. The Spring and Summer Activities of the Dusky Skunk in Captivity, with a Chapter on the Insect Food of the Dusky Skunk, by K. F. Chamberlain. *N.Y. St. Mus. Albany Handbk.*, **4**, pp. 11–103, 59 figs.

567 SHELDON, R. E. 1911. The Sense of Smell in Selachians. *Journ. Exp. Zool.*, X, pp. 51–62.

568 SHELFORD, R. 1901. On the Occurrence of the Mimetic Locustid *Condylodera tricondyloides* (West) in Borneo. *Journ. Straits Branch Roy. Asiat. Soc.*, XXXV, pp. 69–71.

569 —— 1902. Observations on some Mimetic Insects and Spiders from Borneo and Singapore. *Proc. Zool. Soc. London*, pp. 230–84, 5 Pls.

570 —— 1903. Bionomical Notes on some Bornean Mantidæ. *The Zoologist*, (**4**), VII, pp. 293–304, 2 figs.

571 —— 1912. Mimicry amongst the Blattidæ ; with a Revision of the Genus *Prosoplecta* Sauss., and the Description of a New Genus. *Proc. Zool. Soc. London*, pp. 358–76, 1 Pl.

572 —— 1917. *A Naturalist in Borneo.* Edited by E. B. Poulton. London, pp. xxviii + 331, 32 Pls.

573 SHELFORD, V. E. 1917. Color and Color-pattern Mechanism of Tiger Beetles. *Ill. Biol. Monogr.*, 3, **4**, pp. 399–528, 32 Pls.

574 SIMES, J. A. 1933. Adaptable protective Resemblance of an Acridian (Orthoptera) of the Genus *Œdipoda* to the Rocks of its Localities. *Proc. Roy. Ent. Soc. London*, VIII, pp. 138–9.

575 SJÖSTEDT, Y. 1924. Revision der Truxaliden-Gattung *Cannula* Bol. *Arkiv. f. Zoologi*, Stockholm, 15, **21**, 10 pp., 2 Pls.

576 SLUITER, C. P. 1888. Ein merkwürdiger Fall von Mutualismus. *Zool. Anz.*, XI, pp. 240–3.

577 SMEDLEY, N. 1928. A Case of Protective Resemblance. *Malayan Nat. Singapore*, **2**, p. 48.

578 SMITH, E. M. 1912. Some Observations concerning Colour Vision in Dogs. *Brit. Journ. Psych.*, **5**, pp. 119–202.

579 SMITH, MALCOLM A. 1935. *The Fauna of British India. Reptilia and Amphibia.* Vol. II, Sauria. London, pp. xiii + 440, 1 Pl., 94 figs.

580 SOLANDT, D. Y., and HILL, A. V. 1935. Myograms from the Chromatophores of *Sepia*. *Journ. Physiol. Cambridge*, **83**, pp. 13–14.

581 SOLOMON, SOLOMON J. 1920. *Strategic Camouflage*. London, pp. xii + 62, 32 Pls., 7 figs.

582 SONNTAG, C. F., and DUNCAN, F. M. 1922. Contributions to the Histology of the Three-toed Sloth (*Bradypus tridactylus*). *Journ. Roy. Micr. Soc.*, pp. 37–46, 13 figs.

583 SOUTH, RICHARD. 1923. *The Moths of the British Isles.* Vol. II, pp. vii + 388.

584 SPARROW, C. M. 1923. On the Spectral Characteristics of Protective Coloration. *Science*, LVII, pp. 488–90.

585 STARK, A., and SCLATER, W. L. 1900–6. *The Birds of South Africa.* Vol. I, xxx + 322; Vol. II, xiv + 323, 83 figs.; Vol. III, xvii + 416, 141 figs.; Vol. IV, xvii + 545, 163 figs.

586 STEFÁNSSON, VILHJÁLMUR. 1913. *My Life with the Eskimo.* New York, pp. x + 527.

587 STEINACH, E. 1902. Studien über die Hautfärbung und über den Farbenwechsel der Cephalopoden. *Arch. ges. Physiol.*, **87**, pp. 1–37, 2 Pls.

588 STEJNEGER, LEONHARD. 1885. Results of Ornithological Explorations in the Commander Islands and in Kamtschatka. *Bull. U.S. Nat. Mus.*, **29**, pp. 1–382, 8 Pls., 7 figs., 1 map.

589 STEVEN, G. A. 1930. Bottom Fauna and the Food of Fishes. *Journ. Mar. Biol. Assoc.* (N.S.), XVI, pp. 677–700, 4 figs.

590 STEVENSON-HAMILTON, J. 1912. *Animal Life in Africa.* London, pp. xvii + 539, 98 illus., 6 maps.

591 STORER, T. I. 1925. A Synopsis of the Amphibia of California. *Univ. Cal. Pub. Zool.*, XXVII, pp. 1–342, 18 Pls., 42 figs.

592 STOW, GEORGE W. 1905. *The Native Races of South Africa.* London, pp. xvi + 618.

593 SÜFFERT, FRITZ. 1932–3. Phänomene Visueller Anpassung. I Bis III Mitteilung. Die visuelle Wirkung der Raupe und der Puppe von *Colias endusa* (Lepidoptera, Pieridæ), bedingt durch Form, Färbung, und Einstellung zur Lichtrichung. *Zeits. f. Morph. Ökol.*, **26**, pp. 147–316, 5 Pls., 65 figs.

594 SUMNER, F. B. 1911. The Adjustment of Flatfishes to various Backgrounds: A Study of Adaptive Color Change. *Journ. Exp. Zool. Philad.*, **10**, pp. 409–505, 13 Pls.

595 —— 1917. The Rôle of Isolation in the Formation of a narrowly localized Race of Deer-Mice. *Amer. Nat.*, pp. 173–85.

596 —— 1921. Desert and Lava-dwelling Mice, and the Problem of Protective Coloration in Mammals. *Journ. Mamm.*, Baltimore, **2**, pp. 75–86, 1 Pl.

597 —— 1926. An Analysis of Geographic Variation in Mice of the *Peromyscus polionotus* group from Florida and Alabama. *Ibid.*, 7, **3**, pp. 149–84, 3 Pls.

598 —— 1932. Genetic, Distributional and Evolutionary Studies of the Subspecies of Deer-Mice (*Peromyscus*). *Bibliographia Genetica*, **9**, pp. 1–106, 24 figs.

599 —— 1934. Does 'Protective Coloration' protect?—Results of some Experiments with Fishes and Birds. *Proc. Nat. Acad. Sci., Washington*, 20, pp. 559–64.

600 SUMNER, F. B. 1935. Evidence for the Protective Value of Changeable Coloration in Fishes. *Amer. Nat.*, LXIX, pp. 245–66, 4 figs.

601 —— 1935. Studies of Protective Color Change. III. Experiments with Fishes both as Predators and Prey. *Proc. Nat. Acad. Sci., Washington*, **21**, pp. 345–53. 4 figs.

602 —— and SWARTH, H. S. 1924. The supposed Effects of the Color Tone of the Background upon the Coat Color of Mammals. *Journ. Mamm.*, Baltimore, 5, **2**, pp. 81–113, 7 Pls.

603 SURFACE, H. A. 1906. The Serpents of Pennsylvania. *Monthly Bull. Div. Zool., Penn. Dept. Agric.*, **4**, pp. 115–202.

604 —— 1913. First Report on the Economic Features of the Amphibians of Pennsylvania. *Ibid.*, **3**, pp. 67–152.

605 SWINHOE, ROBERT. 1858. A few Remarks on the Fauna of Amoy. *Zoologist*, XVI, pp. 6222–31.

606 —— 1862. On the Mammals of the Island of Formosa (China). *Proc. Zool. Soc. London*, pp. 347–65, 4 Pls.

607 SWYNNERTON, C. F. M. 1915. A brief preliminary Statement of a few of the Results of Five Years special Testing of the Theories of Mimicry. *Proc. Ent. Soc. London*, pp. xxxii–xlii.

608 —— 1916. On the Coloration of the Mouths and Eggs of Birds. II. On the Coloration of Eggs. *Ibis*, Ser. 10, IV, **4**, pp. 529–606, 1 Pl.

609 —— 1919. Experiments and Observations bearing on the Explanation of Form and Colouring, 1908–1913. *Journ. Linn. Soc. Zool.*, XXXIII, pp. 203–385.

610 —— 1926. An Investigation into the Defences of Butterflies of the Genus *Charaxes*. *3rd Int. Ent. Congress, Zürich* (1925), **2**, pp. 478–506, 1 Pl.

611 THAYER, ABBOTT H. 1896. The Law which underlies Protective Coloration. *The Auk*, XIII, **2**, pp. 124–9.

612 —— 1896. Further remarks on the Law which underlies Protective Coloration. *Ibid.*, pp. 318–20.

613 —— 1903. Protective Coloration in its Relation to Mimicry, Common Warning Colours and Sexual Selection. *Trans. Ent. Soc. London*, pp. 553–69.

614 —— 1909. An Arraignment of the Theories of Mimicry and Warning Colours. *Pop. Sci. Mon. N.Y.*, **75**, pp. 550–70.

