

The Comparative Breeding Biology of the African Hornbills (Bucerotidæ).
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CONTENTS.

	Page
Introduction	331
Nest Construction	332
General Behaviour during Nest Occupation	335
Chronology of Events in the Nest	337
Nest Sanitation	339
The Condition of the Female in the Nest	340
Comparative Summary	344
References.....	345

INTRODUCTION.

Bannerman (2) recently summarized the nesting habits of the African hornbills as follows :—" The female lays her eggs in a hollow in a tree, the male (apparently) closing up the entrance with a hard substance and leaving only a small slit through which the female can pass her bill to receive the fruits he brings her . . . While incubating the eggs the female goes through a complete moult, shedding the feathers of the wings and tail . . . Probably all the species have similar breeding habits with the possible exception of *Bucorvus* (the Ground Hornbill), but we require much more information before we can write with authority of their individual characteristics." Bannerman was indeed able to add nothing to the particulars given some years previously by Chapin (6), who collated more information on the subject than any other worker, but himself described it as " fragmentary."

It is still true that what has been learnt of the nesting of African hornbills is very incomplete. Breeding notes, however perfunctory, have been published on only sixteen of the twenty-six African species*. But enough information, largely the product of the last five years, can now be brought together to show that there is great specific variation in the habits of the African hornbills, which may ultimately be reducible to generic variation. Moreover, the new information emphasizes still further the extent to which the hornbills differ from all other birds—not excepting the analogous Toucans (Rhamphastidæ)—in several aspects of their breeding biology.

The bibliography annexed to this paper is believed to be fairly exhaustive for first-hand observations bearing on the nesting, but it is intended to exclude mere oology and casual unverified native information such as constitutes so much of Livingstone's account (17) of *Lophoceros erythrorhynchus*. It is evident that the chief concern of anyone, white as well as black, fortunate enough to find a hornbill's nest has nearly always been to destroy it. The only species for which sustained observations in nature are available are *Bycanistes albotibialis* (7), *Lophoceros flavirostris* (14), *Bycanistes cristatus* and *L. deckeni* (20).

* Twenty-five in the 'Systema Avium Æthiopicarum,' to which must be added the subsequently described *Lophoceros bradfieldi* Roberts. The notes published on the biggest of the African hornbills, *Bucorvus cafer*, which is also the most widely distributed, are amongst the most meagre.

The data under the last reference stand alone as the only histories of African hornbills' nests where there was no fatal nor otherwise conclusive interference by man. Records of the behaviour of captive birds have been included, though they must be used with great caution.

In an attempt to supplement the very incomplete information in the literature I have applied to a large number of ornithologists. For generously supplying me with unpublished observations and for assisting me with references I make my grateful acknowledgments to Mr. G. L. Bates, Dr. J. P. Chapin, Dr. H. Friedmann, Capt. C. H. B. Grant, Herr W. Hoesch, Dr. W. Meise, the Rev. A. H. Paget Wilkes, Capt. C. R. S. Pitman, Mr. C. R. Stonor, Dr. V. G. L. van Someren, Mr. L. S. V. Venables, and Mr. W. L. Sclater, who has given me access to Sir Frederick Jackson's notes. I am further indebted to Dr. Chapin for reading the manuscript critically in the light of his extensive personal knowledge.

NEST CONSTRUCTION.

To the rule that tree-holes are utilized and their entrances plastered the Ground Hornbills evidently provide a generic exception. There is no adequate published description of their nests, but several observers are acquainted with them. Pitman tells me of three Uganda nests, not in enclosed holes, but all in depressions in trees, such as that formed at the tip of a big broken branch. Raymond Hook (*in litt.*) has seen a nest in a similar situation under Mt. Kenya. Swynnerton mentions (34) a Gazaland nest on the top of a large broken-off *Terminalia*. I have information of a regular nesting-site in Usambara, in the cavity formed where several branches spring off together at the head of a tall *Sterculia*. Van Someren (37) has recorded an unusual nest in a cliff at Naivasha. He tells me that it occupied a small cave with a narrow entrance, which was not plastered*.

Apart from the Ground Hornbills a few individual abnormalities of nesting-sites have been recorded. Granvik (10) found that *Bycanistes subcylindricus* had used a cavity between two rocks at 8000 feet on Mt. Elgon. Hoesch (*in litt.*) has also recently found *Lophoceros nasutus* nesting in holes among the rocks on the slopes of the Waterberg (S.W. Africa). *Lophoceros melanoleucos* has been known to nest in a slit instead of a hole and to construct both ceiling and floor (27).

The holes chosen by the small hornbills of the genus *Lophoceros* usually have entrances not much bigger than just sufficient to give the birds entrance. They are often surprisingly narrow, barely 2 in. across. Some *Bycanistes* spp. may, however, use holes that are much wider than their bodies. This was very noticeably so with the two pairs of *B. cristatus* at Amani (20), and I infer the same from Millar's description (18) of his two *B. buccinator* †. On the other hand, Chapin (*in litt.*) has remarked that the "relatively few nests" of West African hornbills he has examined "all had very small entrances, just large enough to admit the bird"; and his experience covers two *Bycanistes* spp. as well as *Lophoceros hartlaubi*, *L. fasciatus*, *Ceratogymna atrata*, and *Tropi-
cranus albocristatus*.

