THE LAKE RUDOLF
CROCODILE (*Crocodylus niloticus* Laurenti) POPULATION

by

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Preface

This work originated as a result of a suggestion by Ian Parker of Wildlife Services Limited to the Kenya Game Department (now Kenya Wildlife Services) that a survey be conducted of the Lake Rudolf (now Lake Turkana) crocodile population to assess its present status and thereby provide the basis for planning its future.

In the past it has been the practice to exterminate crocodiles whenever they begin to conflict with human interests. Nearly all the East African populations have either undergone this treatment or been subjected to indiscriminate exploitation. Lake Rudolf supports the last relatively undisturbed population in Kenya, and to forestall a similar fate an understanding of their ecology has become a matter of urgency.

The Game Department, while supporting the idea, was unable to provide any funds and so the sample of 500 animals killed during the survey was used to finance the work, which was carried out by Wildlife Services Ltd. This proved inadequate as a source of revenue resulting in abandonment of many aspects of the work. Nevertheless, sufficient data were amassed to consider exploitation possibilities and ensure their continued survival.

Summary

1. A 14-month study of the Lake Rudolf crocodile population is described during which 500 animals were killed and examined.
2. Lake Rudolf in northern Kenya is 186 miles long, 6-30 miles wide, with 576 miles of shore. Less than 250 mm of rain falls per annum. Shade temperatures over 24 hours vary between 26.5-30.5^{o}C with little annual variation. There is a strong, persistent easterly wind.
3. The population is estimated by aerial and night ground counts at 12,439 animals in June 1966. Discontinuities in distribution are related to habitat, with high densities in sheltered and low densities in exposed situations, varying from 1-90 per mile. 71.9% of the population occupies the east shore.
4. The main food animals, fish, are caught in shallow water at night.
5. 48.4% of stomachs are found empty, a much higher incidence than is seen in other populations.
6. 90.9% of stomach contents are fish. Of stomachs with fish, 87% contained tilapia (Cichlidae).
7. An annual breeding season is confirmed. In males a quiescent phase in January-March culminates in a peak of spermatogenetic activity in October-December.
8. The relationship between testis weight and cubic dimensions is established to provide a field technique for estimating testis weight in animals near maturity.
9. 50% or more males are mature at testis weights >10g. The mean body length at a testis weight of 10 g is 270 cm.
10. The onset of female sexual maturity is well-marked at 100 cm body length.
11. Seasonal breeding in the female is evident but some reproduction apparently takes place throughout the year.
12. Very old females appear to cease reproducing.

13. The mean clutch size in Rudolf crocodiles is about half that observed elsewhere.
14. Clutch size is shown to increase with increasing body size, the relationship being the same in Rudolf and Uganda animals.
15. Layers are observed in the dentary bone and evidence is presented that they are formed annually. The number of layers increases with length and is used in the male to give absolute values to the age-length relationship.
16. Lens growth is seen to be independent of body growth and is used to show the relative difference in the age/length relationship of males and females.
17. More rapid growth in males results in a difference of size at age between sexes so that the oldest males of 470 cm are 3.5 times as heavy as the oldest females of 500 cm.
18. There is no weight difference between males and females of the same length.
19. Males seldom exceed 470 cm length and females 320 cm.
20. The growth of *Alligator mississipiensis* is compared with that of *C. niloticus* and seen to be similar with the latter species growing larger.
21. Growth in immature crocodiles is analyzed by plotting the frequency of occurrence of different growth rates on arithmetical probability paper. Two modes are obtained and assumed to represent mean annual length increments in males of 52 cm and in females of 20 cm. Growth evidently slows after maturity.
22. Based on immature growth rates and the maximum size obtained hypothetical growth curves for males and females are drawn up using an age scale of 0-60 years.
23. 3 recaptured crocodiles from a sample of 152 marked for growth rate information showed annual length increments of only 1.7 cm indicating that growth in wild crocodiles can be severely inhibited. Captive animals from the same area yielded growth rates of 30 cm per annum.

24. Age specific fecundity is calculated for each age class of breeding females. The age structure of the population being unknown a hypothetical female life Table is drawn up using the observed fecundity values and assuming a net reproductive rate of 1.0.
25. Mortality is discussed. Owing to the high reproductive rate immature mortality can approach 100% in a stable population.
26. The factors affecting the commercial value of crocodile skin are discussed. The incidence of "buttons", a hard deposit in the ventral scales, is seen to be the most important factor reducing value.
27. Skins currently increase in value with increasing body size up to a length of 190 cm, after which the value per unit area remains constant.
28. Evidence is presented that the most valuable age classes of a crocodile population are those near the point of maturity.
29. Ways of exploiting the high potential productivity are discussed and suggestions for reducing the immature mortality rate are made.
30. It is concluded that a management plan for the Rudolf crocodiles could be drawn up aimed at cropping the younger age classes, possibly supplemented by artificial rearing for a period of early life. Exploiting eggs is considered and the dangers of permitting unplanned exploitation emphasized.

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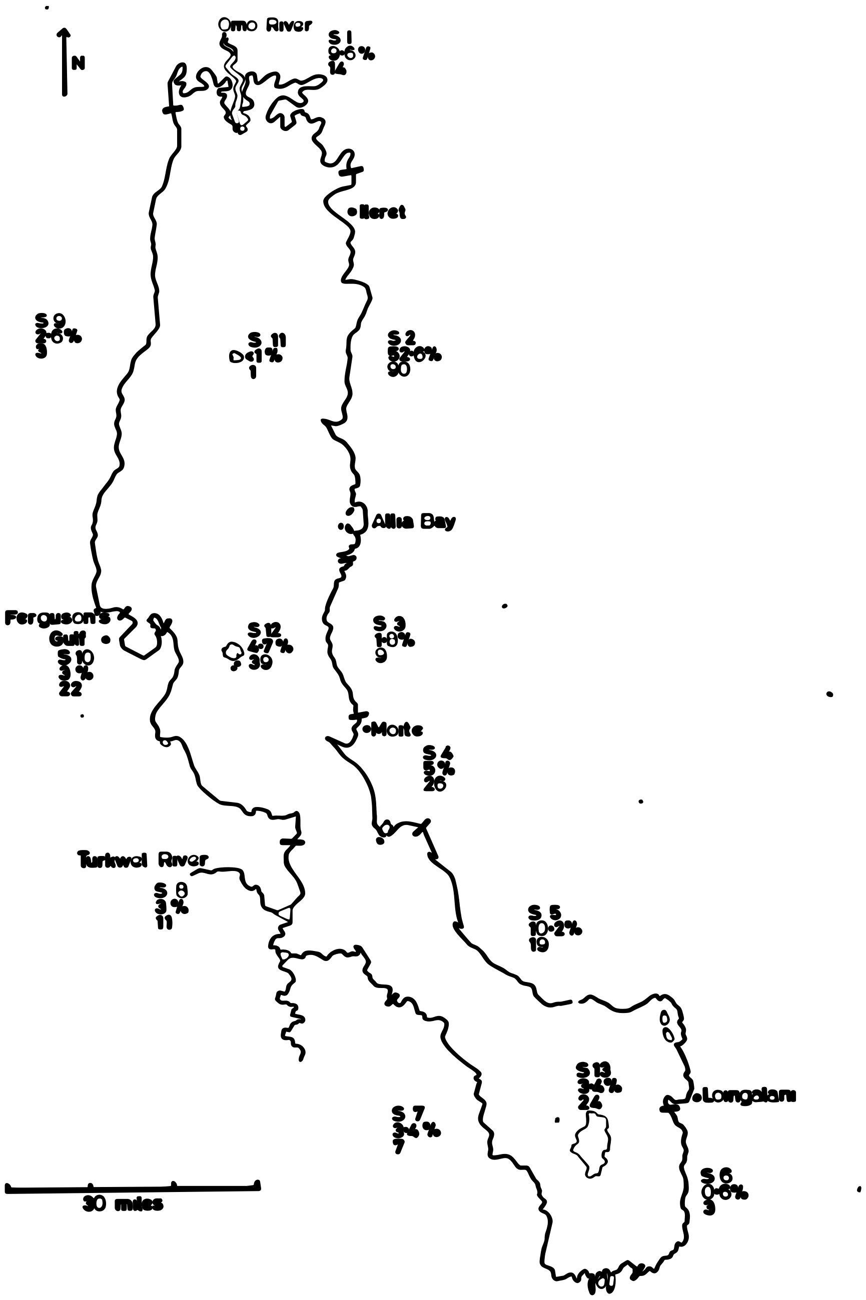


Figure 1. Lake Rudolf showing the location of 13 sections (prefixed "S") described in the text with the proportion of the total population occurring in each section and the density per mile of shore.

Introduction

This thesis comprises information collected during a 14-month survey of the Lake Rudolf (now Lake Turkana) crocodile population. Information was collected on feeding biology, growth and reproduction with the aim of assessing the population as a whole and considering its exploitation possibilities.

The consulting firm of Wildlife Services Limited was engaged by the Kenya Game Department (now Kenya Wildlife Services) to carry out the survey with the East African Wild Life Society Scientific and Technical Committee acting in an advisory capacity. This activity was assumed latterly by the Zoology Department, University College, Nairobi.

No other crocodile population has been subjected to comparable analysis before and information other than of an anecdotal nature is scanty. Hippel (1946) recorded the stomach contents of 587 crocodiles shot on Lake Kioga in Uganda, finding a predominance of fish. Cott (1961) in his monograph on the Nile crocodile gives a good review of the available information up to that time and includes some previously unpublished data of Pitman's. Cott examined 651 crocodiles during the course of his work and records much useful data on feeding, growth and reproduction, and many other aspects of their biology. Peabody (1961) describes growth zones in the dentary of a crocodile and ascribed these to annual climatic variations causing discontinuities in bone growth. Poole (1961) describes the process of tooth replacement in crocodiles which appears to be continuous and notes that there is a constant size increment in each new tooth. Modha (1967) records observations on territorial and reproductive behaviour in crocodiles on Central Island, Lake Rudolf. Reference to other work is made, where appropriate, in the text.

Material and Methods

Detailed methods are set out at the beginning of each section, while a general outline of the work follows. Fieldwork covered the 14 months from July 1965 to September 1966. Preparation of the results occupied the 6 months from February 1967 to July 1967. A 5-day preliminary survey in February 1965 showed most of the population to be on the north east shore of the lake and consequently this was selected as the main study area. The Game Department agreed to 500 animals being killed for investigation, and as no other funds were available the project was financed entirely from the sale of skin from these animals.

Collection of specimens was made from two sites, Allia Bay and Moite (see Figure. 1) with the original intention of collecting approximately 40 per month from each site.

Towards the end, crocodiles were difficult to obtain at Moite and ultimately 305 were collected at Allia Bay, 187 from Moite and 8 from North Island. The first month was devoted to the capture, marking and release of animals at Moite for growth rate studies. The first half of September 1965 was spent on North Island eliminating the crocodiles there as part of a long term experiment to observe the rate of recolonization. Regular collection of specimens began in September 1965 and continued so as to cover a complete twelve month cycle.

A Cessna 182 aircraft was used for most travelling and transport, with a small boat for local movements. The work was carried out entirely by the author although 5 Turkana were engaged as skinners and M. Watson and R. Bell acted as observers during the count in June 1966.

Taxonomic status and Distribution of the Order Crocodylia

The order Crocodylia contains 13 families grouped under 5 suborders. Only the family Crocodylidae remains extant with 8 genera and 25 species. There are 2 genera of crocodiles, *Crocodylus* with 12 species and *Osteolaemus* with 2 species, the latter confined to West Africa and the Congo, the former occurring throughout the Old World tropics and the northern part of the New World tropics. There is one genus of alligators, *Alligator*, with 2 species, one in the South Eastern United States (*A. mississipiensis*) and the other in the lower Yangtze Valley of China (*A. sinensis*.) The related caimans, with 3 genera and 9 species, occur in Central and South America. 2 monotypic genera of gavials, *Gavialis* and *Tomistoma* occur respectively in India and the Malay region. (Schmidt 1944, Wermuth 1953, Darlington 1957.)

Crocodylus niloticus Laurenti, the common African species and known as the Nile crocodile, occurred in recent times throughout Africa, Madagascar, the Seychelles and Comoros. Hunted for its skin, or merely exterminated, it has vanished from much of its former range and significant populations are now confined to parts of Ethiopia, Sudan, Tchad, Botswana, East Africa, Zambia and Mozambique. The first 4 areas, with the largest remaining populations, are being extensively exploited at present. Isolated populations survive throughout most of the former range in rivers and lakes but most of the larger populations are being hunted for skin. Lake Rudolf and Murchison Falls National Park support the only large East African populations that have not been extensively hunted and represent nearly “natural” populations. Deraniyagala (1939) considered the Lakes Rudolf and Baringo crocodiles to differ from those of the Nile system. He accordingly named the Rudolf animal *C. niloticus pauciscutatus* and the Baringo animal *C. niloticus Worthingtoni*. However, until the differences are shown to be other than environmentally caused there seems little value in these sub-species.

Section 1 Density and Distribution

1a Habitat

Geological History

The most widely accepted opinion is that Lake Rudolf has been separated from the Nile system since the beginning of the Upper Pleistocene and Fuchs (1939) presents a detailed account of its geology.

General

The centre of the lake lies approximately 3^{o}30’ North and 36^{o} East. It is 186 miles long and 6-30 miles wide. The shoreline including the 3 main islands is approximately 576 miles and the surface area of water (variable) about 6,870 square miles. The water is saline (Appendix 1), but potable, and the author detected no ill effects after drinking it for 15 months. The taste of the water varies from place to place and is generally saltier near the shore. There is only one permanent river, the Omo, which drains into the lake from the Ethiopian highlands to the North. Numerous seasonal rivers (that do not always flow every year) drain into the lake from which there is no surface outlet. The depth between Central Island and Ferguson’s Gulf averages 174 feet, while Worthington (1932) records a depth of 256 feet near Central Island. No other soundings of the lake appear to have been made. Strong currents are evident in many places, but these have not been studied. From Fuchs (1935) description it appears that the lake today is similar in size to what it was in 1934.

However Fuchs, without giving his sources, states that "during the last 45 years the lake has sunk at least 30-40 feet." There is reason to doubt this statement since the description given by Von Hőhnel (1894) of Allia Bay fits very well its present day appearance. He describes 2 small islands in the bay which are similar in position and size to the islands present today which are less than 10 feet above lake level. The littoral is generally very shallow and changes in depth of 30-40 feet would produce very extensive alterations to the shore-line. However there has been a steady retreat by the lake since the upper Pleistocene which may, in the long term sense, be continuing. The lake is continuously rising or falling over a small range according to rainfall. In 1965-66 the change was about 3 feet, highest in November and lowest in April, but considerable variation exists year to year.

Climate

Occasional recordings of shade temperature were made with a whirling hygrometer. The highest temperature obtained was 56.5°C at 1430 hours and the lowest was 26.5°C at 0600 hours. Similar temperatures have been recorded on Central Island (Modha 1967, p.78). Water temperatures were measured at various times through the 24-hour cycle 15cm below the surface in 50-100cm of water, and ranged from 21-27°C. These may be regarded as typical far the shallows on the east shore, with little variation through the year, or the 24-hour cycle. The area has a probability of less than 25 cm rainfall per annum (Atlas of Kenya, 1959), and Lodwar, 40 miles west, has averaged 12-17cm for the last 30 years. Most rain falls in March, April and May, and lake levels are highest after this time. Insolation measurements are not available, but cloud cover for most of the year is slight, with only occasional cloudy days. Wind measurements are not available, but generally the wind prevails easterly to south-easterly throughout the year. The daily pattern on the east shore I 10 a steady easterly wind throughout the morning, of 10-20 miles per hour, gusting frequently 30-40 miles per hour. After midday there is a tendency for this easterly to be replaced by a slight westerly "sea breeze" until dusk. (Values derived from variations in ground-speed observed while flying.) This pattern is however, erratic, with frequent periods of continuous wind lasting up to 3 days. Calm periods occur on most days at any time in the 24-hour cycle, variable in duration, but not usually lasting more than 12 hours. During periods of rain, this pattern is further disrupted, and it may blow from any direction, usually the north. The importance of this wind on crocodile biology is discussed again in the section on "distribution."