615 —— 1911. Concealing Coloration. *The Auk*, XXVIII, **1**, pp. 146–8.

616 —— 1911. Concealing Coloration. *Pop. Sci. Mon.*, **79**, pp. 20–35.

617 —— 1911. Concealing Coloration : A Demand for Investigation of my Tests of the Effacive Power of Patterns. *The Auk*, XXVIII, **4**, pp. 460–4.

618 —— 1912. Concealing Coloration : an Answer to Theodore Roosevelt. *Bull. Amer. Mus. Nat. Hist.*, XXXI, pp. 313–21.

619 THAYER, GERALD H. 1909. *Concealing-Coloration in the Animal Kingdom. An exposition of the Laws of Disguise through Color and Pattern.* New York, pp. xix + 260, 16 Pls., 140 figs.

620 THÉRY, ANDRÉ, et CERF, F. LE. 1907. Note sur *Phyllomorpha algirica*. *Luc. Ann. de l'Assoc. des Nat. de Levallois-Perret*, pp. 20–1.

621 THOMSON, D. LANDSBOROUGH. 1923–5. Note upon an Association between Spider-Crab and Sea-Anemone. *Journ. Mar. Biol. Ass. Plymouth*, XIII (N.S.), pp. 243–4.

622 THOULESS, ROBERT H. 1932. Individual Differences in Phenomenal Regression. *Brit. Journ. Psych.*, XXII, pp. 216–41, 4 figs.

623 —— 1935. Protective Coloration as a Problem in the Psychology of Perception. *Rept. Brit. Assn. Adv. Sci.*, p. 385.

624 TILLYARD, R. J. 1917. *The Biology of Dragonflies.* Cambridge, pp. xii + 396, 4 Pls., 188 figs.

625 —— 1926. *The Insects of Australia and New Zealand.* Sydney, 560 pp., 44 Pls.

626 TIRALA, LOTHAR G. 1923. Die Form als Reiz. Experimental untersuchung an Libellen und an Vögeln (Wellensittichen und Kanarienvögeln) nebst einer Betrachtung über das Verhältnis von Mechanismus, Biologie und Tierpsychologie. *Zool. Jahrb. Abt. Allg. Zool.*, **39**, pp. 395–442.

627 TOMLINSON, H. J. 1930. A Study in Instinct. *Windsor Mag.*, August, p. 362.

628 TOWNSEND, C. H. 1909. Observations on Instantaneous Changes in Colour among Tropical Fishes. *13th Ann. Rept. New York Rep. Zool. Soc.*, pp. 93–120, 12 Pls.

629 —— 1929. Records of Changes in Color among Fishes. *Zoologica N.Y.*, IX, **9**, pp. 321–42, 27 Pls., 15 figs.

630 TRIMEN, ROLAND. 1869. On some remarkable Mimetic Analogies among African Butterflies. *Trans. Linn. Soc., Zool.*, XXVI, pp. 497–522, 2 Pls.

631 —— 1897. Mimicry in Insects. *Proc. Ent. Soc. London*, pp. lxxiv–xcvii.

✓ 632 TURNER, E. L. 1932. Observations on Insects eaten or rejected by British Birds. *Proc. Ent. Soc. London*, VII, pp. 96–7.

633 TYLOR, ALFRED. 1886. *Coloration in Animals and Plants.* London, pp. xiv + 105, 17 figs.

634 TYTLER, R. C. 1864. Observations on a few Species of Geckos alive in the Possession of the Author. *Journ. Asiat. Soc. Bengal*, XXXIII, pp. 535–48.

635 URECH, F. 1893. Beiträge zur Kenntniss der Farbe von Insektenschuppen. *Zeits. wiss. Zool.*, **57**, pp. 306–84.

636 URQUHART, A. T. 1882. Protective Resemblances among New Zealand Spiders. *N.Z. Journ. Sci.*, I (1882–3), pp. 230–1.

✓ 637 UVAROV, B. P. 1932. The Value of ' Protective ' Adaptations of Animals. *Nature*, **130**, pp. 66–7.

638 —— 1932. ' Protective ' Adaptations of Animals. *Ibid.*, pp. 696–7.

639 VANDERPLANK, F. L. 1934. The Effect of Infra-red Waves on Tawny Owls (*Strix aluco*). *Proc. Zool. Soc. London*, pp. 505–7.

639*a* VARLEY, G. C. 1939. Frightening Attitudes and Floral Simulation in Praying Mantids. *Proc. Roy. Ent. Soc. London*, **14**, pp. 91–6, 1 fig.

640 VERNE, J. 1926. *Les Pigments dans l'Organisme animal. Chimie, morphologie, physiologie, ethologie.* Paris, pp. xv + 608.

641 VERRIER, M. L. 1933. Recherches sur le Champ visuel des Vertébrés. Détermination du Champ de Vision de *Scorpæna scrofa* L. *C.R. Acad. Sci. Paris*, 197, **22**, pp. 1346–8, 1 fig.

642 —— 1936. Recherches sur la Vision des Oiseaux diurnes. *Bull. biol. France-Belg.*, pp. 197–232, 18 figs.

643 VERWEY, J. 1930. Coral Reef Studies. 1. The Symbiosis between Damselfishes and Sea Anemones in Batavia Bay. *Treubia*, Buitenzorg, XII, **3–4**, pp. 305–66, 2 Pls., and map.

644 VIGNON, P. 1924. Sur le mimétisme homotypique chez quelques Sauterelles phanéropterides de l'Amérique tropicale. *C.R. Acad. Sci. Paris*, **178**, pp. 1852–4.

645 WALL, FRANK. 1921. *Ophidia Taprobanica, or the Snakes of Ceylon.* Colombo, pp. xxii + 581, 1 Pl., 98 figs.

646 WALLACE, A. R. 1889. *Darwinism.* London, pp. xvi + 494, 37 figs.

647 WALLS, G. L. 1932. Pupil Shapes in Reptilian Eyes. *Bull. Antivenin Inst. Amer.*, **5**, pp. 68–70.

648 WALSH, J. H. TULL. 1891. On certain Spiders which mimic Ants. *Journ. Asiat. Soc., Bengal*, LX (**2**), pp. 1–4.

649 WARNER, L. H. 1931. The Problem of Color Vision in Fishes. *Quart. Rev. Biol. Baltimore*, VI, pp. 329–48, 4 figs.

650 WASHBURN, M. F., and BENTLEY, I. M. 1906. The Establishment of an Association involving Color-discrimination in the Creek Chub *Semotilus atromaculatus. Journ. Comp. Neurol. Psych.*, **16**, pp. 113–25.

651 WATSON, D. M. S. 1930. Adaptation. Presidential Address, Section D, *Rept. Brit. Assn. Adv. Sci.*, 1929, pp. 88–99.

652 WATSON, JOHN B. 1909. Some Experiments bearing upon Color-vision in Monkeys. *Journ. Comp. Neurol. Psychol.*, **19**, pp. 1–28.

653 WATTENWYL, C. BRUNNER V. 1884. *Ueber hypertelische Nachahmungen bei den Orthopteren. Verhandlungen zool.-bot. Gesellschaft Wien.*, XXXIII, pp. 247–9, 1 Pl.

654 WEBSTER, F. M. 1895. Protective Mimicry in Spiders. *Canad. Entom.*, XXVI, pp. 36–7.

655 —— 1897. Warning Colours, Protective Mimicry and Protective Coloration. *27th Ann. Rept. Ent. Soc. Ontario* (1896), pp. 80–6.

656 WEED, C. M., and DEARBORN, N. 1924. *Birds in their Relations to Man.* Philadelphia, pp. viii + 414.

657 WEIR, J. JENNER. 1869. On Insects and Insectivorous Birds ; and especially on the Relation between the Colour and the Edibility of Lepidoptera and their Larvæ. *Trans. Ent. Soc. London*, pp. 21–6.

658 WEISMANN, AUGUST. 1882. *Studies in the Theory of Descent.* (Trans. Meldola.) London, Vol. I, pp. xxxvi + 400, 1 Pl. Vol. II, pp. 401–729, 6 Pls.

659 WELLS, H. G., HUXLEY, JULIAN, and WELLS, G. P. 1931. *The Science of Life.* VI, **4**, Colour and Pattern in Life. London, pp. 568–77.

660 WERNER, FRANZ. 1907. Das Ende der Mimikry-hypothese. *Biol. Zentralbl.*, Leipzig, **27**, pp. 174–85.

661 WERTH, E. 1915. Kurzer Überblick über die gesamtfrage der Ornithophilie. *Bot. Jahrb.*, **53**, pp. 314–78, 14 figs.

662 WHEELER, W. M. 1913. Notes on the Habits of some Central American Stingless Bees. *Psyche*, **20**, pp. 1–9.

663 WHITAKER, ARTHUR. 1906. The Development of the Senses in Bats. *Naturalist*, pp. 145–51, 1 Pl.

664 WHITE, C. M. N. 1935. Meadow-Pipits eating the ' Magpie Moth ', *Abraxas grossulariata* L. *Proc. Roy. Ent. Soc. London*, pp. 80–1.