* Grant (29) was shown an unoccupied nest stated to belong to this species which was "composed of sticks placed in the topmost forks of strong branches." Gill ('Guide to the Birds of South Africa,' 1936) reports, apparently at third hand, that females lay eggs in a common nest in a hollow tree, where they are brooded by the male, who is fed by the whole company. I must say that this cannot be accepted without the fullest first-hand confirmation.

† The specific name is written *buccinator* by many authors, which is etymologically correct; but Temminck, the original describer, wrote *bucinator*, as Mr. N. B. Kinnear has confirmed for me.

Plastering is carried out by all the species of hornbill except *Bucorvus*, even when the nest is placed in a rock instead of a tree-hole (cf. Granvik's *B. subcylindricus* (10)). Generally the natural entrance is closed so as to leave only a neat vertical slit less than half the width of the owners' bodies and often less than the width of their bills at the base—e. g., in *Ceratogymna atrata* only one inch (16) and in *Lophoceros deckeni* barely three-eighths (20). The one-and-a-half inch slit left by a *Lophoceros flavirostris* (40) seems to be unusually ample.

One apparent individual exception to the plastering habit has been recorded for a small hornbill, namely, when a pair of *L. melanoleucos* occupied a nest with a natural entrance only $1\frac{1}{2}$ in. in width, which was not further constricted (12). This sounds so impossibly small that it is not surprising if the plaster was omitted.

The technique of plastering varies widely. According to Chapin ((16) and *in litt.*) the nests he examined of *Tropicranus albocristatus*, *Bycanistes albotibialis*, and *B. sharpii* had their narrow entrances more or less blocked with dung, presumably that of the bird inside. It might be inferred from this that the blocking of the entrance by these species was perfunctory, and perhaps even fortuitous; when faeces are forcibly voided out through a narrow hole (see under "Nest Sanitation" below) a proportion is sure to stick to the sides.

In *Ceratogymna atrata* the plastering is more elaborate. Bates informs me that he obtained a male of this species that had "clay on the bill and on the helmet . . . Little bits of clay strewed the ground" under the hole, to which unfortunately no one could be induced to climb. Lang and Chapin (16) also found clay in this species' plaster, which sets very hard, with no cracks and perfect adhesion to the bark. When settled inside the hole the female increases the thickness of the wall by adding excrement, which contains insect fragments and seeds.

It is probable that no technique is more specialized and laborious than that of *Bycanistes cristatus* as described by Moreau (20). The plastering of their hole for the first time occupied a pair for several weeks in two successive years. The nest was only completed and occupied in the third season. After the initial clearing out of the hole there was an absolute division of labour between the male and the female. He brought the whole of the material, which consisted mainly of pellets prepared in his interior (probably in his gullet) from earth mixed with his saliva. In addition he supplied a few lumps of dry earth and pieces of bark. All the placing and working of this material was done in the most careful and deliberate manner by the female sitting inside the hole. No dung was incorporated.

From Millar (18) and Stonor (32) it is clear that the same division of labour takes place with *B. bucinator*. Millar, however, records the material brought by both his males as large pieces of mud or clay. If this is a critical observation it may mean that the part of the male bird in elaborating the basic material of the plaster is of less importance in *B. bucinator* than in *B. cristatus*; but in Stonor's captive pair the bulk of the material consisted of pellets regurgitated by the male, although each consignment was "topped off" with a lump of moist clay carried in his bill. Swynnerton (34) described two nests of *B. bucinator* as "mudded up" with a mixture of red earth and the bird's own droppings, containing seeds of figs, etc. Millar (18) also notes that the edge of the partition in one of his *B. bucinator* nests was made of excrement (consisting largely of millipede and beetle remains). It may well be that this excrement had adhered accidentally as it was projected through the slit.

In the nest of *Lophoceros deckeni* observed by Child (20) the male brought to the nest no material specifically for building; the female did the whole of

the work with plaster she herself elaborated from insect remains, probably "cast," and the decaying wood on the inside of the hole. Moreover she worked with surprising speed, for a hole 2 in. across that was plastered one afternoon was closed to a slit less than half an inch wide the following morning at 09.00 hours. The only other evidence we seem to have in the genus *Lophoceros* for the sexes' share in building is for *L. erythrorhynchus* in captivity. The conditions may have been abnormal in (among other respects) larger holes being provided than the birds would have chosen in nature. However, in a pair at Frankfort (39) as well as in a pair at Berlin (22) both sexes worked at the earlier stages of the plastering and used lichen and clay provided for the purpose. The last of the plastering at Frankfort was done by the male after the female had made her final entrance. But at Berlin the female completed the plaster on the day after her final entrance, with material previously stored in the hole.

Various materials have been recorded as composing the plaster of *Lophoceros* spp. Hoesch (14) found that *L. flavirostris* had used clay and remains of vegetation as well as insect fragments, and that the materials tended to be arranged in separate layers, as if the building had been done at intervals with whatever had been available at the moment. A *L. erythrorhynchus* had "made a wall chiefly consisting of cow-dung but also of clay and grasses" (11). For *L. nasutus* Millet-Horsin (19) gave fibres, fruit-skins, soil, and saliva; Carlisle (5), clay, dung, feathers, and beetle wing-cases; Priest (26), excreta and beetle fragments. For *L. melanoleucos* Cowles (8) recorded droppings, feathers (which were all on the inside) and remains of insects.