Habitat

Lake Rudolf is surrounded by arid country, with a gradient north to south of increasing desolation. The west shore is dry and sandy with sparse vegetation for its whole length. There is continuous human activity along this shore with Turkana settlements at several points. No significant numbers of wild mammals occur except in the extreme north-west, where herds of topi and oryx border on the lake. The east shore is generally less arid than the west except in the south-east, where old lava flows predominate, with little vegetation or wildlife. The north-east section is open bush country, with an evidently higher rainfall than any other part, and with numbers of topi, oryx, both species of zebra, Grants gazelle, giraffe, lion, leopard, cheetah, hyaena, wild dog and many small mammals**.** Elephant, rhinoceros and buffalo, common 80 years ago (von Hőhnel 1894) have vanished. Whether the disappearance of these species, and the resident human populations described by von Hőhnel, has been associated with any change in the climate and vegetation, is unknown. The north end of the lake appears to have a higher rainfall than any other part and is extensively cultivated.

Description of the lake shore (Figure. 1)

For the purpose of comparing crocodile distribution and possible future exploitation the lake shore has been divided into 13 sections based on habitat. These are somewhat arbitrary, but serve to make the discontinuities in crocodile density clearer.

Section 1 (Plate 1) Omo River delta. 88 miles of shore, but very variable according to lake level. Marsh made up of extensive reed beds with weed-filled open water. Similar swamp is not found elsewhere on the lake. Moderate crocodile density of 14 per mile. This section is mostly in Ethiopia, with considerable human activity on the shore.

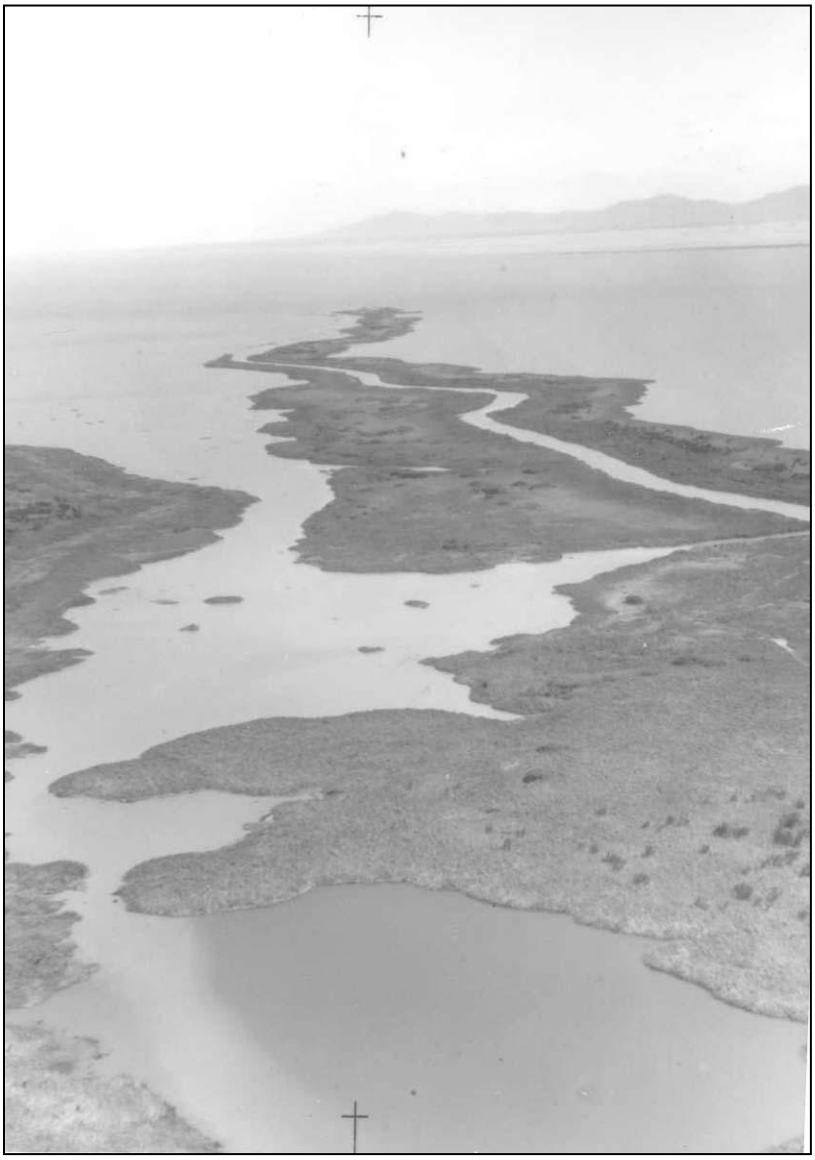


Plate 1. Omo River delta. Extensive marsh of reed beds with weed-filled open water. This comprises the whole of Section 1; similar habitat is not found elsewhere on the lake except for small marshes at the Turkwell and Kerio deltas. Moderate crocodile density of 14/mile.

Section 2 (Plates 2 & 3) Illeret to Allia Bay. 7 miles of shore. Mostly swampy consisting of small scattered reed clumps, grass and inundated bush, with extensive “weed” beds (species not identified). Occasional stretches of sandy beach. Crocodile density of 90 per mile is much higher than anywhere else on

Plate 2A (S2). Illeret to Allia Bay. Extensive weed-beds and inundated bush typical of this section. This photograph is of the northern end of Allia Bay, which supports the highest local density of crocodile on the lake

Plate 2B (S2). A recently flooded area caused by a small rise in lake level. Such sheltered water is favoured by small crocodiles that rapidly accumulate in such transient areas. The section has a density of 90/mile.

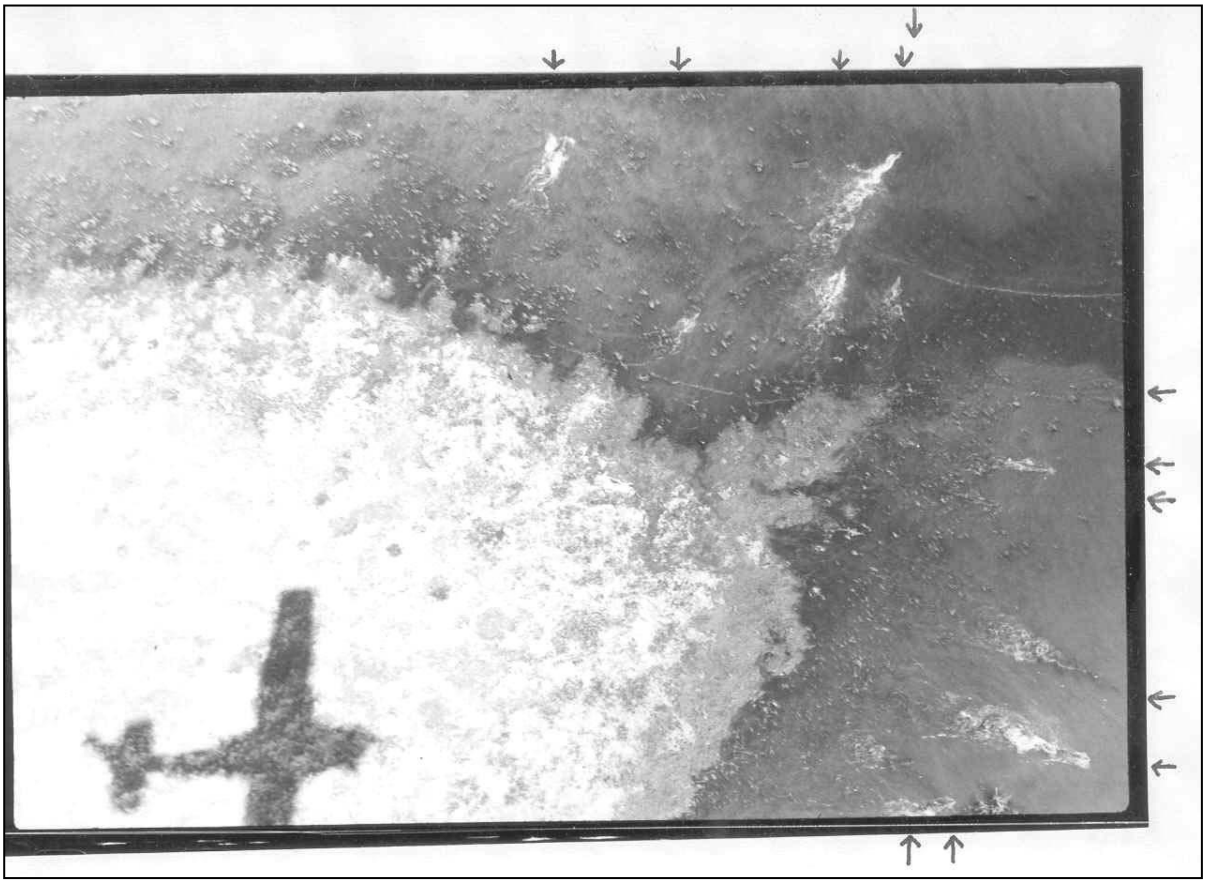


Plate 3A (S2).The passage of the aircraft has disturbed at least 10 crocodiles, while at least 1 remains ashore.

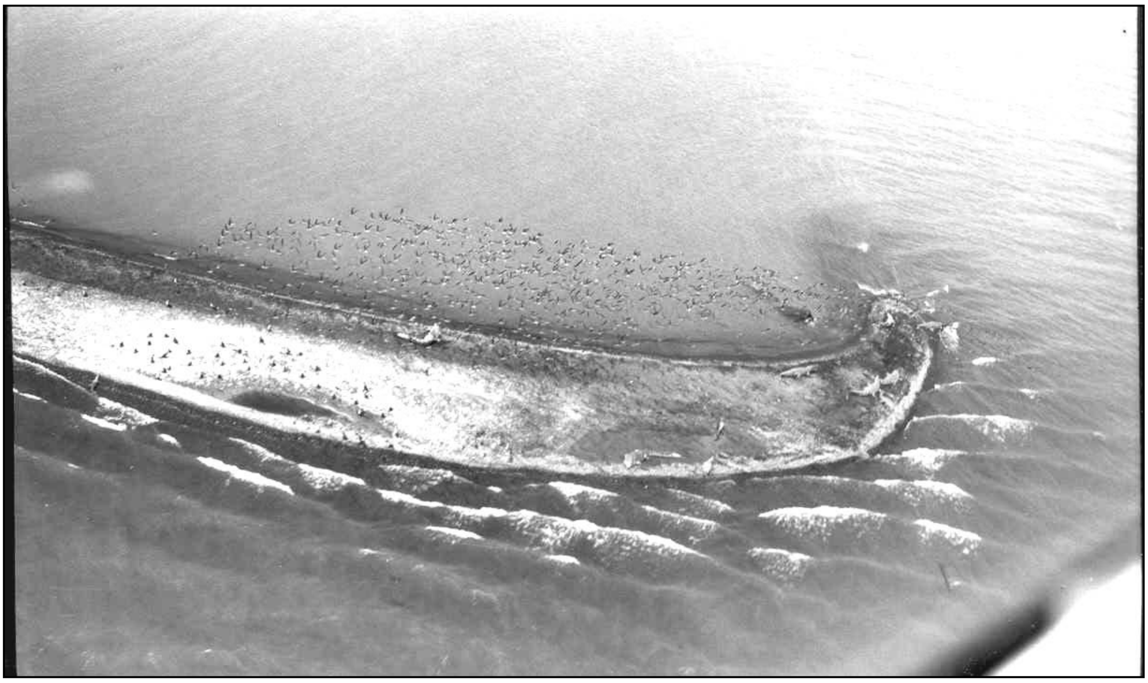


Plate 3B (S2) An isolated sandbank in Section 2 that illustrates the tendency for crocodiles to clump together. The hippo (upper right) and skimmers and Egyptian geese give some idea of scale.

the lake and accounts for 52.6% of the whole population. No resident humans, but subject to sporadic hunting by Merrille from Ethiopia.

Plate 4A (Sections 3, 6 & 7). Extensive sand and shingle beaches interspersed with rocky (lava) stretches. Low densities of 3-9 crocodiles/mile.

Section 3 (Plate 4) Allia Bay to Moite. 24 miles of shore, all rocky or shingle beaches, and backed by a range of hills which provide shelter from the wind. Low crocodile density of 9 per mile.

Section 4 (Plate 5) Moite. 24 miles of shore. Mostly sheltered swampy water, similar to Section 2, and with a high density of 26 per mile. No resident humans, but subject to regular, small-scale hunting by the resident El Molo. Considerable numbers of Rendille and El Molo domestic animals are watered along this section during the dry season, but the nomadic herders do not disturb the crocodiles.

Section 5. (Plate 5) Moite to Loiangalani. 68 miles of shore consisting of isolated stretches of sheltered, swampy water, similar to Moite, separated by

Plate 4B, Sections 11,12 and 13. Volcanic islands with occasional sandy beaches. The high densities of 24-39/mile

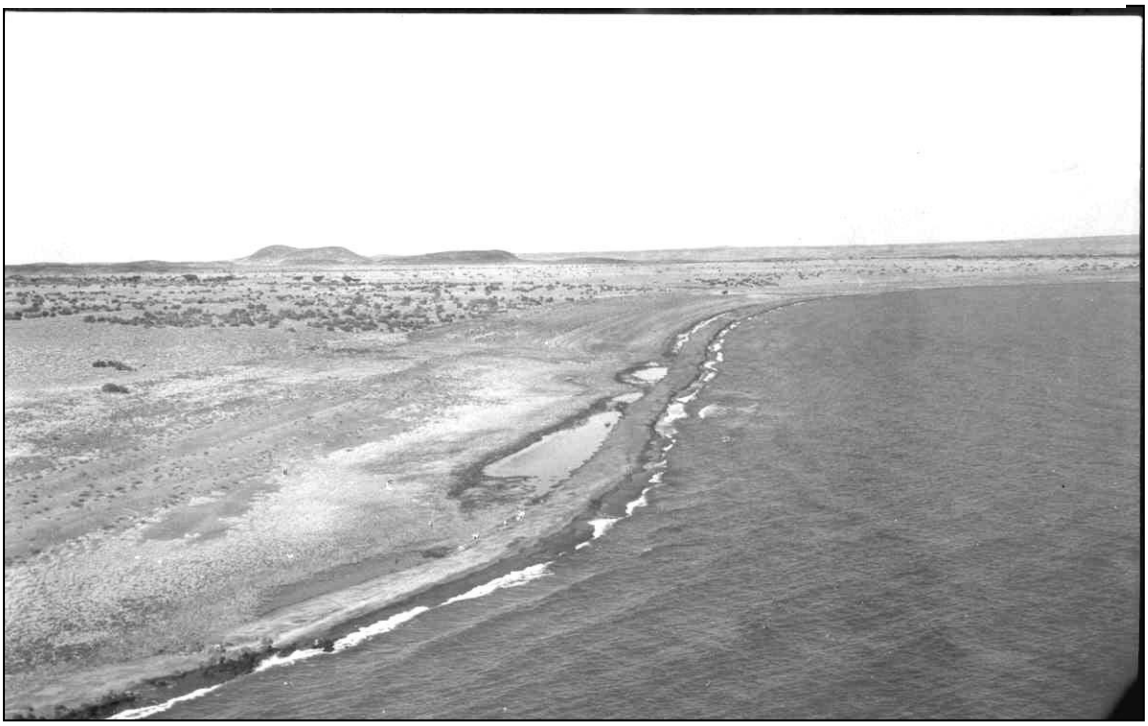


Plate 5. Sections 4,5,8 and 10. Open shore, but with numerous weedy patches and sheltered water. Moderate densities of 11-26/mile is obscure, but possibly associated with nesting.