665 WHITE, GERTRUDE M. 1919. Association and Color Discrimination in Mud Minnows and Sticklebacks. *Journ. Exp. Zool.*, **27**, pp. 443–98.

666 WHITE, STEWART E. (undated). *The Rediscovered Country.* London, pp. viii + 358.

667 WIGGLESWORTH, V. B. 1934. *Insect Physiology.* London, pp. x + 134, 13 figs.

668 WILLEY, A. 1905. Leaf-mimicry. *Spolia Zeylanica*, II, pp. 51–5, 1 fig.

669 —— 1911. *Convergence in Evolution.* London, pp. xvi + 177, 1 Pl., 11 figs.

670 WILLIAMS, C. B. 1918. The Food of the Mongoose in Trinidad. *Bull. Dept. Agric. Trinidad, Port of Spain*, **17**, pp. 167–86.

671 —— 1922. Notes on the Food and Habits of some Trinidad Birds. *Trinidad and Tobago Bulletin*, XX, pp. 123–85.

672 WILLIAMS, C. E. 1904. Notes on the Life History of *Gongylus gonyloides*, a Mantis of the Tribe Empusides and a Floral Simulator. *Trans. Ent. Soc. London*, pp. 125–37.

673 WISSENBURGH, J. C., et TIBOUT, P. H. C. 1921–2. Choix basé sur l'aperception complexe chez les Cobayes. *Arch. néerl. de Physiol.*, VI, pp. 149–62, 1 fig.

674 WITHERBY, H. F. 1920–4. *A Practical Handbook of British Birds.* London, Vols. I, II and III.

675 WOOD, C. A. 1925. Colour Sense of the Satin Bower Bird. *Amer. Journ. Ophth.*, **8**, pp. 120–2.

676 WOOD, F. G. 1870. *The Natural History of Man.* London, II, pp. vii + 864.

677 WOOLLARD, H. H. 1927. The Differentiation of the Retina in the Primates. *Proc. Zool. Soc. London*, pp. 1–17, 4 Pls.

678 WRIGHT, A. H. 1914. North American Anura: Life-histories of the Anura of Ithaca, New York. *Carnegie Inst. Wash. Pub.*, **197**, pp. vii + 98, 21 Pls.

679 YERKES, R. M. 1915. Color Vision in the Ring-Dove. *Proc. Nat. Acad. Sci., Washington*, **1**, pp. 117–19.

680 —— and EISENBERG, A. M. 1915. Preliminaries to a Study of Colour Vision in the Ring-Dove *Turtus risorius*. *Journ. Animal Behav.*, V, pp. 25–43, 1 fig.

681 YOUNG, R. T. 1916. Some Experiments on Protective Coloration. *Journ. Exp. Zool.*, **20**, pp. 457–507, 3 Pls., 8 figs.

682 ZERRAHN, G. Z. 1933. Formdressur und Formunterscheidung bei der Honigbiene. *Zeits. f. vergl. Physiol.*, **20**, pp. 117–50, 20 figs.

683 ZOLOTAREVSKY, B. N. 1930. Sur le Comportement du *Phymateus puniceus* Bol. *Bull. Soc. Ent. Fr.*, pp. 283–6.

684 ZOOND, A., and EYRE, J. 1934. Studies in Reptilian Colour Response. I. The Bionomics and Physiology of the Pigmentary Activity of the Chameleon. *Phil. Trans.*, London (B), 223, **495**, pp. 27–55, 2 Pls.

685 ZUGMAYER, E. 1908. Über Mimikry und verwandte Erscheinungen. *Zeits. wiss. Zool.*, XC, pp. 313–26.

INDEX OF SCIENTIFIC NAMES

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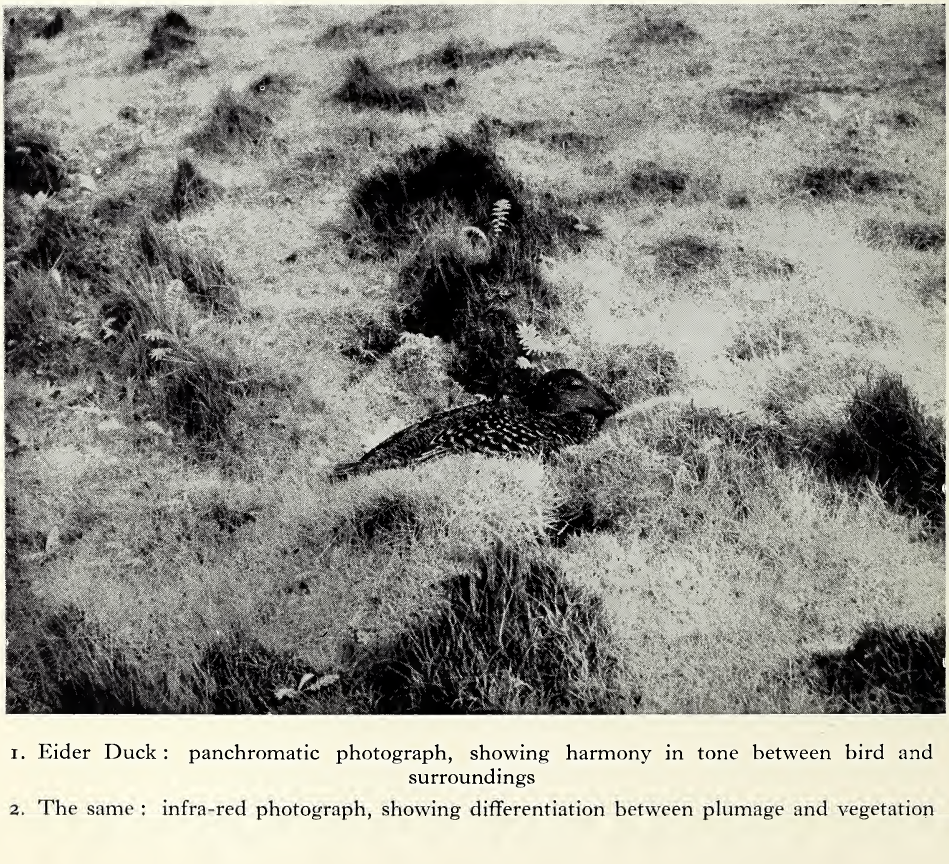
1. *Polychrus marmoratus.* (*Pará*)
2. Abbess Lizard (*Corythophanes cristatus*). (*From a specimen in the Reptile House, Regent's Park*)

PLATE 2

1. Horned Viper (*Cerastes cerastes*). (*From a specimen in the Reptile House, Regent's Park*)
2. Pogge (*Agonus cataphractus*). (*Millport*)

1. *Leptophyes punctatissima :* panchromatic photograph, showing harmony in tone between the grasshopper and the leaf on which it is resting