Dung, presumably the birds' own, has indeed usually been quoted with more or less certainty as an important constituent of *Lophoceros* plaster (cf. also (6) and (24)). But in the only two specimens of plaster subjected to conclusive chemical analysis, one of *L. flavirostris* (14) and one of *L. melanoleucos* (20), it is certain that none of the birds' own dung had been incorporated. It may be suspected, therefore, that dung is not so frequent a component as has been believed. The fact is that it cannot be identified with any certainty without chemical investigation; the food-remains may be—and where of any size most probably are—derived from casts; and I know from personal experience that a plaster looking and smelling as if it consisted largely of dung may contain none at all. Moreover, in examining plaster it is necessary to distinguish dung that has accidentally adhered to the sides of the slit during the occupation of the nest.

On reviewing all the accounts of hornbill walling it appears that earth is not used, or is only a minor element, in the plaster blocking narrow entrances. This applies to all Chapin's West African hornbills, including several *Bycanistes* spp., as well as to *Lophoceros* spp. generally. When *Bycanistes* select cavities so large that prolonged labour is needed to wall up their entrances, then earth forms the staple material. In species of both genera it appears—though it is practically impossible to establish by analysis or any direct method—that saliva is the binding agent; but in *Lophoceros* spp. the salivation of the female is apparently a more important factor than that of the male; while in at least one *Bycanistes*, i. e., *cristatus*, the position is reversed. Indeed, in this hornbill salivation by the male may well be a limiting factor in the breeding process (20).

In Chapin's experience of West African hornbills, they never bring any material to line the nest (6). This generalization can be extended to practically all the African species about whose nest interiors we have any information. The most important exception is that the Ground Hornbills bring leaves ((5) and Pitman, *in litt.*), with which, according to Paget Wilkes (23), "they cover up their eggs . . . to a depth of some inches on leaving the nest." Granvik (11) records a nest of *L. erythrorhynchus* in which the eggs were on a layer

of acacia pods, dry grasses, pieces of paper, cow-dung, and leaves, presumably collected by the birds. It is possible that the bark brought so assiduously to the nest by the male of *B. cristatus* after hatching of the young (20) is converted to nest lining. On occasion food refuse may be retained intentionally for this purpose. A nest of *Ceratogymna atrata* contained such quantities of stones from digested fruit that "they helped to raise the level of the moist bottom" (16).

Chapin (6) has stated that in the Bucerotidæ generally "la femelle, au moment du couvrir, se fait emmurer dans un arbre creux par le mâle." Bannerman's phrasing (2) is more tentative: "the female lays her eggs in the hollow in a tree, the male (apparently) closing up the entrance." More popular references to hornbills' nesting constantly carry the implication that the male to some extent coerces the female, and the words "imprisonment" or "confinement" are used for the period of her residence in the nest. This is without any justification. I have not been able to find a single first-hand account of an African hornbill's nesting in which the male in any way constrained the female. In the pair of *Bycanistes cristatus* whose behaviour has been recorded in greater detail than any other hornbill's (20) the female reduced the width of her own entrance every day; latterly had to struggle hard to get out at the end of each day's building; and went to equally great trouble to force her way in again the following morning. It is of course also true that the plaster is no final barrier to the female's emergence. In both *Bycanistes cristatus* and *Lophoceros deckeni* she simply pecked it away when she was ready (20). Moreover, in three or four of the cases in which the final closing of a hornbill nest is described, namely, for *L. erythrorhynchus* in captivity (22), for *Bycanistes cristatus* (20), and for *B. bucinator* in captivity (32), it was undoubtedly the female who completed her own closing in. In the remaining account, also concerned with *L. erythrorhynchus* in captivity, it is stated that the male put the last touches to the walling after his mate had finally entered (39).

GENERAL BEHAVIOUR DURING NEST OCCUPATION.

The number of eggs laid tends to vary inversely with the size of the hornbill. All the evidence is that the big birds of the genera *Bucorvus*, *Ceratogymna*, and *Bycanistes* (and also the comparatively small *Tropicranus*) rarely, if ever, exceed two eggs to the clutch. Often *Bycanistes* spp., like *Bucorvus* (37), have only one, e. g., *B. subcylindricus* and *B. sharpii* (6) and *B. cristatus* (20)*.

The *Lophoceros* spp., on the other hand, are more variable, with generally larger clutches: for example, in *L. deckeni* 2 (20); in *L. nasutus* 2-3 (25) and 4 (6, 27); in *L. erythrorhynchus* 3 (11), 3-4 (39), 3-5 (6), and 6 (2); in *L. melanolicos* 2 (4) and 3 (20, 27); in *L. pallidirostris* 5 (28).

Marked delay and irregularity takes place in the laying of eggs by all the hornbills for which anything on this point has been recorded. Millar (18) opened one nest of *Bycanistes bucinator* where the female had been in for twelve days and found no eggs; and in another two eggs were laid between seven and nineteen days after the female's entrance. A captive *Lophoceros erythrorhynchus*, having laid her first egg on the day she entered, did not lay a second until five days later (22). Another at Berlin made her final entrance on 16 July, and did not lay her first egg until 23 July (39).