Plate 6A. S9. Uninterrupted sand and shingle beaches, backed in places by doum palms, extending almost the entire length of the west shore. Very low density of 3/mile.

Section 6 (Plate 4) South East Shore. 24 miles of shore consisting of continuous shingle and rocky beaches. With Section 9, this section has the second-lowest density on the lake of 3 per mile. Continuous human activity along the shore.

Section 7 (Plate 4) South West Shore. 64 miles of shore, backed by a range of hills and very similar to Section 3. Rock and shingle beaches with no swamps, exposed to the almost continuous easterly wind. The low density of 7 per mile is made up almost entirely of animals living in sheltered inlets at the extreme south end of the lake. Continuous human activity.

Section 8. (Plate 5) Turkwell and Kerio deltas. 36 miles of shore, very similar to Sections 4 and 5, but less sheltered. Due to the prevailing easterly wind, the swampy areas are confined to irregularities in the shoreline which provide shelter. A moderate density of crocodiles of 11 per mile. Considerable hunting of crocodiles is carried out by the resident Turkana.

Plate 6B. S9. Uninterrupted sand and shingle beaches extending almost the entire length of the west shore, mostly devoid of either aquatic or terrestrial vegetation. Very low density of 3/mile.

Section 2. (Plate 6) Turkwell delta to Omo delta (excluding Ferguson's Gulf (Kalokol)). 121 miles of shore consisting of sand and shingle beaches mostly exposed to the full effect of the surf generated by the easterly wind. A very low density of 3 crocodiles per mile. Resident Turkana exist all along this section, who hunt and collect eggs.

Section 10. Ferguson’s Gulf (Kalokol). 16 miles of shore, enclosing a shallow bay about 2 miles across. Completely sheltered water with small swampy patches. A high density of 22 crocodiles per mile. Resident Turkana all round the bay.

Section 11 (Plate 4) North Island. 5 miles of shore. Mostly recent lava flows with two sandy beaches. Very low density of 1 crocodile per mile. No resident humans.

Section 12 (Plate 4) Central Island. 15 miles of shore, including 2 completely sheltered small lakes. Rocky shore with one beach. The relatively high density of 39 crocodiles per mile is associated with 2 small lakes on the island and along with Ferguson’s Gulf (Kalokol) this Section must be regarded as a special case, as similar habitats are not found elsewhere on the lake. No resident humans.

Section 13 (Plate 4) South Island. 18 miles of share. Mostly rocky but several sandy beaches and same sheltered water formed by partly submerged lava. A high density of 24 crocodiles per mile, possibly associated with the isolation of the Island from the mainland. No resident humans.

Population Counts

Methods

Distribution and density was assessed by aerial counting. As the study area was not large at the resolution of aerial counting total counts were made rather than samples. Two total counts were carried out, one in February 1965, and a second in June 1966.

During the 1966 count a considerable amount of aerial photography was experimented with. Using a military F.24 5-inch format camera, about 10% of the shoreline was photographed from about 800 feet above lake level. The purpose was two-fold: to establish whether photography would confer any advantages over direct visual counting; and to sample stretches of shore to obtain a breakdown of animals into size groups. The only advantage indicated by the use of photography in counting is to eliminate variations in ability among observers. The photographs do not reveal more animals than are seen by an experienced observer and in fact are less efficient in turbulent weather when the resolution on the negatives is impaired by scattered light, despite the use of Polaroid filters. Time and expense prevented a usable sample for breakdown into size groups being obtained as this could only be done in calm periods, which did not occur on suitable occasions.

Day Counts

Counting in February 1965 was by one observer (the author) from a Piper Colt aircraft at 50-100 feet above water level. This gave good results on narrow shorelines, but where the animals were spread out over a wide area counting was impaired due to the relatively small visibility profile of the observer. The June 1966 count used two experienced observers (M. Watson and R. Bell) both counting from the right-hand-side of a Cessna 182 from which the passenger door had been removed to improve visibility. Airspeeds of 70-100 miles per hour were maintained and height at 700-800 feet above lake level. The technique adopted during the June 1966 count was designed with the following points in mind. A total count was made rather than samples to provide an index for the whole lake. An estimate of the actual numbers present was then made by correcting the day count by a factor derived from night counts (Table 2.) Rudolf crocodiles are particularly susceptible to total counting since the area involved is not large and the animals are confined to a relatively narrow belt of open habitat. Water more than 0.25 miles from shore was not examined as in more than 500 crossings of the lake the author saw only one crocodile more than 0.25 miles from land (except in bays such as Ferguson's Gulf (Kalokol).) The height of the aircraft above ground was chosen to provide the observers with a visibility profile wide enough to include the entire habitat. This height meant that virtually no animals less than 100 cm long were seen. This actually improves the consistency of the count as animals this size are difficult to see from any height, and at best will only be recorded erratically when they occur in exposed situations.

In counting by this technique there are 2 main sources of error: those animals simply missed by the observer; and those animals underwater at the time of observation. The proportion of animals missed by the observer varies slightly according to the time of day and counting conditions. Crocodiles are naturally cryptic and when the water is rough, or flying conditions turbulent, somewhat more pass unnoticed than when conditions are calm. One of the major problems in counting crocodiles is a psychological one of having to concentrate on searching for individuals of greatly varying size: there is a tendency to pick on a given size range only. The second source of error, those animals submerged at the time of the aircrafts passage has not been assessed quantitatively. However, general observations suggest that only a small proportion is underwater at any given moment. In assessing this, account must be taken of the pattern of movement in and out of the water during the 24-hour cycle (Cott 1961, p. 217.) Basically, this pattern of activity consists of movement into and out of the water at intervals throughout the day. (Most of the night is spent in the water.) Two peak periods of lying ashore are evident, one in the morning and one in the evening. Crocodiles are somewhat easier to see when lying ashore but this behaviour does not greatly affect the proportion potentially visible as most animals in the water are on the surface, and therefore still visible.

Night Counts

In order to determine and correct the error present in day counts a technique of night counting has been developed. Hunting and capture experience has shown that an accurate estimate of numbers can be obtained by counting eye reflections from a torch. The technique involves moving along a stretch of shore, usually wading to ensure that the entire occupied habitat is in the range of the observer. Distances more than 50 m from the torch (6 volt “Hunter" lantern) cannot be considered accurately counted. Movement of the observer must be continuous, or the animals become disturbed, and the normal precautions of remaining downwind, silent and out of the light must be maintained. Most important is the necessity for an absolutely dark night, as the slightest moon provides enough light for a significant proportion of animals to see the observer. Approximately 3 miles of relatively high density shore gives a sufficiently large sample.

Results

The results of counting are Shown in Figure 1, and Tables 1 & 2. Figure 1 shows Lake Rudolf with distribution expressed by the proportion of the whole population that occurs in each section. Also shown is the actual density per mile of shore. Table 1 shows the results of both visual counts with estimates of actual numbers calculated with correction factors derived from night counts (Table 2). The two night counts in February 1965 gave an average correction factor for day counts of 3.1, and the two night counts in June 1966 an average factor of 2.2. The technique on both occasions was the same and the lower difference between day and night counting in 1966 is attributed to the improved daytime counting on this occasion.

	February 1965			**June 1966**			
Section	Miles shore	Number counted	estimate	Number counted	estimate	Proportion of total (%)	Density per mile
1	88	202		546	1,201	9.6	14
2	73	1,946		2,974	6,543	52.6	90
3	24	162		97	213	1.8	9
4	24	130		288	634	5.0	26
5	68	300		574	1,263	10.2	19
6	24	45		34	73	0.6	3
7	64	114		195	429	3.4	7
8	36	138		173	381	3.0	11
9	121	170		147	323	2.6	3
10	16	41		165	363	3.0	22
11	5	10		2	4	1.0	1
12	15	218		267	587	4.7	39
13	18	97		192	422	3.4	24
TOTALS	576	3,573	11,763	5,654	12,439		

Table 1. Shows numbers of animals seen and estimated in February 1965, and June 1966. The estimates were obtained by multiplying day counts by a factor of 3.1 in 1965 and 2.2 in 1966 (Table 2.)

Locality & size	Date	Numbers (day)	Numbers (night)	Difference	Correction factor used in Table 1
South end Moite Pool 1 X 0.25 miles	Feb1965	67	259	2.86	3.1
Allia Bay 2 miles of shore	Feb 1965	61	205	3.36	
Allia Bay 3 miles of shore	June 1966	344	672	1.96	2.2
North end Allia bay 2.5 miles	June 1966	193	458	2.37	

Table 2. Shows results of 4 night counts and the difference between the corresponding day counts.

Two night counts were made for each day count, and the sections of shore involved were recounted by day from the air to provide the comparative Figures for the correction factors (Table 2.) The total number of animals estimated to be in the lake in June 1966 was 12,439. This Figure was obtained by multiplying the 5,654 animals actually seen by a factor of 2.2, being the average of the two factors obtained from night counts. This total ignores very young crocodiles less than 6 months old, as during the peak hatching period there may be large numbers of newly hatched animals.

It can be seen that 79.9% of the whole population occurs on the east shore of the lake, and 52.6% on the north-east section alone (Section 2.) The whole west shore only supports 12% of the population, and the three major islands 8.1%. Section 9 on the west shore, of 121 miles, only supports 2.6% of the population. Density has been expressed as corrected actual numbers of crocodiles per mile of shore, although the animals are really clumped along the shore, as would be expected. The variation in densities is shown in Figure 1. The highest density occurs in Section 1, with 90 animals per mile, and the lowest density on North Island, of one animal per mile. The west shore (except for the Turkwell delta and Ferguson’s Gulf (Kalokol) supports very low densities of 3-7 animals per mile. The high density of 39 per mile on Central Island is due to the accumulation of crocodiles in the small lakes there.

Density expressed as numbers per mile of shore is useful only for comparative purposes as the animals actually live in the narrow belt made up of the immediate shore and the littoral stretching out 100-500 yards from land, depending on the degree of shelter. Thus the animals actually occupy approximately 144 square miles of habitat (576 x 0.25 miles) and in fact the majority spends most of the time within 100 yards of shore, and thus occupies only about 34.6 square miles (576 x 0.06 miles). This represents a density of approximately 360 crocodiles per square mile of habitat. The highest density is found in Section 2 where 52.6% (6,543 animals) occupy 73 miles of shore. This represents a habitat of 4.38-18.25 square miles (100-500 yards from land) and a density of 358-1,494 crocodile8 per square mile. Based on the age structure indicated in Figure. 13 the total biomass of crocodiles on Rudolf is estimated as 325,000 kg. This represents, in Section 2, 9000-59,000 kg per square mile and compares interestingly with some of the higher densities in terrestrial situations (Bouliere 1963, Lamprey 1964). Their preference for shallow water thus confines them to a relatively small total area of habitat compared to terrestrial animals, a fact not generally appreciated, and one that imposes low limits on the relative numbers of crocodiles in East Africa.

Cott (1961) p. 278, has commented on the apparent scarcity of small crocodiles 60-120 cm long even going so far as to say that these animals" go into retreat," and notes that many other observers make similar comments. This effect is almost certainly a result of confining observations to the day. In order to gain a subjective impression of the numbers of crocodile in any given area it is essential to observe them at night with a torch when a very different impression will be gained to that obtained by day. Crocodiles are exceptionally cryptic, wary animals and even on Rudolf where cover is scant, casual daytime observation reveals only a few larger animals. At night on Rudolf the impression is gained of gradually decreasing numbers with size: certainly no particular size group is absent.

Cott, p. 316, also comments on the segregation of age groups. During the day there is a tendency for the larger animals to be associated with exposed basking sites, but at night, when actively feeding, crocodiles of all sizes may be found together and no pronounced segregation into size groups was observed on Rudolf. As large crocodiles will eat smaller ones there may be same avoidance of bigger animals by small ones at close quarters, but if this occurs it does not result in segregation into size groups.

1c Factors influencing crocodile distribution

At the beginning of the survey 14 days were spent on North Island to eliminate the crocodiles there. It was intended to make regular aerial counts of the Island from then on to observe changes in numbers, but expense prevented this, so the experiment was abandoned. No other experimental work on movement and distribution was attempted.

The main factors influencing distribution on Rudolf are thought to be shelter and possibly food availability. Figure 1 shows that most of the population (79.9%) occurs on the east shore, and locally distribution is clumped with concentrations occurring always in relatively sheltered places. The long sandy beaches of the west, exposed to the surf and with no vegetation, are very sparsely populated.

Ferguson’s Gulf (Kalokol), the only large body of sheltered water on the west shore, is noteworthy in supporting a relatively high density of crocodile despite continuous shooting of crocodiles there by the Game Department, and year-round human activity along the shore. When hunting crocodiles it is very obvious that they avoid rough water. Cott (1961) p. 218 notes that crocodiles show a marked tendency to come ashore during rough weather. It was often observed on Rudolf that during spells of rough weather, particularly when winds blew from unusual directions causing water to surge into normally sheltered places, that crocodiles rapidly moved from such areas. These animals would then accumulate in sheltered spots, often not normally frequented. Rough water generally is avoided and almost certainly is the major factor governing crocodile distribution on Rudolf. The persistent easterly wind generates an almost continuous swell and the resultant surf along the west shore prevents the growth of aquatic plants. The long sandy beaches are only occasionally interrupted by sheltered inlets and the entire habitat is avoided by crocodiles.

The reason for this avoidance of turbulent water is not immediately apparent but may be partly due to difficulty in breathing. Crocodiles swimming in rough water tend to keep the mouth open, so that the nostrils are clear of the surface. Although when not actively swimming they can stay submerged for long periods and rise to breathe for a few seconds only, it is likely that when engaged in continuous activity such as swimming, their oxygen requirements are much greater, necessitating frequent aspirations. Thus merely submerging to avoid waves may not be possible if continuous activity is required as well. While hunting or observing crocodile the impression is gained that long distances are covered by swimming on the surface, not underwater.

Crocodiles on beaches with surf tend to come ashore again rapidly after being disturbed, while crocodiles in sheltered water may remain off-shore for protracted periods, possibly many days at a time, as was observed by the author on North Island. Crocodiles in Ferguson’s Gulf (Kalokol) spend extended periods, probably many days, off-shore, where the continuous human activity discourages them from coming out. It is highly likely that this is in part made possible by the shallowness of the water (10-20 feet,) permitting them to - 27-
rest on the bottom with little effort getting to and from the surface. It is of interest to note here that it is clearly unnecessary for a crocodile to adhere to the normal rhythm of movement in and out of the water in which much of the day is spent lying ashore. The function of this behaviour is not clear, but may be nothing more than for relaxation after the feeding activity of the night. It may also be necessary for the animal to absorb solar energy, but this is possibly still done when floating on the surface.

Associated with the tendency of crocodiles to avoid rough water, and therefore accumulate in sheltered water, is the obvious advantage of calm water in feeding (see section on feeding behaviour.) Further, sheltered water tends to have much more vegetation in and near it, providing the shelter favoured by small crocodiles (Cott 1961, p. 277) and probably necessary for their survival.
To what extent fish densities are affected by the wind is unknown, but casual observation suggests that fish on Lake Rudolf are more numerous in sheltered areas. The availability of food fish may well vary according to the degree of turbulence of the lake and this may be influencing crocodile distribution. - 28-

There is evidence that considerable distances are covered by crocodiles on Rudolf. Modha (pers. comm.) observed crocodiles with pieces of fish net caught on their heads at Central Island: these could only have come from Ferguson’s Gulf (Kalokol), 9 miles away. Much of the lake is only 6-15 miles wide and it is possible that crocodiles regularly cross the lake. A crocodile shot on North Island contained the remnants of a large mammal it must have eaten on the mainland 9 miles away, as none occur on the island. They certainly move along the shore. In the 4 years since 1962 over 500 crocodiles have been shot in Ferguson’s Gulf (Kalokol) by the Game Department and many others wounded and lost. The present population of 363 animals is not noticeably different to what it was in 1962, according to R. McConnell (pers. comm.) the fisheries officer stationed there. As it is unlikely that any eggs laid near Ferguson’s Gulf (Kalokol) escape discovery by the human residents, steady recruitment of the Gulf animals must be occurring from some other source. As it is located on the extensive sandy beaches of the west shore with a density of only 3 animals per mile, there is obviously considerable movement of animals along the shore resulting in an accumulation in the Gulf.