2. The same : infra-red photograph, showing differentiation between the insect and its background

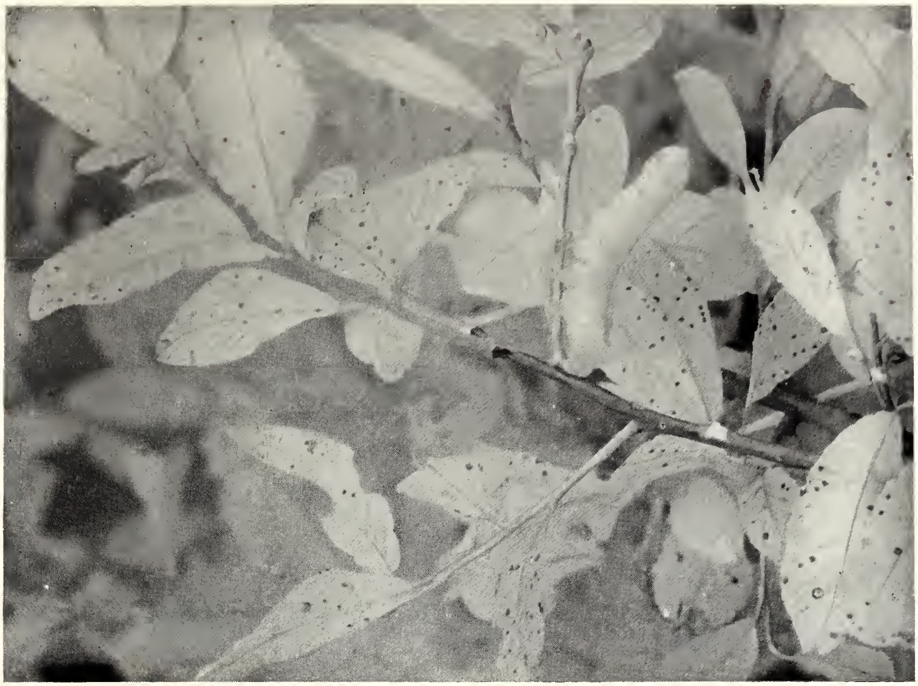


1. Eider Duck: panchromatic photograph, showing harmony in tone between bird and surroundings

2. The same: infra-red photograph, showing differentiation between plumage and vegetation

PLATE 5

Larva of Eyed Hawk-moth (*Smerinthus ocellatus*): panchromatic photograph



The same: infra-red photograph

PLATE 6

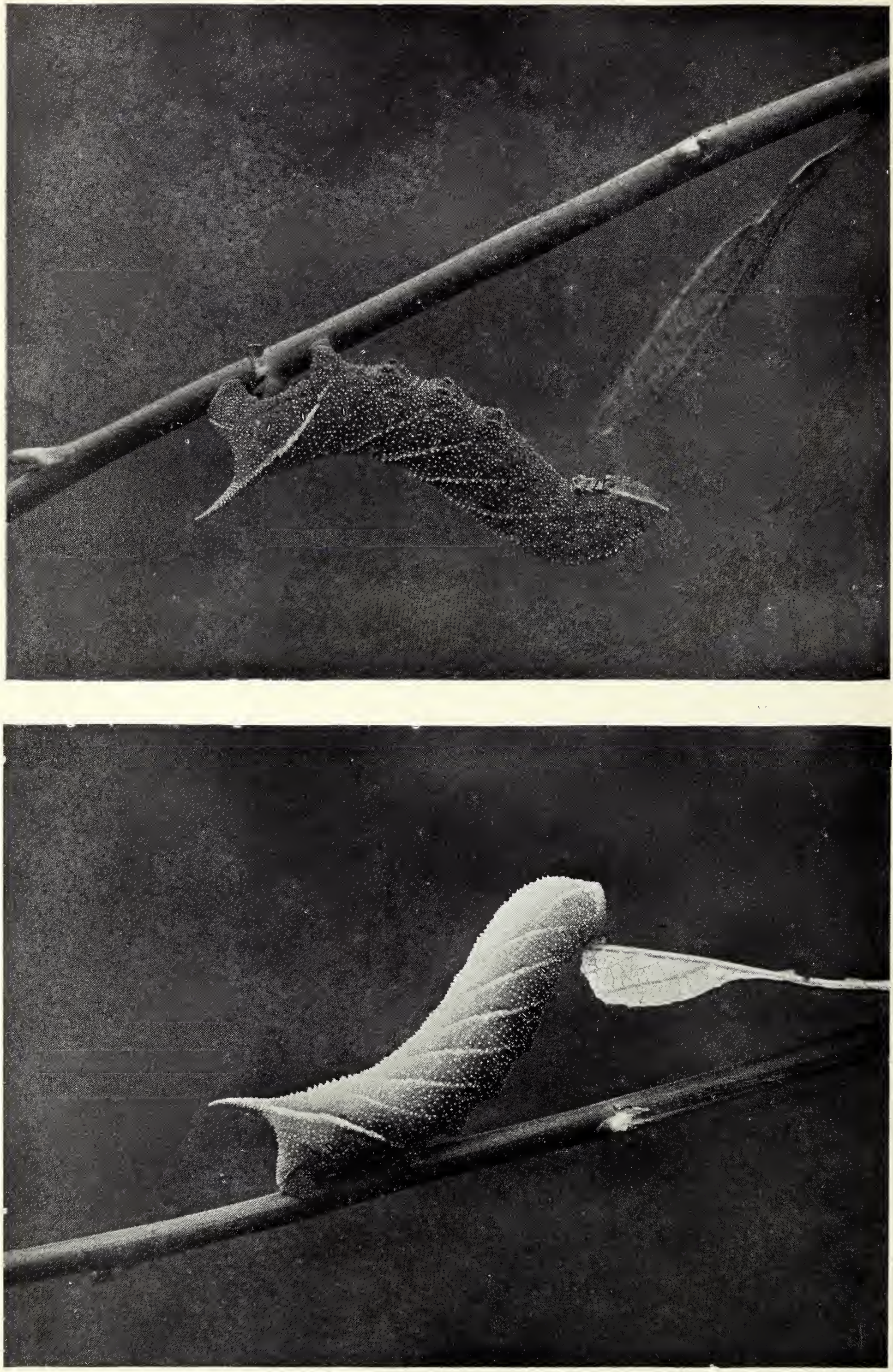
Hyla cœrulea : panchromatic photograph

The same : infra-red photograph

1. Colour resemblance alone is not sufficient to afford concealment. A white cock, photographed out-of-doors in natural diffused daylight, stands out conspicuously against a white background

2. Bush Buck. An example of obliterative shading, the effect of which is greatly to diminish the appearance of solidity due to relief. (*Portuguese East Africa*)

PLATE 8



Larva of Eyed Hawk-moth (*Smerinthus ocellatus*), showing the relation between inverted attitude and inverted countershading: 1. The normal attitude of rest; 2. The same, inverted

1. *Rana adspersa.* (*Portuguese East Africa*)
2. *Ceratophrys cornuta.* (*From a specimen in captivity*)

Garden Carpet Moth (*Xanthorhoë fluctuata*), showing the cryptic effect of a disruptive pattern having some elements which blend in tone with the background while others differ strongly from it—differential blending. (*Hampshire*)

Oak Beauty Moth (*Pachys strataria*). Seen at rest on the lichen-covered bark of an oak, this moth beautifully illustrates the cryptic value of a disruptive pattern. (*Sussex*)

Garden Carpet Moth (*Xanthorhoë fluctuata*) at rest on the bark of an elm. (*Suffolk*)

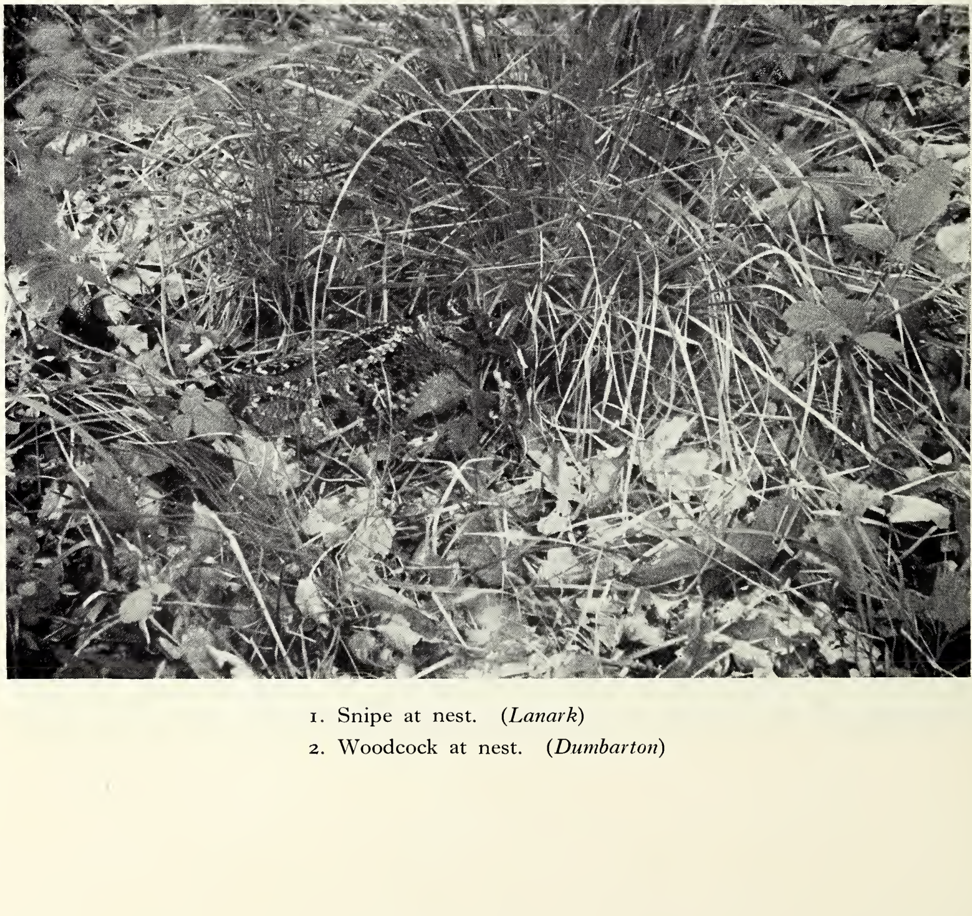
PLATE 13

Young Ringed Plover. The coloration beautifully illustrates the value of a disruptive pattern when combined with countershading, and correlated with the configuration of the environment. Note the disruptive contrast produced by the adjacent light and dark elements in the neck collar, which serves optically to break the chick into two parts. (*Norfolk*)

Scops Owl. (*Pará*)

PLATE 15

Nightjar brooding over eggs. (*Suffolk*)



1. Snipe at nest. (*Lanark*)
2. Woodcock at nest. (*Dumbarton*)

1. Eider Duck at nest. (*Farne Islands*)
2. Golden Plover at nest. (*Dumbarton*)

1. Nest and eggs of Ringed Plover. (*Norfolk*)
2. Nest and eggs of Lapwing. (*Lanark*)

PLATE 19

Young Woodcock. When seen against the irregular patchwork of fallen leaves and deep shadows, the newly-hatched young of this species provide a puzzle for the sharpest eyes. Their concealment is due to the effect of a disruptive pattern of bold contrasts, which catches the observer's eye and distracts his attention from the form upon which it is superimposed. (*Bute*)