It may be objected that the two *Lophoceros* records just cited relate to unnatural conditions, and moreover that in Millar's first *Bycanistes* nest there is no evidence that the female would have laid at all—as the *B. cristatus* who

* Mouritz (21) has recorded a brood of two *B. cristatus* in Katanga; but the record may really belong to *B. bucinator*. Chapin (*in litt.*) tells me that the former species has never been collected in Katanga.

burst out after twenty days in her tree presumably did not (20). But, since after their entrance the females cannot help beginning the incubation of each egg as it is laid, irregularity in laying is also suggested by the marked diversity in size between the members of a brood, which has been remarked upon by several authors, *e. g.*, for *B. bucinator* (34), for *L. melanoleucos* (27), and for four different broods of *L. nasutus* (19, 25). Moreover, there may be as much as four days between the dates on which the members of a brood leave their nest-hole, *e. g.*, in *L. deckeni* (20) and *L. erythrorhynchus* (39). In each of these broods the interval between the emergences is known to agree with the interval between the hatchings, but the interval between the respective layings may be even longer than the interval between the emergences, because in the brood last cited the interval of four days in hatching and in flying compares with the seven days over which the laying extended.

In the records in the last paragraph but one the birds, both *B. bucinator* and *L. erythrorhynchus*, laid all their eggs after their final entrance. Chapin tells me also that a female of *L. fasciatus* was "in the nest for good before her second egg had been laid." Jackson (15) heard of a nest of *L. melanoleucos* that contained one egg and was still open. Clearly, however, Lang's generalization (16) that female hornbills do not "give up their liberty until . . . all their eggs have been laid" cannot stand.

In *B. cristatus* it has been proved that the female remains in the hole continuously until her offspring is ready to fly and emerges on the same day (20). Chapin (6) had evidence that the same thing happened with *B. sharpii*. Of *Lophoceros melanoleucos*, however, Schönland (30) inferred many years ago that the female must come out some time before the young. This has more than once been confirmed (15, 20). A similar habit has been observed in *L. erythrorhynchus* (captive) (39), in *L. flavirostris* (14), in *L. deckeni* (20), in *L. nasutus* (19, 26, and Pitman *in litt.*). Opposed to all these observations is the statement by Paget Wilkes and Sladen (24), which has been reproduced by Bannerman (2), that in *L. nasutus* "the female does not emerge until the young are ready to fly." No details are given; and I cannot help doubting whether this statement is based on personal and reliable observation. Most probably, I think, it is characteristic of the whole genus *Lophoceros* that the female leaves the young alone in the nest, in contrast to the habits of the genus *Bycanistes*.

Of necessity when the female remains in the nest for weeks and months on end the supplying of food devolves on the male. There is no evidence for any African species that he receives assistance from other hornbills, though this has been observed in Asia.

Some detailed observations on the feeding process have been made, mainly for *Bycanistes* spp. Chapin (*in litt.*) found that the male *B. albotibialis* brought food to the hole about twelve times a day. In a long series of notes on *B. cristatus* (20) variation from ten to twenty-four visits a day was recorded, the maximum being attained when the young was well grown. During the time his mate was in the hole this male brought food about sixteen hundred times in all. He carried in his throat up to forty-five berries at a time and disgorged them one by one. There are thoroughly reliable grounds for concluding that the total number of fruits he brought was about twenty-four thousand. In view of the observations on *B. bucinator* (18, 32) it is probably a generic habit of *Bycanistes* males to bring the food to the nest in batches, their procedure closely following that which they adopt when bringing material for walling.

In the genus *Lophoceros*, on the other hand, it appears from observations on *L. melanoleucos* (15, 20) and *L. deckeni* (20) that it is the rule for the parent to bring single morsels, usually insects, more rarely fruit, in the tip of the

mandibles and not to disgorge. It would be expected, therefore, that food would be brought to the nest more frequently by *Lophoceros* spp. than by *Bycanistes* spp. It has in fact been recorded (20) that a male *L. deckeni* brought food to his mate six times an hour, while at the same stage a *B. cristatus* averaged only one visit.

Lophoceros females after their emergence regularly assist the male in bringing food to the young left behind in the nest, cf. (20). Hoesch (14) indeed has noted that the female of a pair of *L. flavirostris* visited the young more assiduously than the male did. The need for such an arrangement is easy to understand. A *Lophoceros* male catering for a growing family is faced with a comparatively much more arduous task than a *Bycanistes* male. As a genus the *Lophoceros* are more insectivorous; they bring food to the nest only a morsel at a time instead of in batches, and on the average their broods are at least twice as large. To such a combination of habits it appears that the early emergence of the *Lophoceros* females is an inevitable complement.

When these females have broken their way out of their holes the entrances are plastered up again, but not by them nor by their mates. Hoesch (14) satisfied himself that in *L. flavirostris* the walling was repaired from inside by a fledgling which used dung and the remains of food. Child found that in a nest of *L. deckeni* it was the elder of the two fledglings which did most of the work, in a few hours and with material elaborated by itself (20). This young bird's plaster appeared to consist of the same elements as that prepared originally by its mother, namely, rotten wood and insect "casts" bound with saliva. It has been observed in *L. melanoleucos* also, by Boscawen (20), that the plaster destroyed by the female is replaced from inside by the young; but it is interesting to note that in this nest two or three days elapsed before the repair was completed. (It should be added that according to Wieschke (39) it was the parents which replaced the plaster in the Frankfort nest of *L. erythrorhynchus* after the female had emerged; under the unnatural conditions the normal procedure of the species may well have been deranged.)

It is a very remarkable fact indeed that, as will be shown in the following section, the young birds capable of such technique are less than four weeks old and only halfway through their fledging period. It is most probable that they are still naked so far as body feathering is concerned, for in a closed nest of another *Lophoceros* sp. (*nasutus*), which contained no female, Millet-Horsin (19) found three young "nus . . . rectrices et rémiges en tuyaux, les rectrices déjà longues," an observation paralleled for the same species by Pitman (*in litt.*).