Section 2. Food choice

Methods

All stomachs were examined in the field and their contents recorded. Unidentified remains were preserved for identification in the laboratory. Three categories were recognized; stomachs containing fresh food, those containing remnants only, and empty stomachs. If fresh enough, the approximate size of the food animals was recorded. Observations of feeding behaviour were made in the field and on captive specimens.

Results

2a Feeding Behaviour

To facilitate comprehension of the observed food choice and the differences between various populations a superficial account of feeding behaviour is presented first.

The Nile crocodile is basically an aquatic, opportunistic predator. Animals at the water’s edge may be taken and there is some evidence that large crocodiles may lie ashore and ambush animals coming down to drink although this may only occur fortuitously. Cott (1961) p. 302, records that very small crocodiles may hunt terrestrial insects on land, but most insects are probably caught near the water’s edge, or after having fallen into the water. As carrion feeders, they will travel considerable distances overland to carcasses and the author has observed a crocodile following a dragged lion kill, presumably by the scent trail. Feeding is done mostly at night. A high proportion of crocodiles are in the water at any given time at night and considerable feeding activity is commonly observed.

Fish, the main food source of Nile crocodiles generally, are caught mostly in shallow water. Observations of animals at night with a torch (most individuals if unaware of the observers are undisturbed by a moderate torch light) show most feeding activity to occur in very shallow water. They float in shallow water with their feet on or near the bottom, mouth open, and eyes half above and half below the surface. Movement is slow, half swimming, half walking, with frequent periods of inactivity. Shoals of fish moving through the shallows are snapped at when within a few inches of the crocodile. Frequently no attempt at catching is made until the fish actually touches the crocodiles head and fish have been observed swimming right into the open mouth. Although no quantitative data exists it is evident that the majority of feeding "bites" fail.

Bites are made with a rapid sideways movement of the head, the closing of the mouth being accompanied by a rolling over of the head about the longitudinal axis, so that the jaws meet with the lateral face of the head parallel to the ground. The function of the turning over of the head is not clear, but in catching fish like tilapia, it may be to overcome the tendency of these fish to escape by leaping out of the water. Rolling the head over the fish will pin it down, reducing the opportunities for escape. In picking up objects from the ground, such as a dead fish, turning the head over allows the teeth to be brought right down over the object concerned.

The tendency to feed in shallow water has the obvious advantage of keeping the prey animal and crocodiles head on the same level, thus minimizing possible avenues of escape. In captive animals a tendency to utilize obstructions such as rocks or the corner of the tank to confine the prey has been observed.

Two other, more specialized, methods of catching fish have been observed.

The first, seen only in captive animals, involves the crocodile approaching a shoal of fish near the shore from deeper water. The crocodile slowly runs aground so that its head becomes half awash. It then gradually curves its body around, so that the tail tip eventually comes ashore. It then bites at the trapped fish, the whole pattern being performed smoothly, in one movement.

The second technique is associated with their observed tendency to approach splashes made by shoals of fish jumping. Any disturbance caused by fish, or by other crocodiles feeding, will often stimulate a nearby crocodile to approach. A crocodile thus alerted, and if within a suitable distance, sometimes leaps right out of the water towards the fish. If the animal lands among the fish, it may bite at them immediately. Often the startled fish become temporarily disabled by swimming or jumping into excessively shallow water.

Crocodiles, like most predators, are quick to notice animals in difficulties and to take advantage. Pitman (1961) gives a description of the attempts by 8 crocodiles to catch a flightless (moulting) spurwing goose that took to the water at the approach of a boat. The bird was evidently recognized as being incapacitated and immediately became an object of attention to the nearby crocodiles. It may be that the primary function of the spectacular leaps that crocodiles frequently make is to frighten fish into situations where they are easier to catch.

Of interest is the fact that identical leaps are sometimes made by crocodiles disturbed by the observer. In such instances, it serves as an escape mechanism to get the crocodile into deeper water rapidly.

Crocodiles frequently catch fish too big and strong to be easily subdued. Several observers have watched such catches being taken ashore and battered on the ground until they cease struggling. In battering a fish thus, the head movements are identical to the feeding bites, except that the jaws are kept closed. The rolling over of the head here serves to ensure that the fish, held sideways in the mouth, is brought into contact with the ground.

The normal fish catching bites are in response to two basic stimulation sources: visual and tactile contact. They will frequently bite at inanimate objects such as stones which are accidentally touched while the animal is moving about

During the survey many nights were spent wading in water up to 5 feet deep while hunting. Crocodiles were frequently seen feeding, but always in very shallow water. Crocodiles have been observed catching fish in deep water (Cott p. 303) but the technique adopted in such instances is unknown. Kinloch (in Cott, page 303) mentions the taking of anglers artificial lures in deep water by crocodiles. These instances may, however, stem from the attraction of an unusual object to the predator, a phenomenon possibly associated with the abnormal movements of distressed animals.

The significance of the extensive weed beds on Rudolf as a high density crocodile habitat is probably associated with the conditions necessary for catching fish. The weed provides support for the crocodiles, and restricts the movement of the fish. Crocodiles have often been observed feeding in the weed beds, where conditions often resemble those of shallow water, the tops of the weed here simulating the ground in the shallows.

In feeding on animals other than fish, two basic techniques may be recognised. Firstly, there is the capture of animals without the use of elaborate stalking or ambush, in which approach is made openly. In this category is the fortuitous catching of passing insects. Secondly, animals which would recognize a crocodile as a potential source of danger, such as most mammals and birds, have to be taken by surprise. In these instances, the crocodile may stalk a watering mammal by approaching underwater, or it may take advantage of ambush.

Like snakes, small crocodiles have to swallow their food whole and thus the size of the food animal taken will be determined partly by the relative size of predator and prey. But with large crocodiles the situation is different, as these can overpower animals too large to swallow, whose inertia as a carcass is sufficient to permit the crocodile to tear off pieces to swallow. Crocodiles feed readily on carrion and descriptions of the techniques for tearing off pieces are given by Attwell (1954). The animal may tear off fragments simply by shaking the head from side to side, like a dog does, or by holding the flesh and then spinning the body about the longitudinal axis, thus tearing off a piece.

2b Analysis of stomach contents

The stomach contents of 493 animals examined during the survey are summarised in Table 3.

Category	Number	Proportion (%)
Total number of stomachs with food	254	51.6
Total number of stomachs without food	239	48.4
Number of stomachs containing fish only	223	45.4
Number of stomachs containing fish and other animals	8	106
Number of stomachs containing animals other than fish	23	4.6

Table 3. Stomach contents of 493 Rudolf crocodiles.

Of those stomachs containing food, 90.9% contained fish, and 87.8% fish only. 9.1% contained other animals only. 48.4% of the stomachs were empty. 22% contained hard food remnants only, such as bones or scales, and 29.6% contained soft, relatively fresh food. No difference in food animals or incidence of empty stomachs was observed between males and females, between crocodiles from Moite or Allia, or from month to month, although slight differences would pass undetected, as the samples generally were small. In addition to food, the stomachs of all 493 animals examined contained stones. Cott (1961) discusses so-called stomach stones at some length and suggests a possible hydrostatic function. No other data on stomach stones were collected during this survey.

Food Animal	Uganda A*	Uganda B*	Lake Bangweulu	Mweru Swamp & Kalunguishi River	Luangwa River	Kafue River	Zambezi River	Zulu-land	Lakes Kioga & Kwania	Lake Rudolf
	L o c a l i t y									
Insects & Spiders	52.3	61	25.5	17	62	38.3	33.9	0	1	3
Crustaceans	7.4	1	1.2	0	0	9.7	17	0	0	0
Molluscs	5.6	5.5	28	19.5	3.3	14	8.5	0	0	0
Fish	13	20.6	27.7	49	4.4	16	27.4	20.5.	74	87.8
Amphibia	6.5	1	1.8	0	8	1	1.2	0	1	1.2
Reptiles	5.6	5.5	1.2	5.8	6	5.5	5.9	16	14.1	4.5
Crocodile Eggs	0	0	0	0	0	0	0	2.7	1	1
Birds	4.7	0	4.6	2.9	4.4	5.9	3.9	9.1	8.7	2.3
Mammals	5	5.5	9.8	5.8	12	8.8	6.7	52.2	1.6	1
Total stomachs with identified food	233	92	173	69	183	239	387	44	440	254

* Uganda A is above and Uganda B below Murchison Falls

Table 4 Compares the occurrence of various animals in crocodile stomachs from 10 localities in Kenya, Uganda and Zambia, expressed as percentages of the total number of food-containing stomachs for each locality. Records from Lake Kioga and Kwania are from Hippel 1946; other Uganda and Zambia records are derived from data given in Cott (1961)

Table 4 shows the proportion of various food animal types in the Rudolf sample and compares this with 9 other localities. Individual samples are too small for critical comparison, but the results are sufficient to illustrate a number of points. Firstly, in the majority of localities, insects are the most frequently recorded food animal. However, as pointed out by Cott, p. 279 they are taken exclusively by small crocodiles. Insects are not recorded from crocodiles >250 cm long, presumably owing to the size difference between predator and prey. After insects, fish are the most frequently taken food animal. Cott found crocodiles of all sizes feeding on fish and this is the case on Lakes Rudolf, Kwania and Kioga.

Molluscs are frequently taken and in a wide range of localities. Reptiles, mammals and birds form a significant part of crocodile diet in most localities and crustaceans (mainly crabs) are eaten where they occur. Fish are clearly the most important food source for Nile crocodiles generally as they are taken throughout life and in higher proportions than other animals. Cott, p. 278, concluded that the very wide variety of food animals that have been recorded from crocodile stomachs reflected a progressive change in diet with age. His data do not however support this conclusion. Of the 9 animal types recorded by Cott, 6 are eaten by crocodiles of all sizes from 50 cm onwards. Three groups only eaten by very small crocodiles were insects, spiders and amphibians, almost certainly a reflection of the discrepancy in size between larger crocodiles and arthropods and amphibians. It seems more likely that crocodiles will eat any available animal and the stomach contents of any particular crocodile will reflect the local availability of potential food animals and the relative sizes of predator and prey.

Crocodiles from Rudolf, compared to most other habitats, show two striking differences: a high incidence of empty stomachs, discussed later, and an almost exclusive feeding on fish. This latter is readily explained by the very obvious lack of other food animals in and around the lake, such as large insects, amphibians and small mammals. Also scarce are small birds (except waders), lizards and snakes. Molluscs and crustaceans available to crocodiles are non-existent. The lake and its surrounds constitute, from the biological point of view, a very barren environment compared to other East African crocodile habitats.

The incidence of reptiles (other crocodiles and chelonia) taken is similar to elsewhere, but birds evidently fewer. Here again, the difference is probably due to the lower incidence of darters and cormorants which are the birds most commonly recorded by other observers. The only birds common on Rudolf (except in isolated suitable habitats such as Ferguson's Gulf (Kalokol) and Central Island) are various waders and Egyptian Geese, which are probably infrequently taken as their occupation of shallow water could be expected to make it easy for them to detect and avoid an attacking crocodile.

Table 5 compares the incidence of various fish types in stomachs of crocodiles from 11 localities in Zambia, Uganda and Kenya. Again samples are mostly small, but trends are detectable. Firstly, cichlids, mostly tilapia species, are everywhere except lakes Mweru and Kalunguishi taken in relatively high numbers and must be considered the most widely eaten fish type. Other types are taken in variable proportions, but mochokids (*Synodontis* spp.) clariads (*Clarias* spp.) and characins, (*Hydrocyon* and *Alestes* spp.) are taken in the widest range of habitats. All these fish frequent the shallows. But the fish most frequently taken varies considerably. In Uganda above Murchison Falls (including Lakes Kioga and Kwania) it is a *Protopterus*; in Mweru and Kalunguishi almost exclusively *Clarias mossambicus* Peters, and on Rudolf almost exclusively *Tilapia nilotica vulcani* Trewavas. In other areas more than one variety may be taken in equal proportions.

	Locality									
Family	Uganda A*	Uganda B*	Lake Bangweulu	Mweru Swamp & Kalunguishi River	Luangwa River	Kafue River	Zambezi River	Zulu-land	Lakes Kwania & Kioga	Lake Rudolf
Lepidosirenidae	41								33	1
Mormyridae	18	5.5	6				2.5		1	
Characidae		22	15	3	28	9.5	2.5			1
Cyprinidae	25	11				5			30	2
Bagridae		17							6.5	
Schilbeidae			15							1
Claridae		6	6	97		31	40		7	10
Mochokidae		22	22		44	10	21	25		4
Anguillidae								25		
Cyprinodontidae						6				
Plectorynchidae								25		
Centropomidae		6								1
Cichlidae	18	11	38		28	38	33	25	23.5	87
Total number of stomachs with identified fish	17	18	16	31	7	21	76	4	326	177

* Uganda A is above, and Uganda B is below Murchison Falls. Where percentages total more than 100, it is due to two or more species in the same stomach.

Table 5 Shows the incidence of 13 fish types in stomachs of crocodiles from 11 localities in Zambia, Uganda and Kenya, expressed as percentages of all identified fish for each locality. Data for Kioga and Kwania from Hippel (1946) and for Uganda adapted from Cott (1961.)

The preponderance of tilapia in Rudolf stomachs is obscure. To superficial observation *Clarlas mossambicus* and *Alestes* spp are common fish of the shallows and could be expected to form a more important part of their diet. Of interest are Cott's observations from Mweru wa Ntipa where 49% of all stomach contents were fish. Of these, 97% were *Clarias mossambicus* despite the abundance of tilapia. There are obviously many factors influencing food choice.

Table 6 compares the incidence of empty stomachs among crocodiles from Rudolf and other habitats. Cott’s data, which he does not present separately, are from a variety of Uganda and Zambian localities.

Locality and source	**Sample**	**Percentage of stomachs with food**	**Percentage of stomachs empty**
Zambia Cott (1961)	591	85.9	14.1
Lakes Kioga and Kwania (Uganda) (from Hippel (1946)	587	76	24
Rudolf	493	51.6	48.4

Table 6. Compares the proportion of empty to food-containing stomachs in crocodiles from 3 localities.

The very much higher incidence of empty stomachs on Rudolf (48.4%) compared to elsewhere (Hippel 24%; Cott 14.1%) is outstanding and unexplained. The highest local incidence recorded by Cott was 27.5% (Mweru and Kalunguishi), still much lower than for Rudolf. In both these localities fish form a high proportion of all stomach contents and in both instances there is almost exclusive feeding on only one fish species.

Cott, p. 282, found a higher incidence of empty stomachs in crocodiles over 180 cm than in immatures (29.5% and 9.1% respectively) but on Rudolf the proportions were similar (51% and 41% respectively.)

The relatively high incidence of empty stomachs on Rudolf is not accompanied by any obvious deterioration in the physical condition of the animals. Less than 1% of the animals examined were described as being in "poor condition". Nevertheless, they obviously feed less frequently than crocodiles elsewhere and while this may only mean that fish are a more easily convertible food source than other animals, it is suggested here that it is a consequence of some unexplained function of availability. Young crocodiles in captivity if supplied with an excess of fish will feed every day. This suggests that the high incidence of empty stomachs on Rudolf is a consequence of low food availability and that the animals would feed more frequently if they could. If, as postulated, the animals are not obtaining a maximal amount of food then a likely compensation would be a lowering of growth rate. This is discussed further in Section 4.