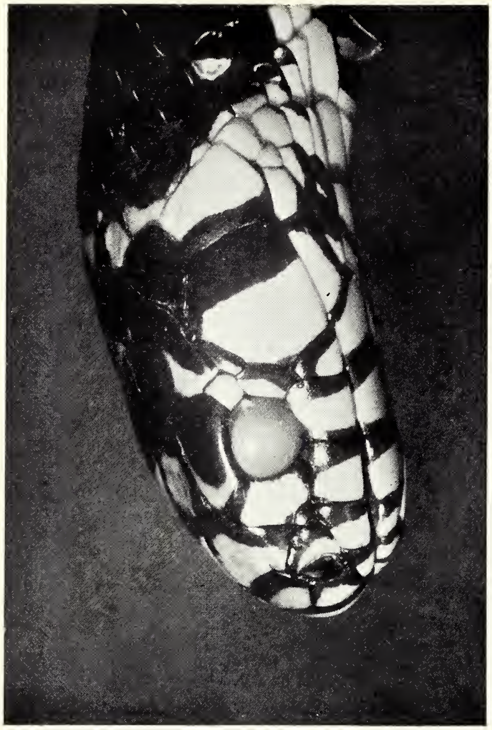
Young Arctic Tern. (*Farne Islands*)

PLATE 21

Megalixalus fornasinii. (*Portuguese East Africa*)

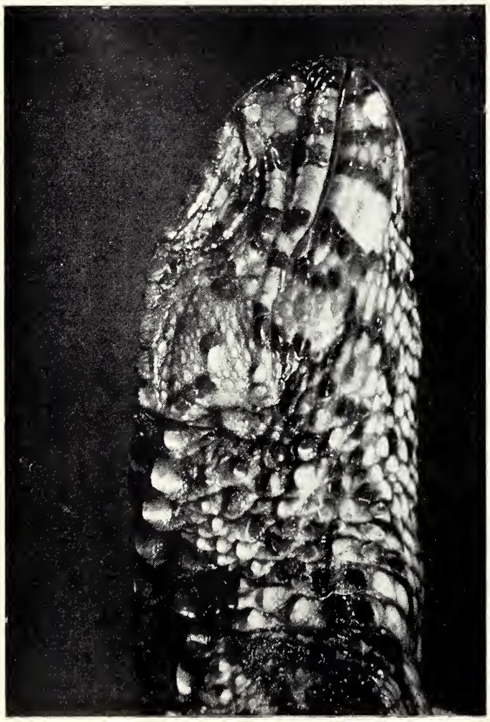
Kassina senegalensis. (*Portuguese East Africa*)

PLATE 22



Spilotes pullatus

Vipera superciliaris



Shinisaurus crocodilurus

Corythophanes cristatus

Edalorhina buckleyi

Bufo valliceps

Bufo typhonius

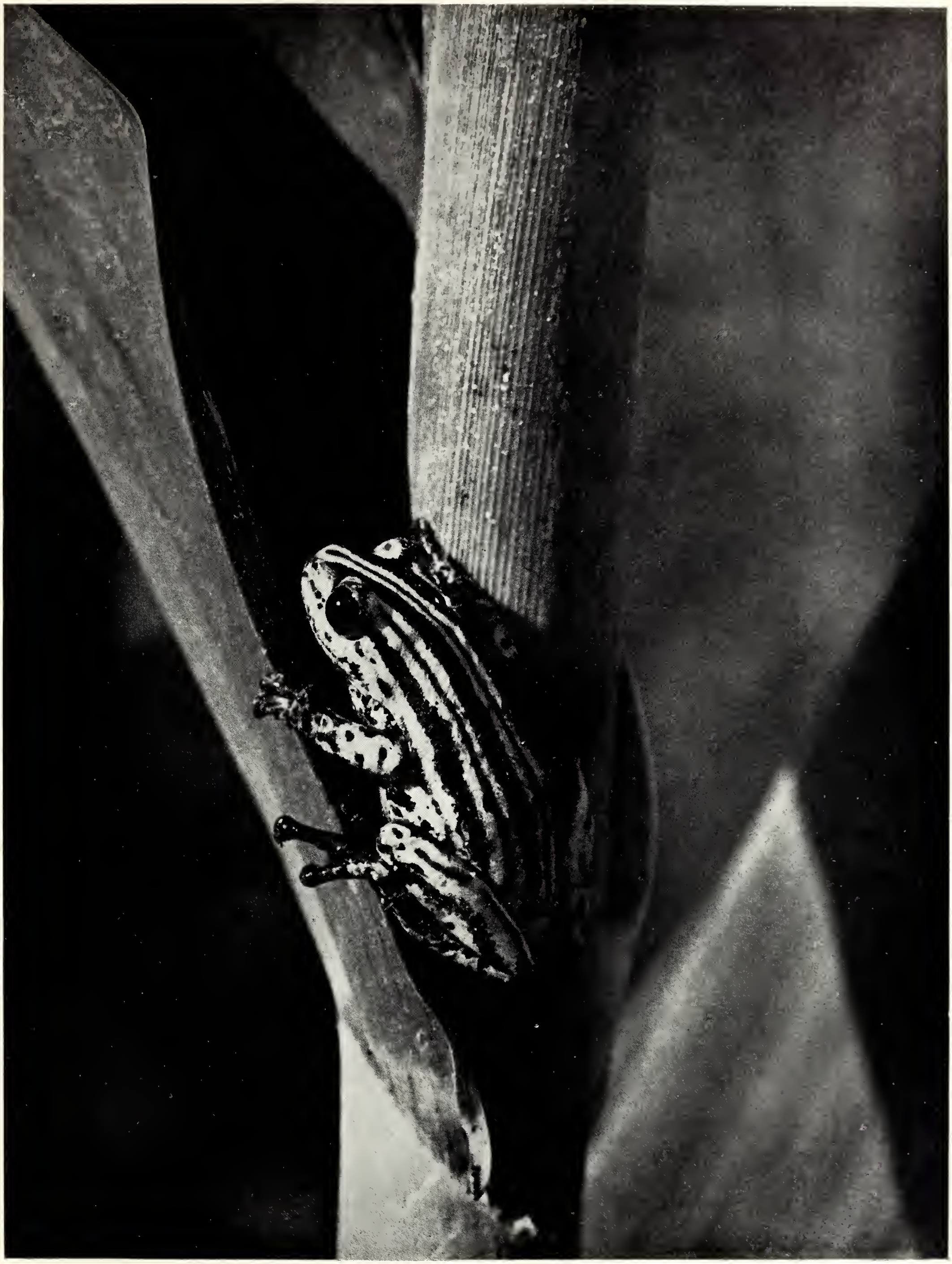
Bufo typhonius

PLATE 24

Concealment of the eye by coincident disruptive patterns: 1. *Rana temporaria*. (*Sussex*.) 2. *Constrictor constrictor*. (*From a specimen in the Reptile House, Regent's Park*)

1. Gaboon Viper (*Bitis gabonica*)
2. Gemsbok (*Oryx gazella*)

1. Larva of Pale Tussock Moth (*Dasychira pudibunda*). (*In captivity*)
2. Blood-vein Moth (*Timandra amata*). (*Hampshire*)