There is, I think, no doubt that such precocity in building ability is without its equal among birds, and moreover it extends to the cleaning of the nest after the female has left it (14).

CHRONOLOGY OF EVENTS IN THE NEST.

Chapin (6) suggested fifteen to twenty days as a likely period for incubation and at least a month for the growth of the young. He thought it certain therefore that the females of many hornbills—though he would except the *Lophoceros* spp.—passed more than six weeks in their holes. The additional data that have accumulated since Chapin wrote show that these time allowances must be greatly increased, in some species beyond all reasonable expectation.

A *Bycanistes cristatus* remained in her nest no fewer than 108 days (20), a period that is, I think, probably often exceeded by this species. There is an indication that her single young one was hatched about fifty days after her entrance. The apparently unreasonable length of this period may be due

Incubation and other Periods in the Genus *Lophoceros*.

Species.	Reference.	Number of days.				
		Total female in. (3)	Female in after first hatching. (4)	Incubation period. (5)	Fledging period. (6)	Young in after female's exit. (7)
(1)	(2)	(3)	(4)	(5)	(6)	(7)
<i>L. erythrorhynchus</i> (captive)	Wieschke (1928).	61	26	(36)	?	?
Ditto.	Ditto.	59	24	27-29	43	20-24
<i>L. nasutus</i>	Priest (1934).	?	?	?	?	21
<i>L. flavirostris</i>	Hoesch (1934).	?	?	?	?	28
<i>L. deckeni</i>	Moreau (1936).	?	?	?	?	24
Ditto.	Ditto.	44 ± 13	?	?	?	28
Ditto.	Ditto.	57	24	(33-37)	46	22
<i>L. melanoleucos</i>	Ditto.	about 70	?	?	?	about 14

to her not laying the egg as soon as she entered the nest, for delay and irregularity in laying have been shown to be characteristic of the hornbills. In any case, however, it follows that the fledging period of *B. cristatus* must be fifty-eight days at the least.

The *B. bucinator* that recently attempted to nest in the London Zoo occupied her box for ninety-four days (32).

For *Lophoceros* spp. the records lately accumulated are less scanty and also more complicated. They can most conveniently be presented in the accompanying table (p. 338). It will be observed that the figures in column three justify the tentative estimate quoted by Stark and Sclater (30), namely, seven or eight weeks, for the length of time spent in the nest for a female of *L. melanoleucos*.

In column five only the figures not bracketed are exact incubation periods, based on a knowledge of the dates the eggs were laid as well as when they were hatched. The figures bracketed are calculated only from the date of the female's entrance, after which several days may elapse before an egg is laid.

It appears that when the *Lophoceros* females leave the nest the body-feathers of their young are still not grown ((10) and Pitman, *in litt.*). I note that Priest (26) mentions a brood of young *L. nasutus* "just fledged and the female inside as well"; but since he adds that they did not fly until four weeks and two days after this observation, it is evident that the word "fledged" is used in no ordinary sense.

In review there is no doubt that the total period of broody inactivity is longer in *Bycanistes* than in any other birds. The actual incubation period is uncertain, but in *B. cristatus* it is probably nearer forty days than thirty. The incubation period of the *Lophoceros* spp., which may now be taken as established at not less than four weeks on the average, is much longer than the average for birds of their weight, which is, according to my records, about two hundred grams. A parallel to the *Lophoceros* weight—time relation is, however, provided by small owls (13).

The fledging periods of all the hornbills mentioned in this section—over six weeks for the *Lophoceros* spp. and apparently over eight for a *Bycanistes*—are also longer than could have been expected. At the same time it is interesting to note that the former period agrees with that of a Toucan (38) of comparable wing-length though double the weight. It may be recalled that the young of *Lophoceros* are in a class by themselves for constructive ability, and, moreover, that young hornbills do not seem to have to learn to fly when they leave the nest. Both *B. cristatus* and *L. deckeni* have been ascertained to fly from the nest-tree and its neighbourhood directly they come out of their hole (20).

NEST SANITATION.

The sanitation of a family of birds that remain continuously in their nest-holes for several months is of special interest. The primary provision is that the inmates defecate towards the entrance with surprising force, like kingfishers. With *Lophoceros* spp. the result is a strip of whitish dung extending for several feet away from the point below the nest, as Livingstone (17) noted long ago. These accumulations are so conspicuous that they often direct attention to a nest otherwise by no means obvious. The *Lophoceros* spp. eject other things besides dung. Cowles (8) observed that egg-shells, feathers, and other rubbish were dropped outside by *L. melanoleucos*. Pitman (25) has remarked on the clean condition of *L. nasutus* nests. Hoesch (14) found no food-remains nor dung in the nest of *L. flavirostris*. He tells us that the female had at intervals a thorough "spring-cleaning", on which occasion rubbish of all kinds came

hurtling out of the slit. When she had left the hole her half-fledged young continued to clean it with equal care.

In the big hornbills it appears that, generally speaking, the attention paid to sanitation is less careful. They do defecate forcibly towards the entrance, but this has gone unremarked until the recent observations on the London *B. bucinator*, because, as Chapin has noted in West Africa (*in litt.*) and I have since observed in Tanganyika, the dung of the big hornbills is brownish and not conspicuous. As mentioned under "Nest Construction" above, Chapin found that the birds' own dung contributed to the walling of several West African species. He thinks that whatever dung adhered to the sides of the entrance in being projected outwards was pressed into place by the birds' beaks as food was passed through.