2c Quantity of Food Consumed

There are no quantitative data on the amount of food consumed by wild crocodiles and the results just discussed show that this varies considerably. However, it is possible to calculate approximately the amount of food that could be consumed by a wild population from a consideration of captive animals.
Pooley (pers. comm.) has extensive, as yet unpublished, data on the amount of food consumed by captive animals. He observed hatchling crocodiles to consume approximately 3.8% of their weight in food per day under conditions where excess food was available. Further, he found that they consumed similar quantities per meal whether they were fed daily, or at 3-day intervals, suggesting that a stomach fill is digested in 24 hours. Essentially similar results

were observed by the author in 3 captive hatchlings from Rudolf that were kept in Nairobi in a tank with the water temperature maintained at approximately 260^{o}C and fed on live fish. Cott (1961) describes observations on 2 crocodiles of 230 cm which consumed an average of 0.8% of their weight in food per day, although the details of the conditions under which they were kept are not given. Nevertheless, a falloff in the rate of food intake would be expected to accompany a falloff of growth with age.

Based on the age structure in Figure. 13 the biomass of crocodiles on Rudolf has been estimated as 525,000 kg. Ingesting 3.8% of their weight in food per day would represent 4,000,000 kg fish per annum (90.9% of food is fish). Wild crocodiles on Rudolf, at their current density, are obviously feeding at a much lower rate and will consume only a small fraction of this maximal amount. Nevertheless the Figure is of interest to the prospective crocodile farmer who will aim at maximising the rate of growth in his animals.

Section 3 Reproduction

The purpose of this section is to describe, superficially, the reproductive process in both sexes, emphasizing those aspects relevant to crocodile population dynamics at the expense of a more detailed treatment of the mechanics of reproduction.

3a Reproduction in the male

Methods

All animals killed were examined in the field and their reproductive state assessed. Testes were weighed on an Ohaus triple beam balance, measured (length, breadth and depth) and the vas deferens examined for the presence or absence of semen. Several entire reproductive tracts were collected. Semen samples were examined microscopically on the spot for the presence of sperm. Testis tissue from 52 animals of all sizes and at all times of the year was collected and fixed in a 10& formaldehyde solution. Tissue from 24 animal ranging in length from 150-470 cm was ultimately sectioned for histological examination. Sections were cut at 5 µ and stained with a standard haematoxylin/eosin technique. Tissue stored in fixative for up to 18 months was found to be satisfactory for the determination of spermatogenesis and the measurement of tubule diameters.

Results

A well established breeding season occurs in most reptiles and is described for the Nile crocodile Cott (1961) and Modha (1967). Basically, in the male there is an annual build up of spermatogenetic activity culminating in a period of sexual activity. This is followed by a quiescent phase during which no spermatogenesis occurs and the testis decreases in size. In the male crocodile the events accompanying the onset of maturity and the cycle of reproductive activity are briefly as follows. In the immature animal the testis is small, weighing less than 10 g. With the onset of spermatogenesis the testis increases in size, weighing, in an animal 470 cm long, over 700 g. The active testis is pink in colour while the mature but inactive testis darkens to a mottled purple; this is not however an accurate indication of the state of sexual activity of the testis. With the production of sperm, seminal fluid begins to accumulate in the vas deferens. Microscopic examination up to 4 hours post mortem of semen from both the testis and the vas deferens shows a dense mass of motile sperm. A tendency for the sperm to occur in clumps of 15-30 arranged symmetrically with the sperm bodies together and tails radiating outwards was frequently observed. Histologically, the immature testis is characterized by extensive interstitial tissue and small tubules with a relatively thin germinal epithelium. As spermatogenesis begins the epithelium starts proliferating and the tubules enlarge until their diameter is three times that of the immature testis. Very little interstitial tissue is present and the testis is composed almost entirely of seminiferous tubules. In the mature but quiescent testis the tubule diameter is reduced by almost half and no spermatogenetic activity is seen.

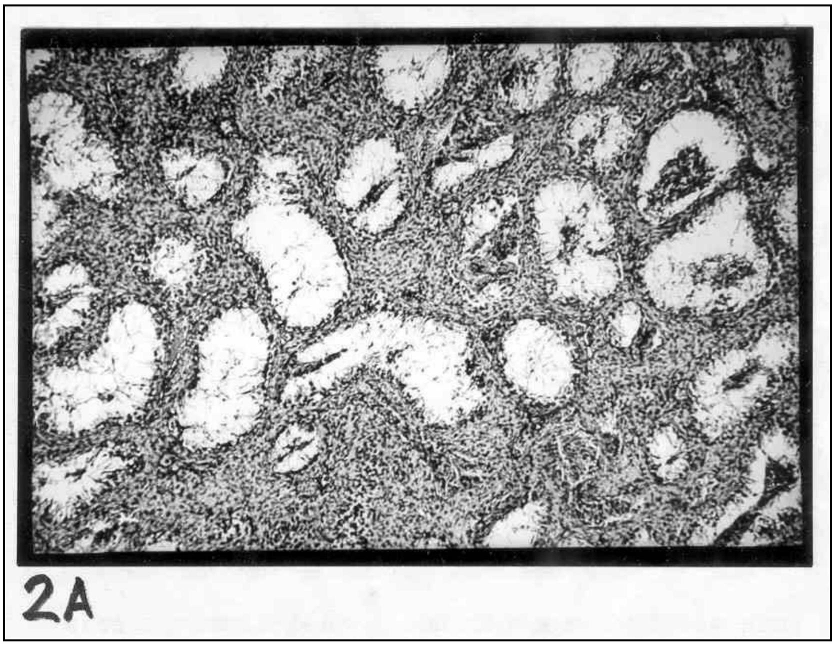


Figure 2.A. Z.67. Immature testis with extensive interstitial tissue, small tubules with only a thin germinal epithelium. 63 diam.

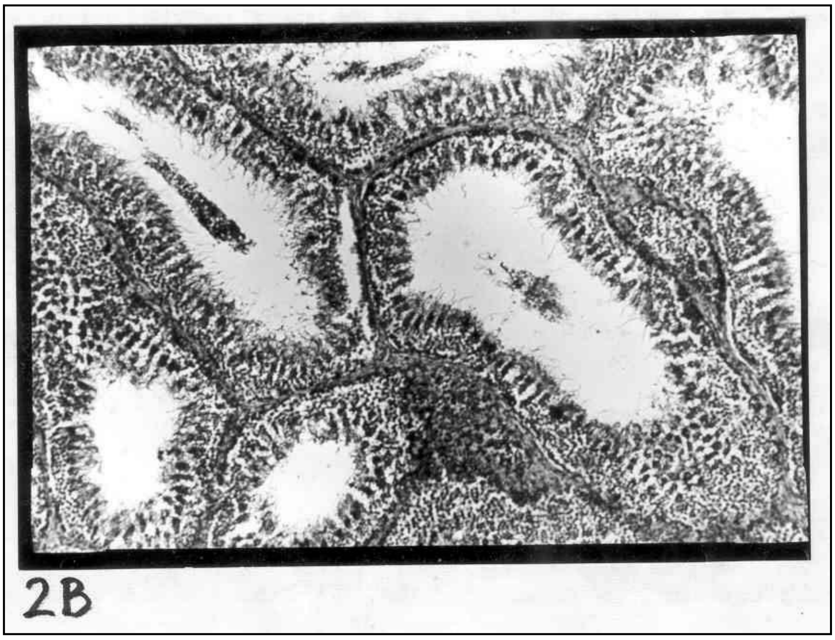


Figure 2.B. Z 68. Mature testis at the height of spermatogenesis. The tubules make up most of the testis volume and interstitial tissue is reduced to a thin layer between tubules. A thick germinal epithelium is present with a columnar appearance. Clumps of sperm tails are seen projecting into the lumen of the tubule. 63 diam.

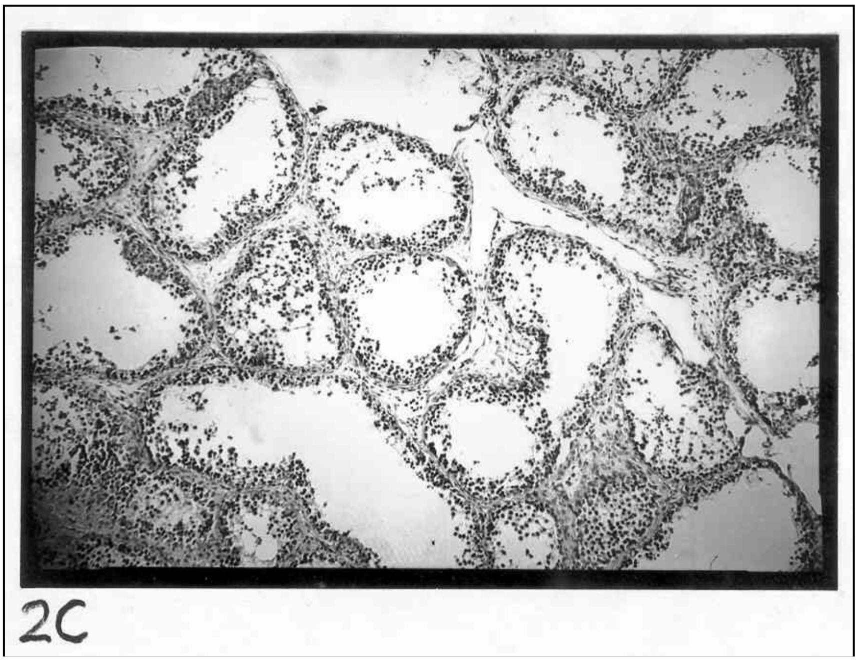
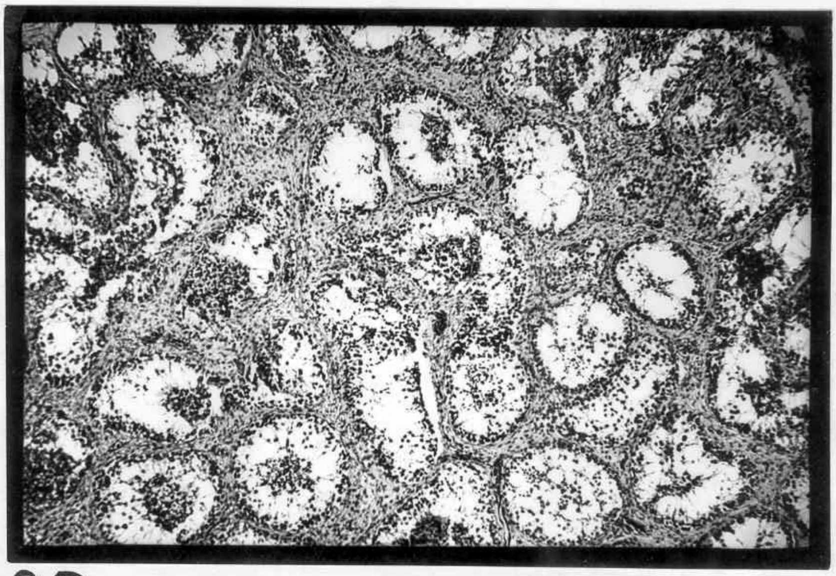


Figure 2.C. B.10. Mature but quiescent testis. Tubule diameter is reduced, there has been an increase in interstitial tissue and the germinal epithelium is reduced and somewhat disorganized. 63 diam.



2D

Figure 2.D. X.3. Mature testis considered to have become non-functional. Tubules are similar in size to an immature animal's and the interstitial tissue is extensive. The germinal epithelium is almost completely broken down. 63 diam.

The 3 basic conditions of the male testis, namely immature, mature and, active and mature but quiescent are shown in Figs. 2A, 2B, 2C and 2D.

The product of length, breadth and depth in 35 animals with testis weights in the range 1-40 g are listed in Table 7 with the corresponding testis weights. These data have been plotted in Figure 3 as the cubic factor against weight and the regression of cubic factor (y) on weight (x) calculated. The regression coefficient was 1.5492. This was done to provide a ready means in the field, where an accurate balance may not be available, of determining the testis weight in animals that are near the point of sexual maturity.

Testis wt (g)	Testis cubic factor (cm)	Testis wt (g)	Testis cubic factor (cm)
1.0	0.6	16.5	22.5
2.0	1.4	16.5	24.0
2.7	2.7	17.0	27.6
3.5	4.3	18.0	36.0
4.5	5.5	18.5	22.6
5.0	5.5	19.0	44.8
6.0	10.5	20.5	30.2
7.0	22.1	20.0	37.8
9.4	12.4	21.0	35.0
10.0	11.2	20.0	40.0
11.0	19.1	23.0	50.4
11.0	18.5	24.0	28.0
13.0	33.6	25.0	30.4
14.0	35.8	25.0	38.5
14.0	22.5	29.0	50.0
15.0	35.0	35.0	45.0
15.0	24.4	38.0	61.0
16.0	32.5		

Table 7. Lists testis weights and the corresponding product of testis length, breadth and depth, in 35 animals with testis weights in the range 1-40 g.

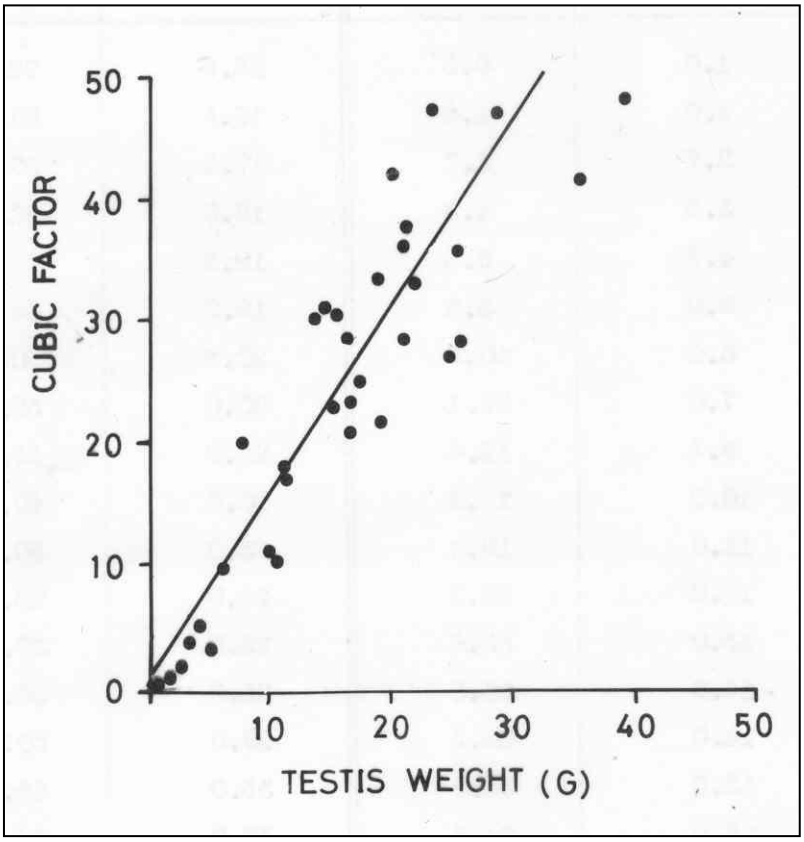


Figure 3. The product of length, breadth and depth plotted against weight in 35 testes in the range 1-40g. The regression coefficient was 1.5492

Determination of Sexual Maturity

It is important to determine the point of sexual maturity, but in an animal where the mature but quiescent testis superficially resembles that of an immature animal this is not always easy. Cott (1961) p. 253, recognized "breeding" males as those with testes "enlarged and distended." During this survey the criterion of sexual maturity adopted was testis weight, and the criterion of sexual activity was the presence or absence of semen in the vas deferens. There is no other structure in the male reproductive tract capable of storing significant quantities of semen and it is assumed therefore that any male in this condition is mature and potentially capable of fertile copulations. Whether recently matured males do in fact breed is unknown. Observations by Modha (1967) p. 83, suggest that it is the older males that are chiefly involved in reproduction. This, however, probably depends on the age structure of the population concerned with the younger males reproducing where no older males are present.