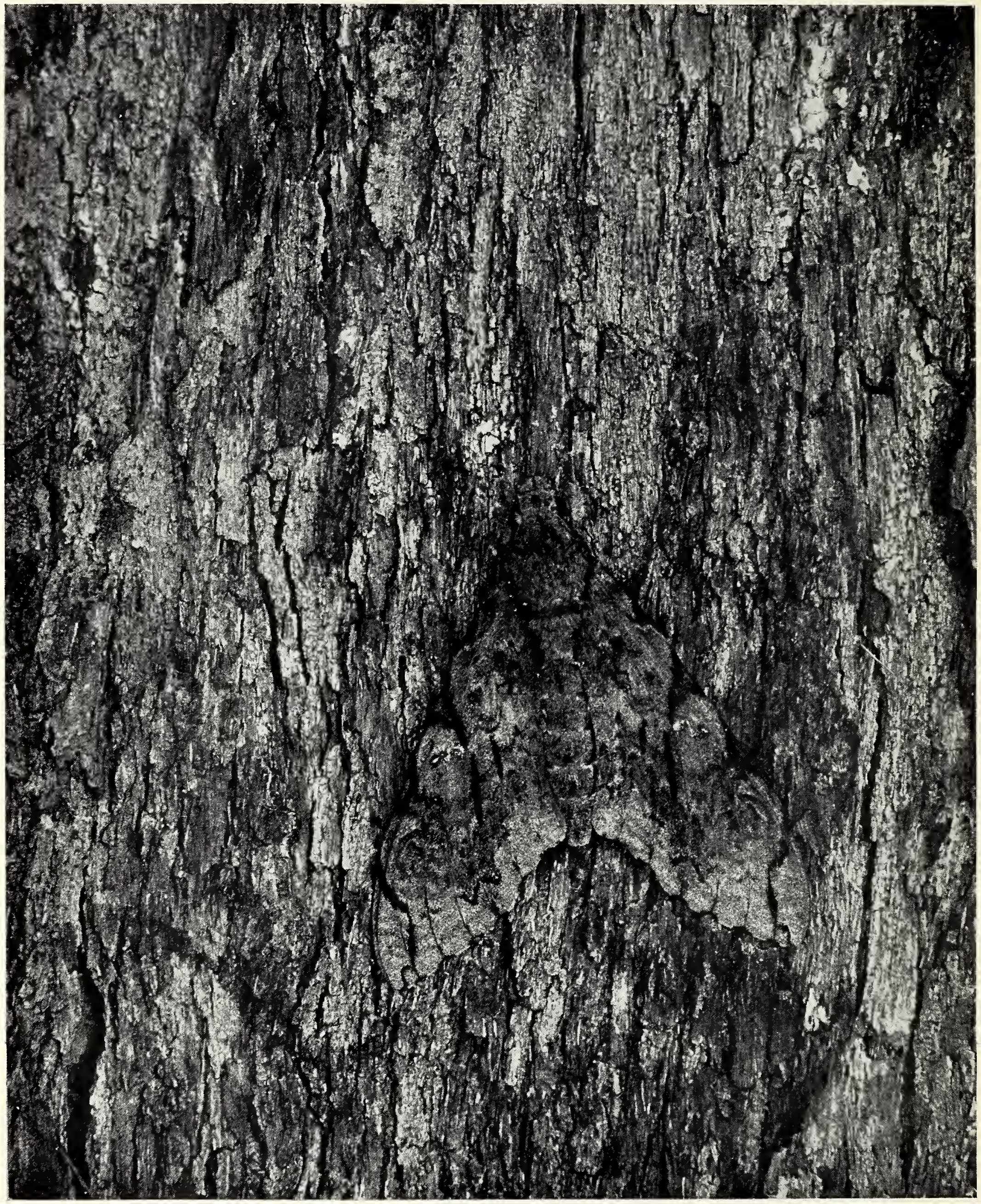


Hyperolius marmoratus. (*Lower Zambesi*)

1. *Chiromantis xerampelina*, an East African tree-frog, whose coloration affords good concealment on the grey branches among which it lives. (*Lower Zambesi*)

2. *Rana temporaria*, as it appears in its natural surroundings. Colour harmony, countershading and characteristic pattern are combined in the frog's cryptic dress. (*Sussex*)

Cryptic resemblance to a background of rock: 1. *Tarentola delalandii.* (*Hierro, Canary Islands.*) 2. Marbled Beauty Moth (*Bryophila perla*). (*Wiltshire*)



An East African Hawk-moth (*Xanthopan m. morgani*), seen in its natural attitude of rest. This moth attains a wonderful degree of concealment through the pattern on its wings, which closely reproduces that of the tree on which it rests. It will be seen that the dark markings are correlated with the carriage of the wings, so that in the natural resting posture they form an approximately parallel series ; that the moth instinctively alights with its body parallel to the tree trunk, so that the wing-pattern lies parallel to that of the bark which it simulates ; and that the insect applies itself flat against the surface, thus eliminating tell-tale shadows. (*Beira*)

1. Painted Lady (*Pyrameis cardui*), showing the interrupted marginal pattern which serves to confuse the outline of the wings. (*From a mounted specimen in the Museum of Zoology, Glasgow University*)

2. Grayling (*Satyrus semele*), showing the cryptic appearance of the butterfly when at rest in its natural surroundings. (*Hampshire*)

Scarce Tissue Moth (*Eucosmia certata*). Many moths whose wing-pattern lies at right angles to the body orientate themselves, when alighting, with the body in a horizontal, instead of a vertical, position—thus bringing the cryptic colour-scheme into closer relation to their immediate surroundings. (*Surrey*)

Willow Beauty Moth (*Boarmia gemmaria*). (*Hampshire*)

Tropical Rain Forest. (*Pará*)

PLATE 35

Bufo typhonius photographed in its natural forest surroundings of the Lower Amazon. This small toad is a wonderful example of special resemblance. Its likeness to a leaf depends upon a combination of form, coloration and habits. The form is extremely depressed ; the snout is pointed like the tip of a leaf ; the flanks are drawn out sideways into a sharp flange, which simulates the leaf-margin ; there is a mid-dorsal line which suggests a midrib ; and two jet-black spots on the back simulate deep shadow seen through holes in the ' leaf '. (*Pará*)

1. *Phyllium crurifolium.* (*From a specimen in captivity*)

2. *Sphodromantis virdis.* (*Portuguese East Africa*)

1. Buff-tip Moth (*Phalera bucephala*). (*Hampshire*)

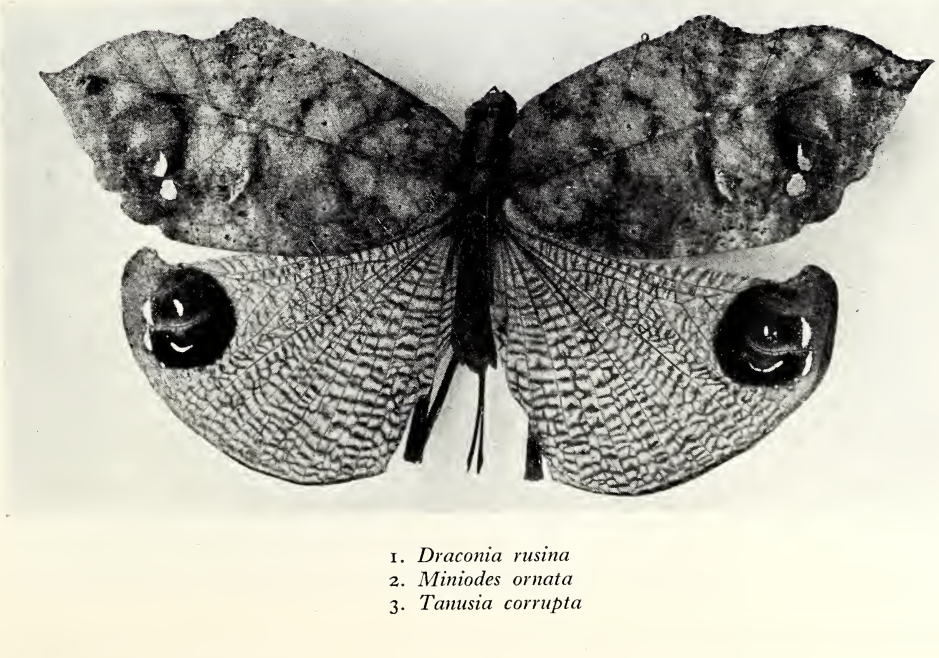
2. *Bufo superciliaris*. (*From a specimen in the Reptile House, Regent's Park*)

PLATE 38

3. *Chitoniscus feedjeanus*

1. *Cycloptera* sp.
2. *Cycloptera excellens*

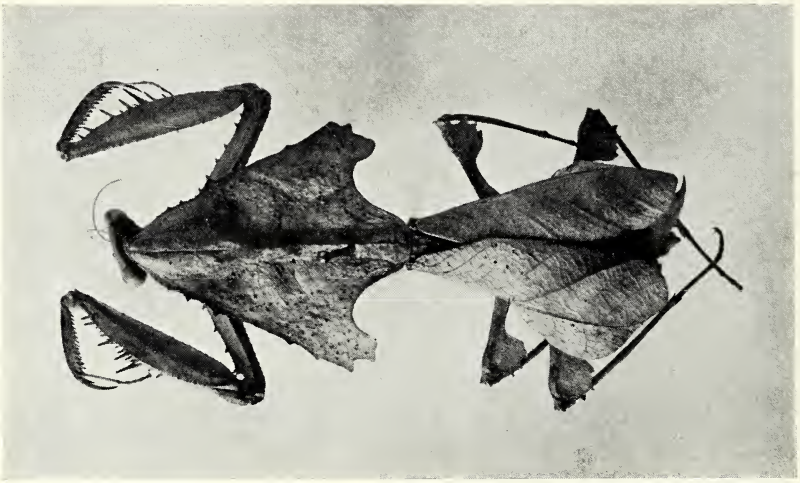
PLATE 39



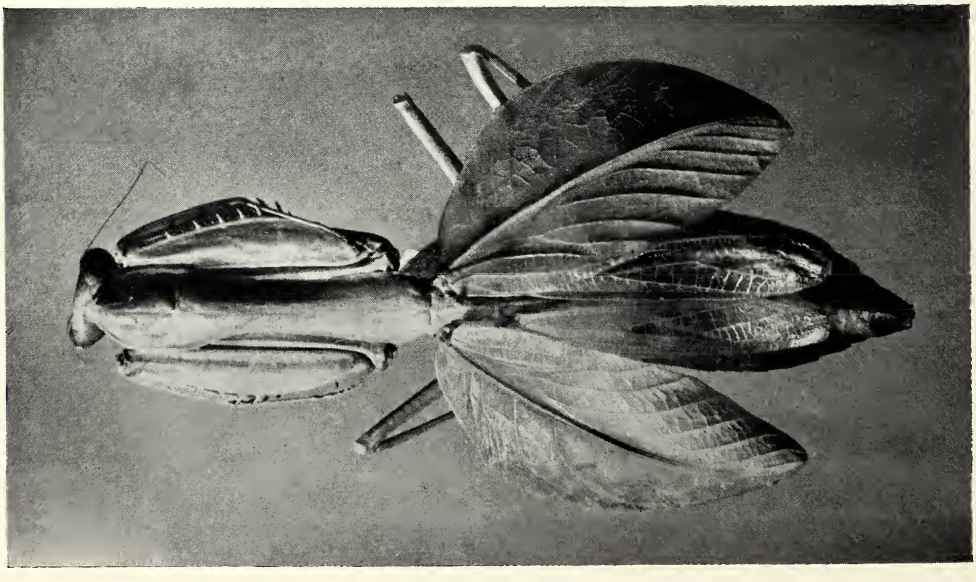
1. *Draconia rusina*
2. *Miniodes ornata*
3. *Tanusia corrupta*