Another method of disposing of waste matter is by "casting." Experiments kindly made by Stonor at the London Zoo at my request have shown that this is a regular procedure with fruit-stones, but it is not invariable—Stonor has found a fruit-stone in the intestine of a *B. sharpii*—and in nature they are not all ejected from the nest. A *Ceratogymna*'s hole contained remains of food and a great quantity of fruit-stones (6). A *B. cristatus* threw out large numbers of cleaned fruit-stones, but probably by no means all the twenty thousand or so that the male brought (20). Millar (18) found excrement, remains of fruit, and feathers in the nest of *B. bucinator*.

The conditions in these big hornbills' nests should be favourable for coprophagous or commensal insects, which might play a part in the sanitation, as recently shown to take place with a kingfisher (35). Personally I have never examined the interior of a hornbill's nest, but I am indebted to Chapin for the information (*in litt.*) that a nest of *B. albotibialis* contained a number of wingless roaches that were presumably coprophagous, and a few larvæ, probably of tineid Lepidoptera. The whole insect fauna of the nest was, however, not sufficient to be of much importance in its sanitation. The point is worth attention by anyone who opens a hornbill's nest.

THE CONDITION OF THE FEMALE IN THE NEST.

Not much appears to have been recorded on the general physical condition of nesting females. Cowles's *L. melanoleucos* (8) was "very weak and emaciated," but according to Stark and Selater (30) in this species she is "generally found to be very fat." Mouritz (21) examined a *B. cristatus* "nearly through with her moult [nature unfortunately not specified] but very fat and in good fettle." Probably there is much individual variation in this respect. Lang and Chapin (16) remark, however, that the plump condition of females and young is "proverbial among natives."

It has long been known that female hornbills moult in the nest. As Friedmann puts it (9), while they are "confined in the small space all the old rectrices (and the remiges too) are dropped and new ones are grown." Bannerman's generalization (2) on this point is that "while incubating the eggs the female goes through a complete moult." Only one exception seems to have been published, a captive *L. erythrorhynchus* (39), which, as Wieschke states explicitly, in two successive years did not moult in the nest. This is undoubtedly an individual variation due to the unnatural conditions; for in wild nests of this species noted by van Someren (*in litt.*), Granvik (11), Alexander (1), and Fischer (27) the moult had taken place.

It is practically certain that the Ground Hornbills form a generic exception to the rule, because their females are not subject to the same restrictions nor afforded the same protection as other members of the Bucerotidæ. And

Paget Wilkes (*in litt.*) has more than once put a Ground Hornbill, which was able to fly normally, off incubated eggs. There appears to be another specific exception, for I have just been informed by Hoesch that in the little-known *L. bradfieldi* which he had under observation in Damaraland "males and females come into moult after the nesting time and both in the same manner." Further details and any explanation of this peculiarity will be awaited with interest.

Accepting the moult of the female in the nest as the rule, we have still much to learn about the course of the moult, and particularly how far a flightless period is general. The widespread opinion that it is so seems to depend on the evidence from three species of *Lophoceros*. Of *L. melanoleucos* Stark and Selater (30) have stated that the female "before entering the nest begins to moult and during the imprisonment . . . the process continues so that she is often helpless and unable to fly." It is possible that the qualifying "often" in this extract was inserted uncritically: females of this species have several times been reported as flightless, *e. g.*, (4) and by Friedmann (*in litt.*). In *L. nasutus* Carlisle (5) records an incubating female unable to fly, and Millet-Horsin (19) one with two eggs who had lost all her remiges and rectrices. He goes on to make impossible demands on our credulity by adding "dégarni par les soins du mâle." Alexander (1) found a *L. erythrorhynchus* who was "unable to fly in her filthy, featherless condition," and van Someren (*in litt.*) a female of the same species with young (stage not stated) and wing-feathers only about four inches long. Recent evidence from Priest (26) and Hoesch (*in litt.*) demonstrates a flightless period in a fourth species, *L. flavirostris*. Taken together these statements justify the opinion, also expressed by Chapin (*in litt.*), that this condition is common to the genus *Lophoceros* as a whole. I can find no definite evidence for the other species, but it may be noted that a female *L. deckeni* made no attempt to escape when her plaster was chipped away twelve days after her entrance (20).

Some accounts given by observers who have destroyed *Lophoceros* nests are sufficiently precise to enable the progress of the moult to be related to the other events in the nest. Belcher's (4) female *L. melanoleucos* had eggs, was "quite unable to fly," and had "wing and tail-feathers just sprouting." In another incubating bird of this species, which had two naked young and an egg chipping, the moult was almost over but replacement of the feathers was not far advanced (8). In a third *L. melanoleucos* with naked young her feathers were half grown (27). A female *L. pallidirostris* on three eggs and two newly hatched young had "moulted all her long wing and tail feathers" (28). In *L. nasutus* a bird with three eggs lying on her old feathers had quite moulted (5). Her new feathers were beginning and she was unable to fly. A *L. fasciatus* with one egg was very worn but apparently had not begun to moult (6). For *L. flavirostris* Priest (26) has given valuable comparative details: a female on one egg had lost neither wing nor tail-feathers; another on two much incubated eggs had lost all her wing and tail-feathers and the new ones were about an inch long; two more females with young each had "feathers of the tails about an inch in length, but nothing could be seen of those in the wings." Wilson (40) found a female of this species on 17 October with one egg "quite fresh and clean, the other stained and slightly incubated," who looked "very dishevelled," was "barely able to flutter up into a bush close to" and had "lost all her tail-feathers." This bird's moulting process must have been a rapid one, because only twelve days before, on 5 October, she was flying normally and the plastering of her hole had only been started. Finally, Hoesch has noted (*in litt.*) for this species that a bird with two half-grown

young had her tail-feathers a little short of full size, and that three days after this observation she broke her way out of the hole and took to the wing.