In order to determine the weight at which the testis begins to mature the presence or absence of semen in the vas deferens has been related to testis weight in 70 males examined between July and December, the period of greatest reproductive activity (Table 9 and Modha 1967.) Animals examined during the first half of this year were eliminated to minimize confusion with mature but quiescent individuals. From Table 8 it is evident that no animals with testis weights of < 5 g are mature. In the range 6-10 g 35.7% were producing semen while from a testis weight of 11 g onwards 50% or more are mature. Those testes in the weight range 11-35 g that were not producing semen may have been quiescent rather than immature, but short of histological examination there is no way of deciding. For the purposes of this survey 50% or more males are considered to be mature at a testis weight of 11 g.

Testis weight (g)	Sample	Number with semen	Percentage with semen
0-5	17	0	0
6-10	14	5	35.7
11-15	5	3	60
16-20	5	3	60
21-25	6	3	50
26-30	1	1	100
31-35	4	2	50
>36	18	18	100

Table 8. Shows the incidence of semen in the vas deferens of 70 male crocodiles examined between July and December, expressed as the percentage of animals with semen in the sample for each of 8 testis weight ranges.

The mean length of 21 animals with testes weighing 5-15 g was 270 cm, varying from 212-336 cm. Cott found in a sample of 65 animals from Zambia that none were breeding until 280 cm length suggesting that crocodiles on Rudolf mature at shorter lengths than animals from other localities.

The Breeding Season

The incidence of semen in the vas deferens of 144 crocodiles recorded over a 12 month period is shown in Table 9.

	Testes <10g			**Testes >10g**		
	Sample	No with semen	Percentage with semen	Sample	No with semen	Percentage with semen
Jan-Mar	20	0	0	13	0	0
Apr-Jun	7	0	0	34	19	56
Jul-Sep	12	5	41.6	18	12	66.7
Oct-Dec	19	0	0	21	20	95.3

Table 9. Shows the incidence of semen in the vas deferens of 58 crocodiles with testes weighing less than 10 g and 86 crocodiles with testes weighing more than 10 g collected over a 12 month period. The results are expressed as percentages of animals with semen in the samples for each 3 month period.

In the sample of animals with testis weights of more than 10 g it can be seen that there is a well-marked cycle of sexual activity through the year, with no animals active in January-March and 95.3% active by October-December. It is interesting to note that by April-June 56% were potentially active. How much reproductive activity actually accompanies the appearance of these potentially active males is not known. Modha (1967) did not observe copulation on Central Island until the second week in October, lasting until December; but this is certainly not a true reflection of the events on the mainland where hatching nests were found in late August and September at Allia bay. Fertilization of these eggs would have occurred in May-June which agrees with the condition observed in the female. These points are discussed again below.

3b Reproduction in the female

Methods

All animals killed were examined in the field and their reproductive state recorded. Ovaries and oviducts were weighed on an Ohaus triple beam balance whenever possible. The number and size of developing follicles or ova was recorded. Ovary and oviduct tissue from a representative sample of animals was fixed in a 10% formaldehyde solution for histological examination. Whenever possible the whole ovary was collected and preserved. Four entire reproductive tracts were collected.

Results

Reproduction has not previously been described in any crocodilian, but a number of workers have investigated various lizards, snakes and turtles. Cagel (1944) working on the turtle *Pseudemys scripta* found that the mature ovary has 2-3 sets of enlarging follicles, development of which result in one set a season maturing. In *Lacerta agilis* (Marshall 1956) the various stages of oogenesis may be seen at any time of the year but mature follicles are present only in April and May. In many reptiles the ovarian follicle after discharging the ovum develops into a structure that has been considered analogous to the mammalian corpus luteum (Marshall 1956 p. 468.) The function of these "corpora lutea" is unknown. Accompanying development of the follicles the oviducts increase in size and vascularization.

In the Nile crocodile the immature ovary is small, weighing up to approximately 26g, and consists of a clear cortical tissue with numerous clusters of oocytes distributed evenly throughout the organ. The clusters are close together, giving the whole ovary an even, granular appearance.

As the animal matures, follicles begin developing. These grow and begin to protrude from the ovary, eventually separating almost entirely from it. Development continues until the ova are 4-5 cm in diameter and weigh 30-40 g. At this stage they are shed through an aperture on the surface of the follicle and pass into the proximal oviduct. After ovulation a "corpus luteum" develops from the ruptured follicle. This consists of a thick-walled brownish sac about 1 cm in diameter) which, in recently ovulated ovaries, is found everted and connected to the ovary by a short stalk. More usually it is inverted with the body of the structure visible through the clear cortical tissue of the ovary. After ovulation the corpus luteum regresses, eventually vanishing altogether. The time taken to do so is unknown, but it appears that by the time the next set of follicles is well developed no signs of the previous corpora lutea remain.

Immediately after the ova are shed the ovary is flabby, enlarged and heavy, weighing, in animals of 275-320 cm, 400-2,000 g. It then undergoes resorption eventually be corning small and firm, 30-300 g in weight, with corpora lutea in various stages indicating recent activity. The ovary then appears to go through a stage of quiescence as regards oogenesis (Table 12). Of 121 sexually mature (but not senescent) animals examined, 15 (12.4 %) were evidently quiescent with no large follicles developing. 106 of these 121 animals were either ovulating or had just laid, and of these 16 (15.1%) had another, smaller set of follicles developing concurrently, producing a condition of the ovary similar to that observed by Cagel (1944) in *P. scripta*. Thus some animals may only have one batch of ova developing at a time, while others have 2 batches. The inconsistency on this point and its significance is unclear, but it appears that: either an animal may produce one batch of eggs with no other follicles developing until regression of the corpora lutea is well advanced or complete, which cycle of events probably occupies a complete season (one year); or maturation of a batch of ova may be accompanied by development of another, younger batch so that soon after egg deposition a second set of ova may be near maturity. The obvious consequence of this latter condition is that 2 batches of eggs might be produced in one season. This point is discussed again in the section on breeding season.

Of the total of 127 mature females examined 6 (4.7%) appeared to be totally inactive rather than quiescent. No corpora lutea were present and the ovary presented a smooth mottled appearance caused by confinement of the oocytes to small, widely spaced clusters so that the cortical tissue comprised the major part of the ovary. Such ovaries had probably ceased producing ova altogether, particularly as they were all from large (and presumably old) females of >290cm.

Altogether, 35 animals >290 cm long were examined of which 6 (18%) were inactive. It thus appears that in the older females a cessation of reproduction eventually occurs, suggesting that senescent processes affect crocodiles, which will have some consequence on their population dynamics.

The oviduct consists of 2 readily distinguishable sections. The first part, here called the proximal oviduct, is thin-walled, much convoluted and slightly longer than the second part. It is more extensively vascularized, blood vessels being especially prominent in the mature, active animal. The second part, or distal oviduct, is shorter, less convoluted and with much thicker and whiter walls. The whole length is deeply folded longitudinally presumably to allow for expansion when containing eggs. After ovulation the ova pass into the proximal oviduct.

No animals were found during the survey with ova in the proximal oviduct suggesting that they do not remain there for long. Fertilisation possibly occurs here and it may participate in the initial formation of the egg membranes and shell. The distal oviduct may be found containing eggs, either still soft with very little of the hard shell formed, or with fully formed and shelled eggs Thus the distal oviduct is where at least part, if not all, of shell formation occurs. Prior to deposition the eggs are seen fully formed and covered in a thick, gelatinous substance.

The oviducts lead straight into the cloaca and the only other macroscopic organs which may be accessory to the reproductive tract are the cloacal glands. These are small and lie lateral to the cloaca with a short duct opening into it and secrete a viscous orange substance with a strong, distinctive smell. Their function is unknown.

At this point it is worth mentioning the gular glands which are almost identical in size and appearance to the cloacal glands, and secrete what appears to be the same substance. Their function is also unknown.

The final stages in the reproductive process have been described by Cott (1961) and Modha (1967). When ready to deposit the eggs the female comes ashore and digs a hole in the ground, usually somewhat above high water level and not far from the shoreline. The environment of the nest site does not appear to be critical as nests may be made on exposed sandbanks, with the eggs only 10 cm beneath the surface, or in sheltered positions in vegetation. The eggs after deposition are covered up and throughout the ensuing 3-month incubation period the female tends to spend considerable time ashore on or near the nest. If disturbed by activities such as hunting the females may not actually lie ashore, but evidently continue to frequent the vicinity as such animals unearth the ready-to-hatch eggs in the normal manner. The hatching embryos emit a variously described "squeak" which probably stimulates the female to unearth the eggs. Most nests seen on the east shore were constructed in a substrate which, during incubation, becomes so hard that the young are unable to dig themselves out. Unearthing by the parent is essential in these cases for survival. In the authors experience it has been the rule rather than the exception for the young to require digging up by the female and the significant feature of the females presence by the nest during incubation is probably the necessity for unearthing it rather than any factor concerned with incubation.

The consequence of this behaviour on crocodile conservation is of great importance as severe disturbance of females before the nests have been dug up will result in high egg mortality. The female also acts in a “guarding" capacity as evidenced by the aggressive behaviour observed by Modha (1967) p. 90, although her continued presence near the eggs may attract rather than repel predators such as monitor lizards (*Varanus niloticus*), hyaenas (*Crocuta* species) and baboons (*Papio* species).

Length (cm)	Sample	Number mature	Percentage mature
< 160	30	0	0
161 – 170	19	1	5
171 - 180	23	1	4
181 – 190	23	10	43
191 - 200	23	11	47
201 – 210	35	18	51
211 – 220	42	33	79
221 - 230	18	10	55
231 - 240	2	1	50
241 – 250	9	3	33
251 - 260	3	2	67
261 - 270	4	3	75
271 - 280	5	4	80
281 – 290	8	7	88
291 - 300	13	11	85
301 +	23	23	100

Table 10. Lists the numbers of mature animals in each of 16 length groups in 280 female crocodiles from Lake Rudolf

The onset of sexual maturity

This was determined simply by considering an animal potentially mature when developing follicles were visible in the ovary. Cott (1961) used a similar criterion when he considered females with ova more than 0.2 cm in diameter to be mature. The same criterion was adopted during the present work**.**

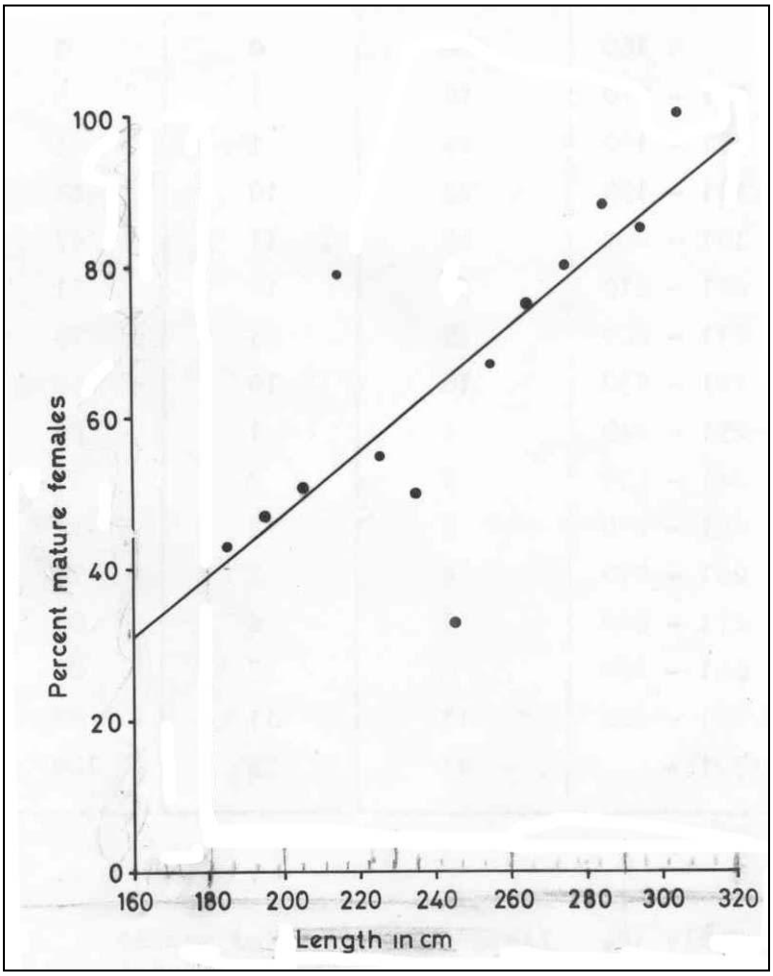


Figure 4. The proportion of mature females in each of 16 size groups plotted against body length for 280 female crocodiles from Rudolf. The regression coefficient was 0.4065

Table 10 shows the proportion of mature to immature animals in each of 16 length groups in 280 females from Rudolf. It can be seen that although some animals are maturing at lengths of 161-180 cm, the onset of maturity in Rudolf crocodiles may be considered well-marked from 180 cm onwards. An increasing proportion of mature animals is seen with increasing length and in order to derive a value for age specific fecundity for use in the female life Table the regression of maturity (y) on length (x) has been calculated. The regression coefficient was 0.4065 and the result is shown in Figure 4. Comparable data for crocodiles elsewhere does not exist, but Parker (unpublished data) has records of 8 mature and 15 immature animals from the Galana river, shown in Table 11.

Length (cm)	Sample	Number mature	Number breeding
<190	14	0	0
191-200	2	1	0
201-210	2	2	1
211-220	0	0	0
221-230	3	3	2
231-240	0	0	0
241-250	1	1	0
251-260	1	1	0

Table 11. Shows proportion of mature animals relative to length in 23 female crocodiles from the Galana river (Kenya). (Parker: unpublished data).

Although too small a sample for critical comparison the absence of mature animals <190 cm length and the onset of maturity at about this length is consistent with the Rudolf data.

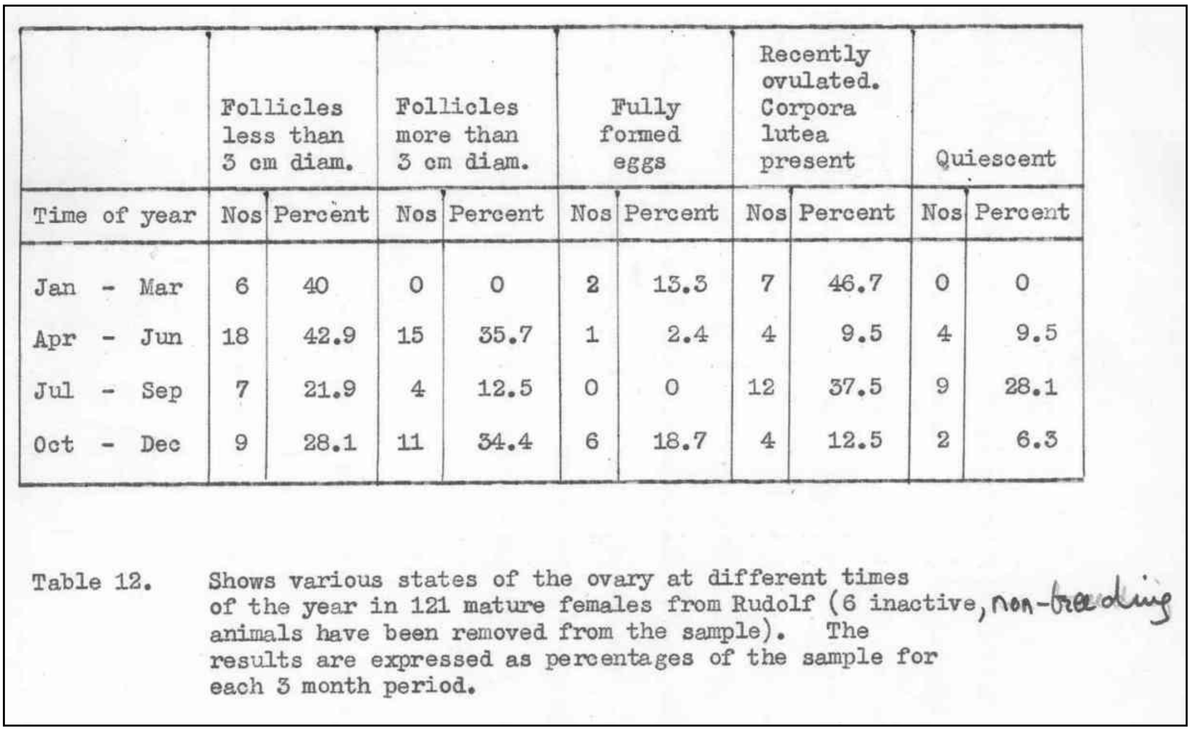
Cott (1961), while giving no details, states that for crocodiles from several Zambian localities about half the females are breeding at 300cm length. The smallest breeding female he found was 238 cm. These comments suggest that maturity is attained at considerably longer body lengths than on Rudolf. Cott (1961) p. 254, also quotes previously unpublished data of Pitman’s, collected during a Uganda Game Department campaign to exterminate crocodiles on Lake Victoria. He records a sample of 855 females shot and measured on the "breeding grounds" and therefore considered to be representative of the female breeding population. The mean length of these 855 females was 318 cm, varying from 219-462 cm. Less than 2% were breeding at lengths below 244 cm suggesting that maturity is reached, as with Zambian animals, at much longer body lengths than on Rudolf.