PLATE 40

Chæradodis rhomboidea

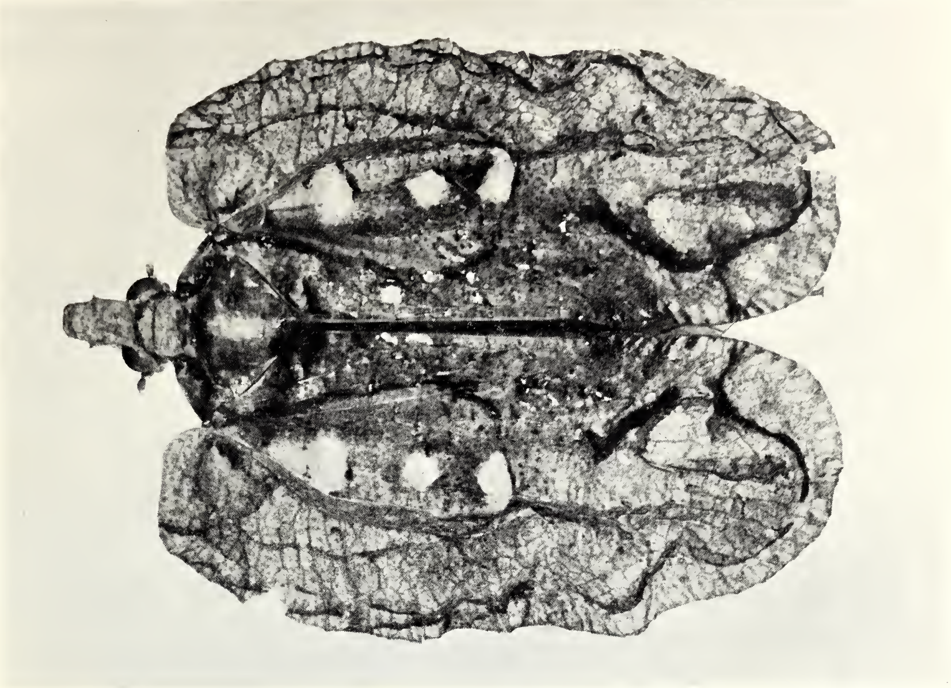


Deroplatys sp.



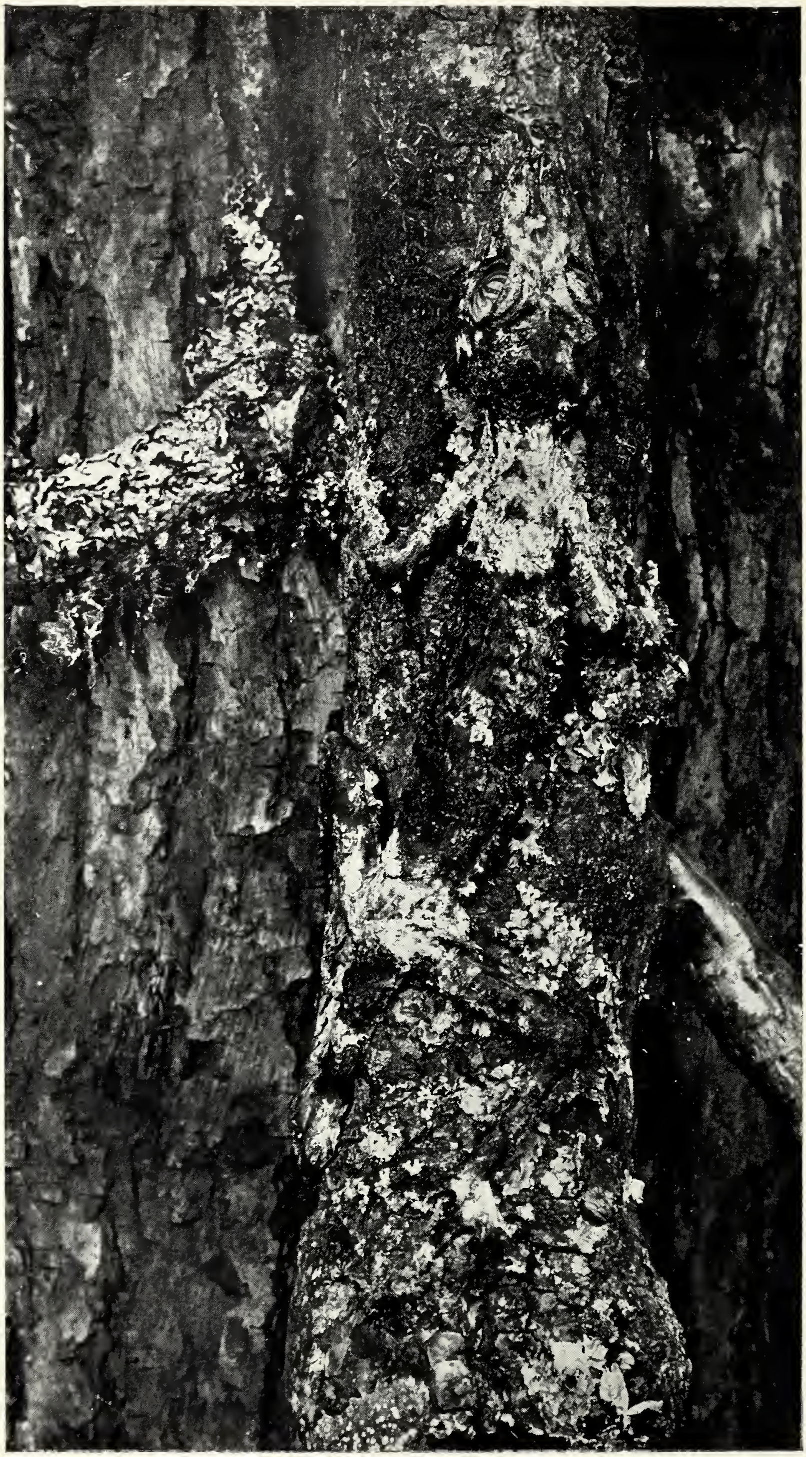
Stagmatoptera sp.

PLATE 41

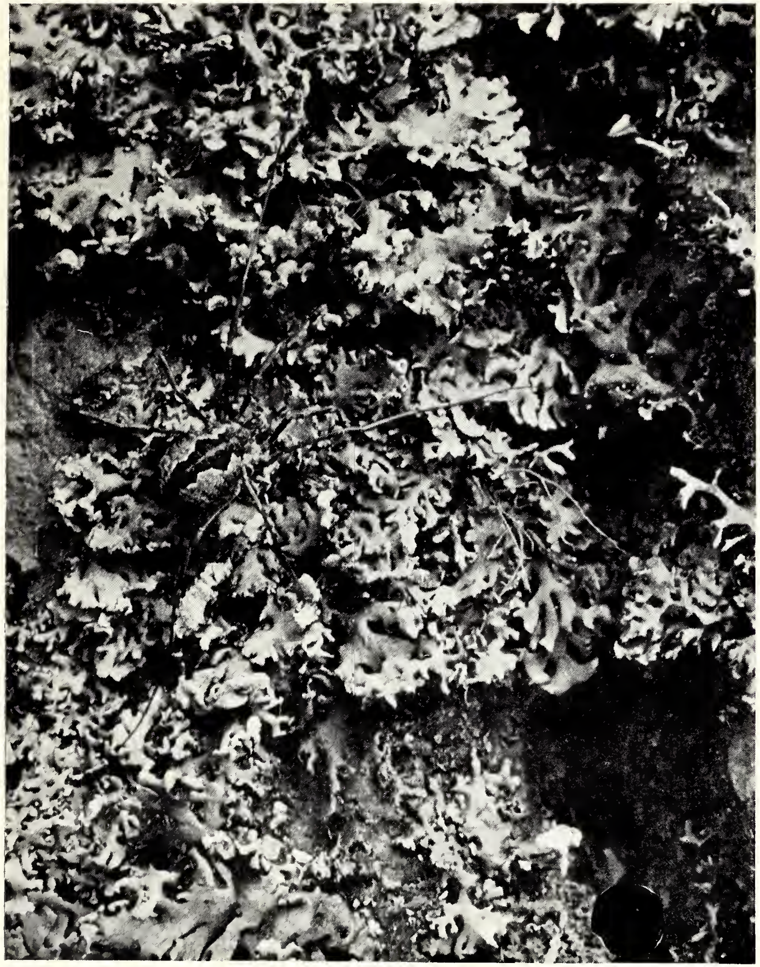


Flatoides dealbatus

Hyla langsdorfii



Malagasy Bark Gecko (*Uroplates fimbriatus*), showing the close adpression of the body to the bark, and the lateral flap-like expansions of the tail, which serve to reduce visibility due to shadows cast by the animal on its surroundings. (*From a specimen in the British Museum, Natural History*)