On collation of these references it appears that the females of *Lophoceros* spp. begin their moult very shortly after the first egg is laid, if not actually before, and lose the power of flight rapidly, probably soon after the clutch is completed. At least some of them shed the tail completely before the wing-feathers. The new plumage is often only beginning to sprout when the young are hatched, and thereafter the females remain in the nest about three and a half weeks. It is clear from the last-quoted observation of Hoesch's that a female *Lophoceros* may emerge almost before her feathers have finished growing, though she would probably have been capable of flight of a sort some days earlier still.

The data collated in the table (p. 338) show that the females remain in the nest for seven to nine weeks altogether. It is probable therefore that they are incapable of flight for some six to eight weeks as a maximum.

The question whether the body feathers participate in this sudden moult has received little consideration. There are several casual references to the "naked" condition of female hornbills discovered in their nests, but the only critical published statement I know of is Belcher's (4). He found a *Lophoceros melanoleucos* with wings and tail "just sprouting, the body feathers were down and the back of the neck quite bare." Chapin tells me that in his experience of *Lophoceros* spp. and of *Tropicranus* the females in the nest "seen not to shed any of the body plumage at all—and not even the wing-coverts." Nevertheless, to do so is obviously characteristic of *L. melanoleucos*, because Stonor tells me that in a family group at South Kensington Bird Gallery a female with wings and tail about two-thirds grown has "a fair number of her contour feathers still with some sheath but almost full grown." Moreover, Van Someren (*in litt.*) has handled a female *erythrorhynchus* with sprouting wing-feathers of about four inches and "most of the body feathering, except on breast, almost complete." To establish how generally *Lophoceros* females shed their contour-feathers is therefore a point needing much more specific investigation.

In the other hornbills the evidence is both more scanty and more various in its implications. A *Tropicranus albocristatus* with young about a week old was "certainly unable to fly" (Chapin, *in litt.*), having lost all her wing and tail-feathers at once. On the other hand, it has been stated (16) that in *Ceratogymna atrata* the female "does not emerge with a complete set of new feathers. Only a few of the larger quills are shed inside the nest and . . . the process of moulting is not always completed during the breeding period." I am informed, however, by Chapin that these statements cannot be accepted as proven, only as likely.

Within the genus *Bycanistes* there appears to be specific variation in the course of the female moult. Pitman (*in litt.*) found a *B. subcylindricus* (with a naked nestling) that "could not fly, although the moult was mainly over and the new primaries and rectrices were well advanced." He thinks that "most certainly all the primaries had been shed at the same time." This agrees with Bates's native information (3), according to which a hole belonging to this species contained "a mother bird and a young one, both naked like two big squabs." On the other hand, in two nests of *B. albotibialis* Chapin (*in litt.*) satisfied himself that the females had moulted gradually enough to retain power of flight. What happened in the case of the *B. bucinator* that attempted to breed in the London Zoo is not certain: her state on emerging, as described by Stonor (32), was compatible with her having shed her flight-feathers practically all together, but her tail-feathers in pairs at intervals. On the other hand, in a spirit-specimen of *B. sharpii*, of which he has kindly given me particulars, the whole

of the tail-feathers were missing and only one pair showed any signs of growing again. The wings were beginning a moult that may have been gradual, because in the only three pairs of feathers that had been shed the new ones were already well on their way to full size. Of the contour-feathers "many in all the tracts were just sprouting, but quite a number had not recently been shed." The ovary contained one egg the size of a pea, and from the absence of tail-feathers it is reasonably certain that the bird was secured in her nest-hole, but the collector gave no particulars.

On the evidence brought together in the foregoing paragraphs it may be accepted as a characteristic of the genus *Lophoceros* and of the monotypic *Tropicranus* that the female passes through a period when she is incapable of flight; but this does not apply to *Ceratogymna*, and within the genus *Bycanistes* there appears to be specific variation, which it is very desirable to confirm. It may be remarked parenthetically that it is probably only under the conditions of a nesting hornbill, which combine physical inactivity with liberal feeding, that a complete simultaneous regeneration of the plumage is possible. It has been found that in passerine nestlings the weight and growth curves flatten when the curves of feather growth rise rapidly (31).

In those numerous species in which a flightless period takes place, three questions at once arise:—

(1) What explanation can be offered for this type of moult? I fail to see how it can be regarded as an adaptation of value to the bird. I am inclined to adopt the hypothesis put forward by Stonor (32), according to which sudden moult is a consequence, through the agency of the pituitary gland, of the abrupt reduction in the female's light ration when she has shut herself up in the nest. Certainly, however, a grave difficulty to this hypothesis is presented by those cases of *Ceratogymna* and *Bycanistes*, where birds occupying closed nests do not moult suddenly. Attention must also be drawn to the statement by Stark and Selater (30) that the female of *L. melanoleucos* begins to moult before she enters the nest. Critical confirmation is desirable; but it is at least clear from the evidence collected, especially Wilson's (40), that heavy moult sets in very quickly, within a week of the female's entrance.