The Breeding Season

Seasonal breeding in crocodiles is well known and is described by Cott (1961): Modha (1967) has confirmed its existence on Central Island. Cott observed that in 14 Ugandan and Zambian localities, egg deposition occurs from 1-3 months before the time of lowest water level so that hatching after the 3-month incubation period takes place during, or shortly after, the time when the water level begins to rise. The onset of the rains and resultant rise in water level could be expected to favour survival in young crocodiles. The habitat is enlarging and there is an increase in emergence of insects, important in small crocodile diets. It is obvious, too, that egg deposition should take place sometime during the year when water levels are subsiding as the danger of inundation of nests by rising water is great in African waters characterized by seasonal flooding.

Modha (1967) describes a clearly defined breeding season on Central Island during 1965-66. Copulation was observed beginning in October and lasting until December with a peak in November. Nesting started at the end of November, lasting until January with a peak in the second half of December. Hatching lasted from February to April with a peak at the end of March. The lake level was lowest in April, rising again in that month and the pattern of the breeding season was thus seen to be the same as that described by Cott for crocodiles in Uganda and Zambia.

Modha's observations suggest that ova are maturing in October and November and that the interval between fertilization and the completion of egg formation is approximately one month, the time between the observed peaks of copulation and egg laying. There is then a 3-month incubation period.



	Follicles less than 3 cm diam.		Follicles more than 3 cm diam.		Fully formed eggs		Recently ovulated. Corpora lutea present		Quiescent	
Time of year	Nos	Percent	Nos	Percent	Nos	Percent	Nos	Percent	Nos	Percent
Jan - Mar	6	40	0	0	2	13.3	7	46.7	0	0
Apr - Jun	18	42.9	15	35.7	1	2.4	4	9.5	4	9.5
Jul - Sep	7	21.9	4	12.5	0	0	12	37.5	9	28.1
Oct - Dec	9	28.1	11	34.4	6	18.7	4	12.5	2	6.3

Table 12. Shows various states of the ovary at different times of the year in 121 mature females from Rudolf (6 inactive, non-breeding animals have been removed from the sample). The results are expressed as percentages of the sample for each 3 month period.

Table 12 shows the condition of the ovaries of 121 mature females examined on the east shore over a 12-month period in 1965-66. It is evident from Table 12 that no clear sequence of events emerges from an examination of the ovaries. While this is in part due to the small samples it is probably also a reflection of a much more diffuse breeding season than that recorded by Modha on Central Island. Animals with follicles in all stages of development are found throughout the year and while a peak of egg production occurs at the end of the year there is evidence of some reproductive activity throughout the year.

This could mean that either some animals reproduce more than once a year, or that there is considerable variation in the time of reproduction. The time sequence of events would permit an animal to breed twice. From fertilization to hatching occupies about 4 months. An animal with two batches of ova developing concurrently could, after maturation of the first batch, be ready to produce the second in a few months time, say shortly after the first lot of eggs have hatched. On Rudolf where fluctuations in water level are relatively slight there may not be so close an association of nesting and time of year, since this is not as critical as it may be on most rivers where changes in water level are more pronounced.

Number of eggs produced

Table 13 lists mean clutch sizes from 7 sources. +While the various Ugandan and Zambian records are similar, much smaller clutches are found on Rudolf. Cott (1961) p. 275 observed that larger clutches were from larger animals: this

Table 14 lists clutch sizes and corresponding body lengths of 19 crocodiles recorded by Cott (1961) from Uganda and Zambia, and 10 crocodiles from Rudolf.

Locality & source	Mean clutch size	Range	Sample
Uganda, L. Victoria. Carpenter (1920)	59.9	38-76	13
Uganda, L. Victoria. Pitman (in Cott 1961)	60.4	25-95	775
Uganda, Murchison. Cott (1961)	54.9	-	17
Uganda, Murchison. Parker (1967) unpublished.	52	32-67	22
Zambia. Cott (1961)	56.2	-	23
Rudolf, Central Island. Modha (1967)	33.5	14-46	65
Rudolf, Sections 2,3 & 4. This study	33	16-55	18

Table 13. Nile crocodile clutch sizes from 7 localities.

Uganda & Zambia		**Rudolf**	
Clutch size	Body length	Clutch size	Body length
40	275	16	207
57	290	28	250
45	292	37	275
55	292	40	283
50	293	44	294
49	302	49	302
50	306	41	305
55	307	55	307
45	308	35	316
46	309	52	316
60	309		
66	311		
50	313		
69	313		
65	316		
70	319		
87	330		
69	333		
70	345		

Table 14. Lists clutch sizes and body lengths of 19 crocodiles from Uganda and Zambia, and 10 crocodiles from Rudolf

means that the difference in mean clutch size between Rudolf and other localities might be due either to a difference in the number of eggs produced relative to crocodile size, or a difference in the mean size of breeding females.

These two samples are compared in Figure 5 which shows the cube root of clutch size plotted against length. The regression coefficients of clutch size (y) on length (x) have been calculated and were 0.0150 (Uganda and Zambia) and 0.00978 (Rudolf). These were not significantly different at the 5% level.

It is evident that clutch size bears a direct relationship to length and that this is the same for the 2 samples considered. The differences in mean clutch size between Rudolf and Uganda and Zambia therefore reflect differences in the mean size of breeding females. Of interest are observations of Pitman's (in Cott 1961, p.274) in which the mean size of 775 clutches from Lake Victoria was 60.4, varying from 25-95. Recorded concurrently with these observations were the lengths of 855 females from the same localities, in which the mean length was 318 cm varying from 220-470 cm. Inspection of the regression line for Cott's data shows that a clutch size of 60 corresponds to a length of 315 cm.

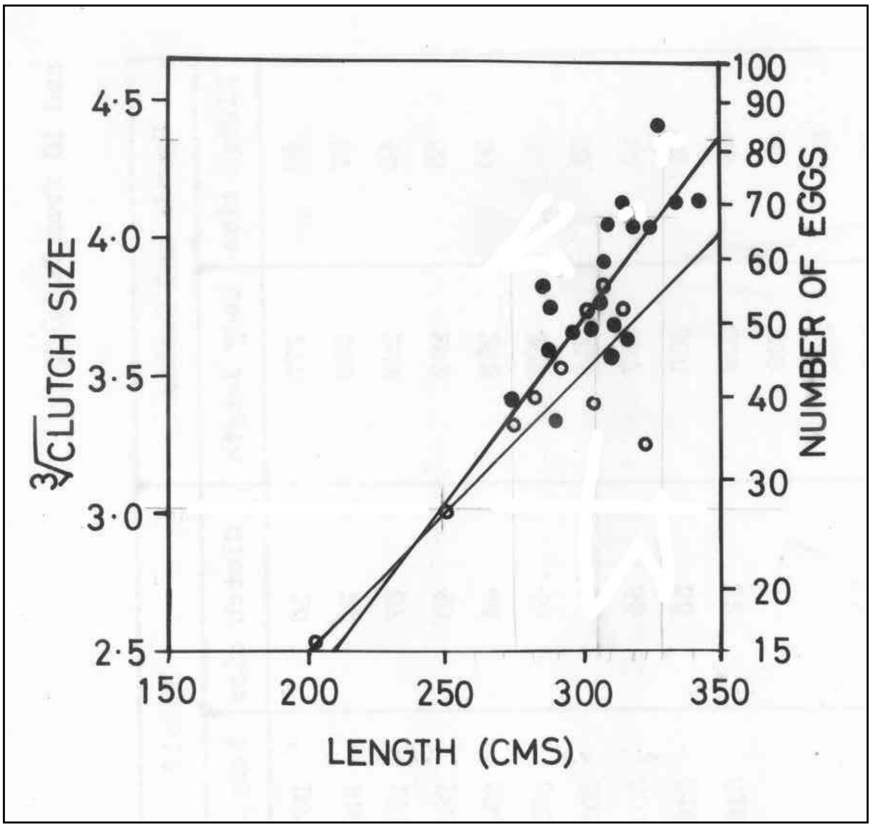


Figure 5. the cube root of clutch size plotted against body length in 19 Uganda crocodiles (Cott 1961) and 10 Rudolf crocodiles. The regression coefficients were respectively 0.015 and 0.00978. Closed circles: Uganda. Open circles: Rudolf

Section 4. Age and growth

Attempts to establish age criteria for Rudolf crocodiles were hindered by the absence of sequential, morphologically different structures, such as occur in mammalian molar teeth, so that even a crude division of animals into relative age groups was not possible. Generally speaking, an adult crocodile is simply a larger replica of a juvenile with the most obvious and easily measured expression of age being size. Evidence is presented later that for most, if not all, of the animals life growth is continuous, of which the most convenient measure is body length. Throughout this work attempts to relate length to age have been made.

Nothing on ageing crocodiles has been published and information on rate of growth is scant. Cott (1961) p. 240 records data on one wild and 6 captive, known age animals), and Pooley (1962) records growth in 10 captive hatchlings. Poole (1961) describes tooth replacement in crocodiles and concludes that as each successive tooth is larger by a constant increment the total number of replacements in any individual can therefore be determined. In the absence of information on the rate of replacement it is, however, impossible at this stage to relate tooth size to age, although this could be a fruitful line of research.

Laws (1965 B) and Watson (1967) have used growth layers in the teeth of various mammals as age indicators. These layers are formed in response to environmental changes at known intervals that were, in the case of wildebeeste (Watson ibid.) the alternating wet/dry season and its accompanying changes in food supply and metabolism. Although layers are present in crocodile teeth, investigation was abandoned in favour of a similar investigation of the layering that occurs in the dentary bone. Attempts to relate tooth layers to age are hampered by ignorance of the replacement rate, and the high incidence of damaged teeth seen in Rudolf animals would prevent the same tooth being available from each jaw.

Peabody (1961) described zones in the dorso-lingual region of the dentary in a specimen of *C. niloticus* from Ngamiland (Botswana), ascribing these zones to variations in growth caused by the well marked summer and winter climate of the region. He assumed that differences in growth rate were reflected in differences in the formation of bone, seen as symmetrical layers of alternating darker and lighter bone, and that each layer represented a year’s growth. He describes 4 layers in the specimen he examined concluding that it was thus in its fifth year. The animal in question was 81 cm long and Pooley (1962) found that captive crocodiles in Zululand grew to similar lengths in 2 years with an optimal food supply. It is not unlikely that a wild crocodile living under more rigorous conditions and with a less favourable food supply might take 4 years to attain the same size. As similar layering was present in Rudolf animals a series of jaws was sectioned and examined.

Methods

Cross sections were cut through the ramus of the mandible at 4 sites along its length. The most suitable was found to be that between tooth number 8 and 9 (counted from the front). This section goes through the dentary and splenial, layering being especially obvious in the dorso-lingual region of the dentary. Peabody does not state where his section was cut but in appearance it is similar to those of the present study. Of 68 sections cut, 23 male and 24 female sections were finally compared. The remaining 21 were rejected owing to damage during preparation or because they were too obscure for interpretation.

The technique used for preparing the sections was similar to Peabody’s and is essentially the same as the geologists’ method of preparing rook sections. Sections were ground down with carborundum compounds until thin enough to mount on a microscope slide in a mounting medium, thickness being judged by eye. Examination was made under the low power of a binocular microscope with oblique reflected lighting.

Results

The 47 sections considered are listed in Table 15.

Males		Females	
Body length (cm)	Dentary layers	Body length (cm)	Dentary layers
146	14	157	15
150	8	164	19
159	10	167	19
164	21	171	18
168	23	176	20
175	17	181	14
190	21	183	23
202	22	190	14
203	15	190	21
206	18	191	29
216	18	197	22
235	30	198	16
237	30	198	18
244	33	198	30
270	20	203	29
283	33	205	24
287	35	209	26
291	28	215	29
297	35	215	31
308	40	219	26
309	24	223	18
309	44	226	17
453	51	227	28
		272	25

Table 15. Lists body length and the corresponding number of dentary layers in 23 male and 24 female crocodiles from Lake Rudolf.

The data have been plotted in Figure 6 as the number of layers on length. The regression of layers (y) on length (x) was calculated in the male sample and the regression coefficient found to be 0.1295. In the female sample there was no regression of layers on length, which is probably due to the restriction of the sample to a small body length range of 160-270 cm. It was expected that in the female a greater number of layers at a given body length would be found, and the limited data in Figure 6 do suggest this as the female scatter tends to lie above the male regression line. However, in the absence of a better distributed sample it is impossible to determine the relative difference, if any, between male and female dentary layers relative to length.

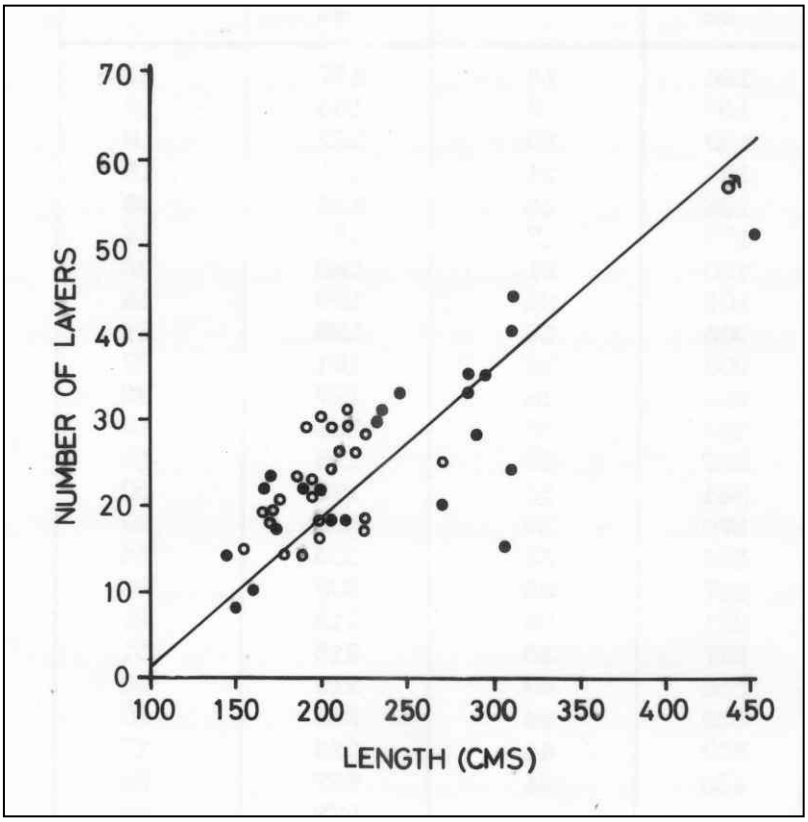


Figure 6. The number of growth layers in the dentaries of 23 male and 24 female crocodiles from Rudolf, plotted against body length. The male regression coefficient was 0.1295. Closed circles: males. Open circles: females.