Phalangium opilio, on the bark of a Scots Pine. The cryptic function of a disruptive pattern is greatly enhanced if its lightest and darkest elements are placed in juxtaposition as seen, for instance, in this phalangid, which well illustrates the principle of maximum disruptive contrast. (*Northumberland*)

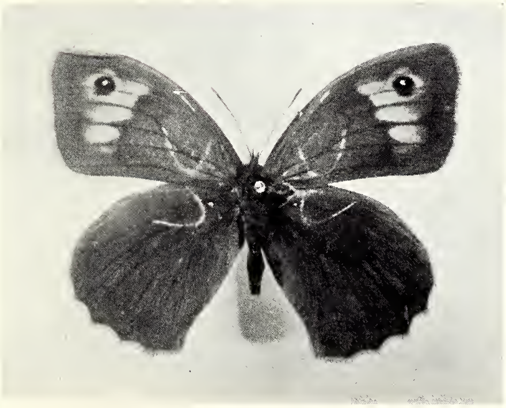
Lithinus nigrocristatus. Two specimens of this black and white, lichen-like Weevil (in addition to the mounted specimen) are seen above against a background of lichen-covered bark. (*From a preparation in the Museum of Zoology, Glasgow University*)

1. *Acrida turrita.* (*Gran Canaria*)
2. *Eremocharis insignis.* (*From a specimen in captivity*)

PLATE 45








1. *Cilix glaucata*
2. *Problepsis œgretta*
3. *Pararge megœra*
4. *Nemeobius lucina*
5. *Epinephele ianira*
6. *Haetera diaphana*

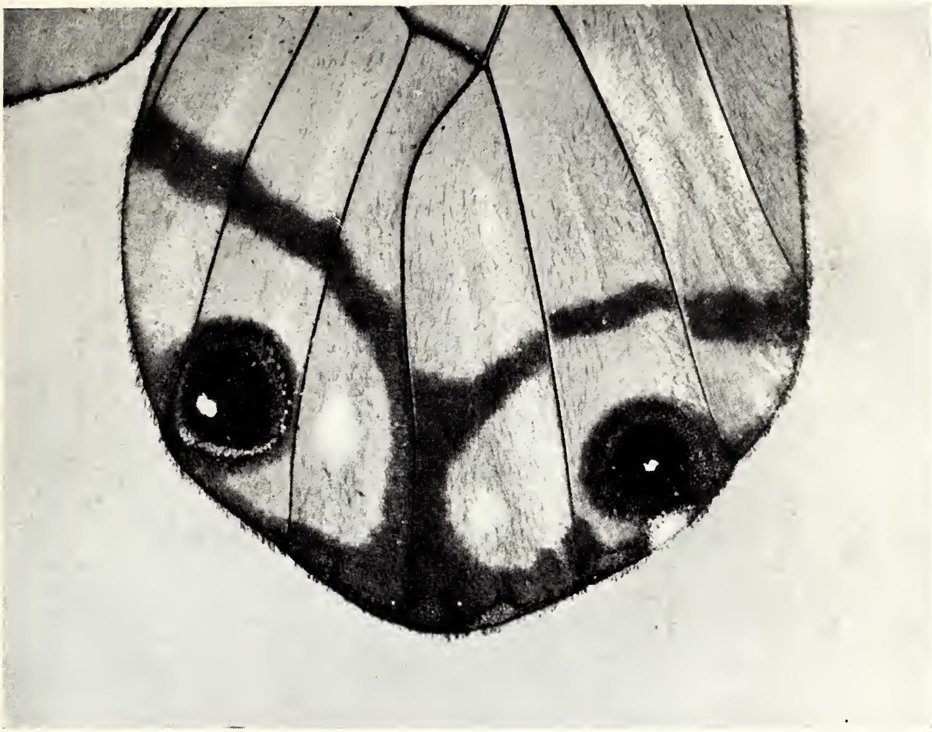
Lepidoptera: (1 and 2) showing special resemblance to excrement; (3 to 6) showing beak- or mouth-injuries

Edalorhina perezi

Leptodactylus mystacinus

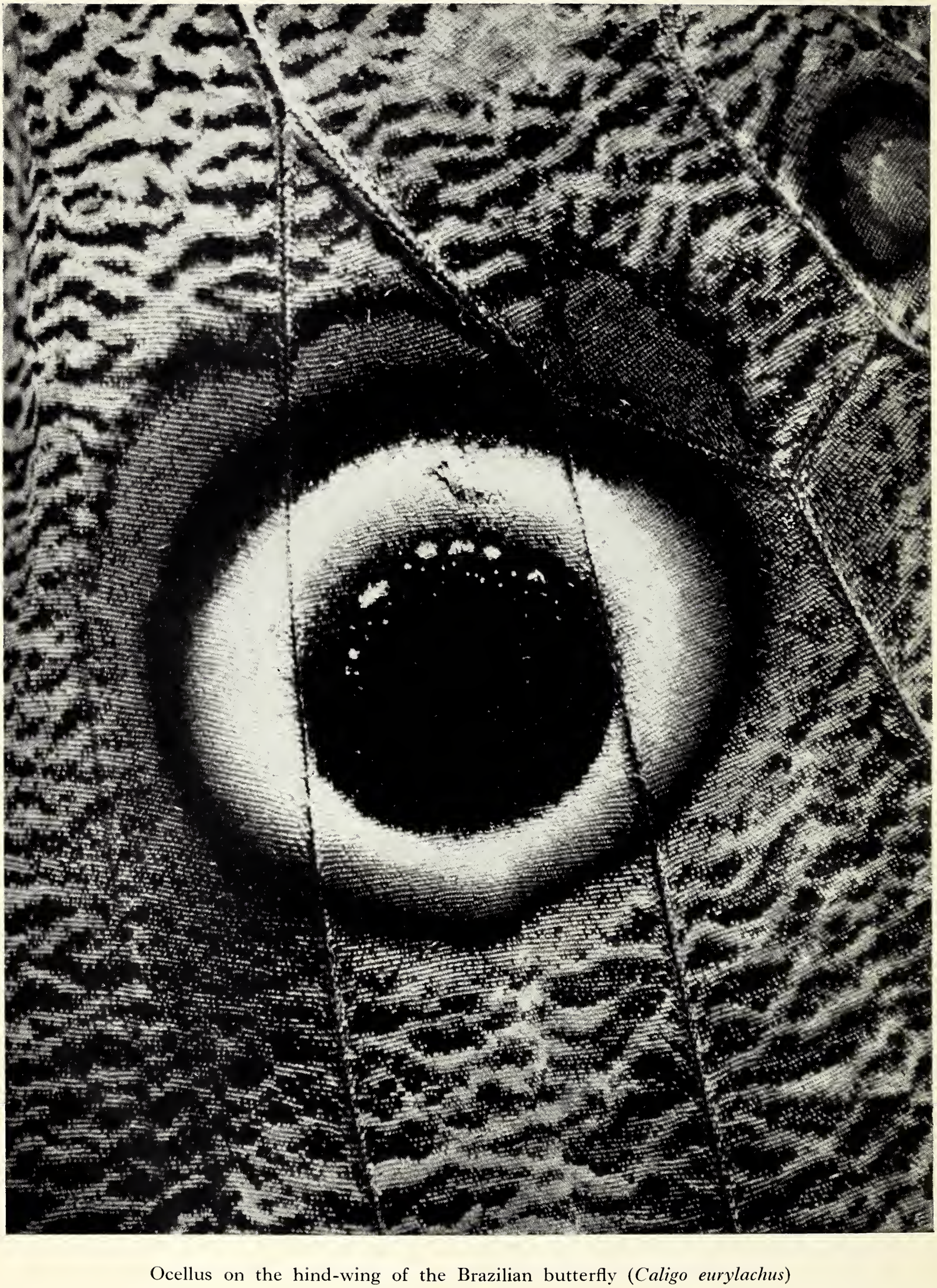
Eupemphix nattereri

Gastrophryne elegans



1. *Haetera diaphana :* Extremity of hind-wing
2. *Laternaria servillei*

PLATE 48



Ocellus on the hind-wing of the Brazilian butterfly (*Caligo eurylachus*)

Date Due

Due	Returned	Due	Returned
JUL 21 1987	JUL 20 1987 JA		
FEB 03 1996	DEC 21 1995		