(2) What is the sequence of moult in non-breeding females? It seems most unlikely that they would have to—or be able to—endure a flightless period of several weeks while living in the open air; and on Stonor's hypothesis there is of course no reason to suppose that they moult in any other way than the great majority of birds, including their own males. It would go far to settle the point if museum specimens of females showing normal type of moult could be cited for any of the species in which sudden moult while breeding has been demonstrated. I have examined scores of skins in the National Collection without finding one to the point, but some may well exist elsewhere*.

It may be recalled that a *Bycanistes cristatus* that burst out of her hole after being inside for nearly three weeks was perfectly well able to fly and showed no signs of moult (20); and I have had females of this species collected on the wing that were undergoing gradual moult. But unfortunately the course of moult in the brooding bird of this species has still to be established.

(3) If the female in the nest loses her mate does she break her way out and attempt to provide for herself? Statements are quoted, *e. g.*, in (36), to the

* Since the above was written a record has been published of a female *Lophoceros pallidirostris neumanni*, presumably shot in the open, since the contrary is not stated, that was "moulting the body plumage and the inner primaries" (Bull. Mus. Comp. Zool. Harvard, vol. lxxxii, p. 171).

effect that other hornbills take over the care of the bereaved female. References for which I am indebted to Stonor show that this is based on observations on certain Asiatic species. Nothing of the kind has been recorded in Africa. The question might easily be settled experimentally.

COMPARATIVE SUMMARY.

Some particulars, for the most part fragmentary, have been recorded on the nesting of sixteen out of the twenty-six African species of hornbills.

The scanty data for *Bucorvus cafer* make it practically certain that the Ground Hornbills fail to exhibit any of the peculiarities in breeding biology that distinguish the Bucerotidæ as a family from all other birds, including the analogous Toucans. The features common to all the other African species we know anything about may be summarized as follows :—

They choose holes with narrow entrances which they constrict with plaster so as to leave a vertical slit barely the width of their own bills. They build mainly with earth when the entrance is comparatively wide, with food-remains and fibrous matter when it is small. Dung has probably been reported too often as a constituent of their plaster ; it cannot be identified without chemical analysis. As a rule no lining is brought for the nest. The males in no way coerce the females, who wall themselves in and remain inactive from two to four months continuously, moulting meanwhile. During this period their mates are solely responsible for the food-supply of the family. Irregularity in egg-laying is general. A first egg may not be laid for nearly a fortnight after a female's entrance, and a second may follow five days after the first. This is reflected in unevenness in size within a brood and in their irregular emergence. The primary provision for the sanitation of the nest is that the occupants defecate forcibly towards the entrance.

Within this general framework of habit the African species of hornbills show much variation in detail :—

(a) The plastering may be perfunctory in some of the West African hornbills, but it is most careful in *Lophoceros* spp. and in some *Bycanistes* spp. In *Ceratogymna* the male brings the material and both he and his mate fix it. In *Bycanistes* there is division of labour between the male, who brings the whole of the material, and the female, who does all the actual building. In *B. cristatus* the plastering of a hole can occupy a pair for months, the progress of the work depending on the male and probably on his salivation. In *Lophoceros* spp., on the other hand, the plastering process takes only a few days, or no more than a few hours, and the male's part in it is relatively unimportant.

(b) *Bycanistes* females do not come out until their offspring are ready to fly. A *B. cristatus* was in her hole for 108 days, the egg probably hatching about the fiftieth day. In *Lophoceros* the females remain inside for 50–70 days and emerge 14–28 days before their young, the incubation period of which averages 30 days and their fledging period 45.

(c) In *Bycanistes* the male is responsible for the entire food-supply of the family until they all fly. In *Lophoceros* the female helps to feed the young as soon as she emerges. The fact that the *Lophoceros* bring the food to the nest in single morsels, not in batches like *Bycanistes*, and, moreover, have much bigger families to cater for, would probably make it impossible for the *Lophoceros* male to bring up his family without the relief afforded to him by the early emergence of his mate.

(d) The fledglings of *Lophoceros*, only 25 days out of the egg when the mother leaves them, at once elaborate plaster, re-seal the hole, and take over

the sanitation of the nest. There is no evidence of precocity in *Bycanistes* fledglings.

(e) Sanitation appears to receive more attention from *Lophoceros* spp. than from *Bycanistes* and *Ceratogymna*, in the nests of which the insect fauna should be examined for scavengers.

(f) In the genus *Bycanistes* some species moult so suddenly as to lose the power of flight, and some do not. In *Lophoceros* spp. and *Tropicranus* the females drop all their wing and tail-feathers very rapidly, in *Lophoceros* by about the time their clutch is complete. They are probably flightless for at least six weeks, because their new feathers have made but little progress by the time their young hatch. There may be specific variation in the extent to which the contour feathers participate in the sudden moult.

This habit of sudden moult raises several problems. It cannot be explained teleologically, and may be a physiological consequence of the brooding bird's reduced ration of light.

In conclusion, it is to be emphasized that the African hornbills include species that are in several respects unique among birds, though no one of them combines all their peculiarities, namely: the length of time the female remains in a state of broody inactivity; her sudden wholesale moult, that results in a period when she is not only incapable of flight, like a wild goose, but practically naked; the prolonged devotion of the male to the duty of feeding his whole family; and the technical ability displayed by nestlings long before they are fledged.

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