The results for the male sample in Figure. 6 suggest a relationship between layers and age, and in order to determine this in absolute terms it is necessary to consider what might be governing their formation. Seasonal changes on Rudolf are so slight that it is unlikely that they could be directly influencing growth to the extent observed by Watson (ibid.) in wildebeeste. But a well-marked cycle of reproductive activity, particularly in the male, is present, which appears to have evolved in response to the seasonal fluctuations in water level that occur in tropical Africa as a result of the alternating wet and dry seasons. The continuation of this cycle in Rudolf despite its separation from the Nile system since the middle Pleistocene indicates the fundamental nature of this reproductive cycle. The build to a peak of reproductive activity, followed by a sudden cessation and quiescent phase, is likely to be accompanied by a gross cycle of metabolism that could result in discontinuities in bone growth such as occur in other animals. The considerable variation in the male scatter could be due to several factors. Variation in individual growth rate, variation in the age at sexual maturity and the possibility that some animals do not breed every year.

From the foregoing it seems possible that growth layers in the dentary are formed on an annual cycle in response to a rhythm of reproductive activity with intervals of a year. Assuming the number of dentary layers to represent an equal number of years the data in Figure. 6 for males has been replotted in Figure 7 as body length on age. Ignorance of the form of the growth curve in crocodiles precludes any transformation of the data at this stage; consequently, the regression line has been drawn in as for Figure. 6. The corresponding curve for absolute age in the female has been derived from the relative age difference in males and females indicated by the relationship between lens weight and body length. This is discussed further in the next section.

Eye lens weight and age

Since in some mammals (Lord 1959) it has been shown that lens weight increases with age after growth of the organism as a whole has ceased, so that lens weight can be used as an age indicator, a collection of lenses was made to determine whether a similar phenomenon occurred in crocodiles. Since absolute ageing of any lenses has not been possible the series proved useful only in indicating relative ages.

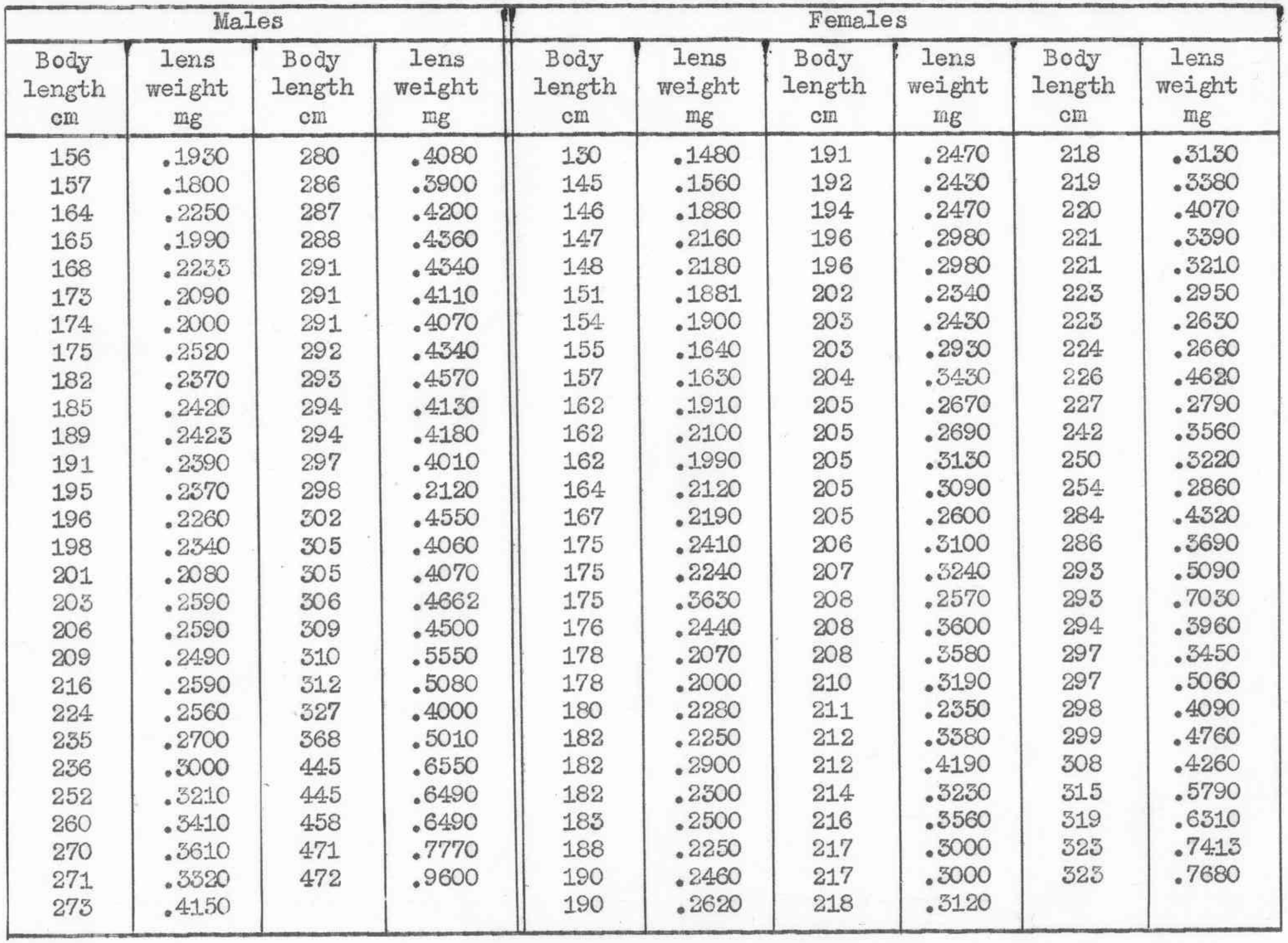
Methods

Lenses were collected by dissecting the eye, removing the lens and ciliary body together and preserving this in a 10% formaldehyde solution. In animals killed by day lenses were discarded if not collected within 4 hours post mortem: in animals killed at night lenses were collected up to 18 hours post mortem, provided the eyes had not been exposed to the sun. Since all animals were shot through the brain many lenses were accidentally damaged, but one or both lenses (273 in all) were obtained from 180 animals. In the laboratory the fragment of ciliary body and the suspensory ligament were dissected off leaving the lens capsule free of extraneous tissue. Minor damage was detected at this stage and resulted in 42 of the 273 lenses being discarded, as it was found that even small injuries to the capsule resulted in significant weight losses. Lenses were dried in an oven at 78-80^{o}C to constant weight. Weights in milligrams were measured on a sensitive balance. A test series showed that drying was slow, so that after 10 days, a loss of 2 mg a day was still occurring. By 20 days weight loss was insignificant and these weights were taken as constant. The full series of 231 was dried under the same conditions for 25 days.

Results

Comparison between right and left lenses

Right and left lenses of the same individual were collected undamaged from 51 animals and their weights compared. The mean difference between pairs was 1.5% and did not exceed 4% of the weight of the heaviest lens.

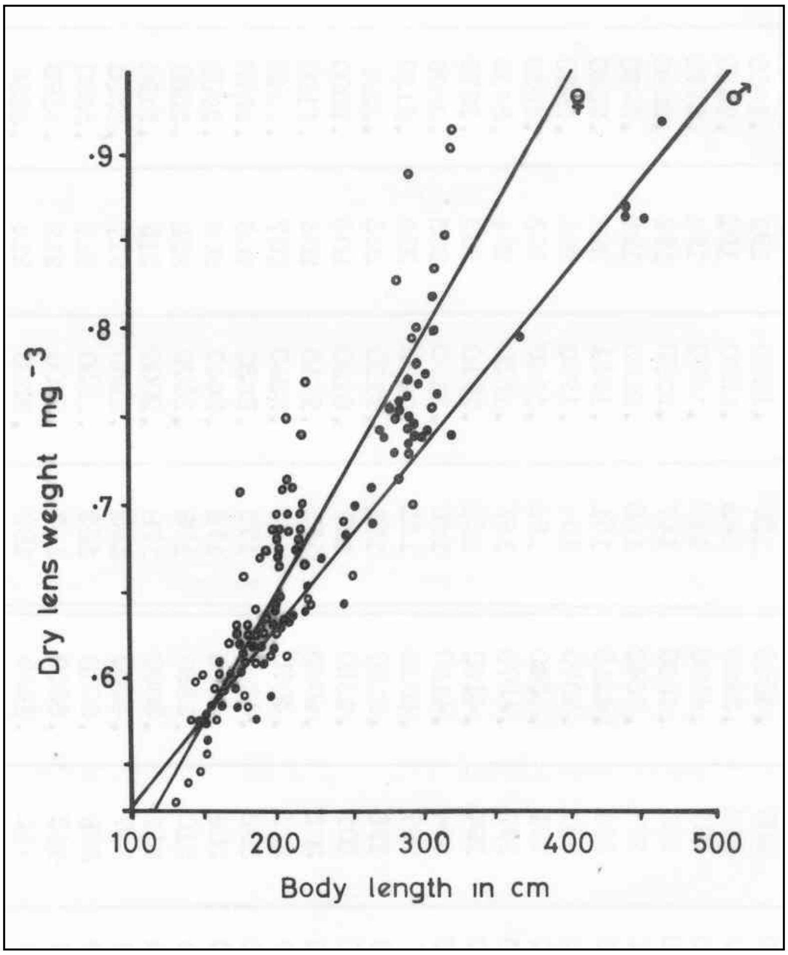


Males				Females					
Body length cm	lens weight mg	Body length cm	lens weight mg	Body length cm	lens weight mg	Body length cm	lens weight mg	Body length cm	lens weight mg
156	.1930	280	.4080	130	.1480	191	.2470	218	.3130
157	.1800	286	.3900	145	.1560	192	.2430	219	.3380
164	.2250	287	.4200	146	.1880	194	.2470	220	.4070
165	.1990	288	.4360	147	.2160	196	.2980	221	.3390
168	.2233	291	.4340	148	.2180	196	.2980	221	.3210
173	.2090	291	.4110	151	.1881	202	.2340	223	.2950
174	.2000	291	.4070	154	.1900	203	.2430	223	.2630
175	.2520	292	.4340	155	.1640	203	.2930	224	.2660
182	.2370	293	.4570	157	.1630	204	.3430	226	.4620
185	.2420	294	.4130	162	.1910	205	.2670	227	.2790
189	.2423	294	.4180	162	.2100	205	.2690	242	.3560
191	.2390	297	.4010	162	.1990	205	.3130	250	.3220
195	.2370	298	.2120	164	.2120	205	.3090	254	.2860
196	.2260	302	.4550	167	.2190	205	.2600	284	.4320
198	.2340	305	.4060	175	.2410	206	.3100	286	.3690
201	.2080	305	.4070	175	.2240	207	.3240	293	.5090
203	.2590	306	.4662	175	.3630	208	.2570	293	.7030
206	.2590	309	.4500	176	.2440	208	.3600	294	.3960
209	.2490	310	.5550	178	.2070	208	.3580	297	.3450
216	.2590	312	.5080	178	.2000	210	.3190	297	.5060
224	.2560	327	.4000	180	.2280	211	.2350	298	.4090
235	.2700	368	.5010	182	.2250	212	.3380	299	.4760
236	.3000	445	.6550	182	.2900	212	.4190	308	.4260
252	.3210	445	.6490	182	.2300	214	.3230	315	.5790
260	.3410	458	.6490	183	.2500	216	.3560	319	.6310
270	.3610	471	.7770	188	.2250	217	.3000	323	.7413
271	.3320	472	.9600	190	.2460	217	.3000	323	.7680
273	.4150			190	.2620	218	.3120		

Table 16. Lists the body length and corresponding dry lens weight in 55 male and 83 female crocodiles from Rudolf.

Comparison of male and female lenses

Dry lens weights were obtained for 55 male and 83 female crocodiles and are shown in Table 16. These data have been plotted in Figure. 8 as the cube root of lens weight against body length. The regressions of lens weight (y) on length have been calculated and the regression coefficients were 0.01097 (males) and 0.01610 (females). For males and females up to a length of 180 cm no difference is detectable, but from this point on lenses of females are heavier than males of the same body size. This is what would be expected if lens growth continued independently of body growth since male crocodiles after maturity grow faster than females. Assuming lens growth in the two sexes to be similar the discrepancy between the male and female regressions is taken to



(x)

Figure 8. Shows the cube root of dry lens weight plotted against body length in 55 male and 83 female crocodiles from Rudolf. The regression coefficients were respectively 0.01097 and 0.0161. Closed circles: males. Open circles: females.

represent the relative difference in ages. This relationship has been utilized in Figure 7 so that a curve for the absolute ageing of females may be obtained. The male curve in Figure. 7 has been taken directly from Figure. **6.** The female curve is the lens weight curve relative to the male lens weight curve after the latter has been adjusted to the same scale as that for male dentary layers.

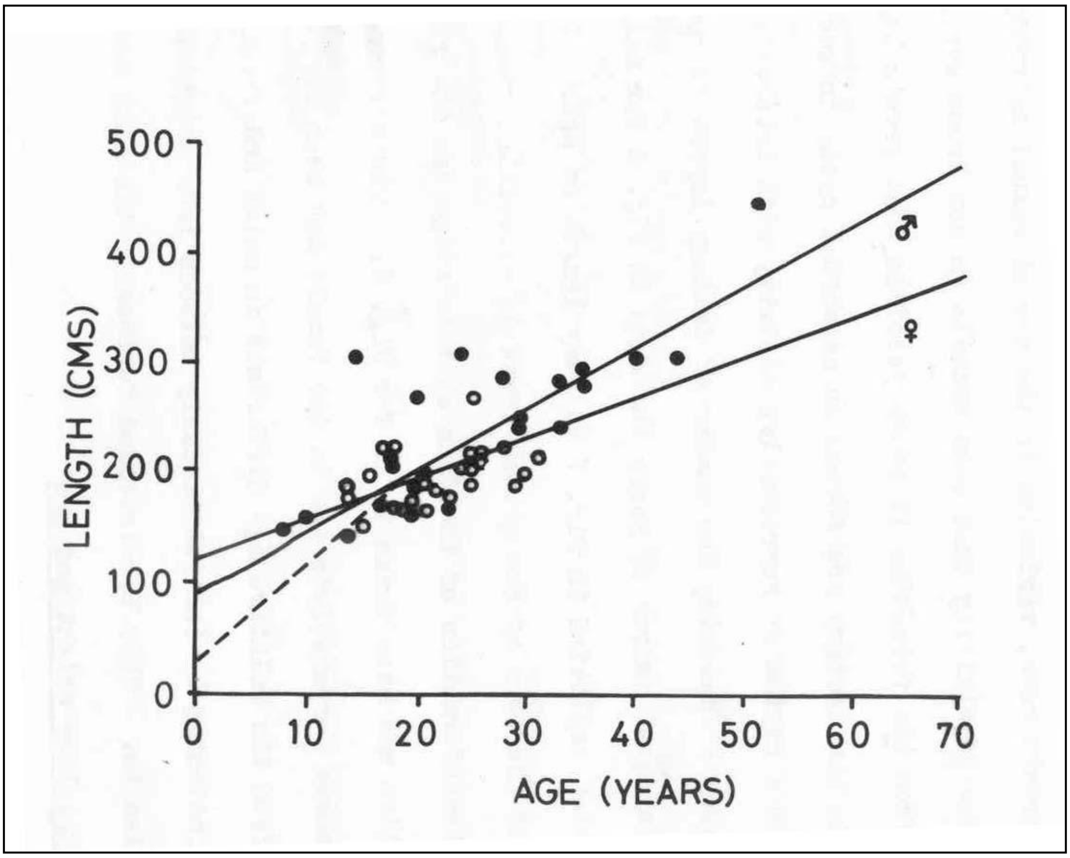


Figure 7. Shows the male data from Figure 6 repotted as body length on age in years (where years equals dentary layers). The female curve is female lens weight (Figure 8) relative to male lens weight after the latter has been adjusted to the same scale as male layers. The broken line represents immature growth.

In the absence of other evidence the curves in Figure. 7 have been used as the means of ageing Rudolf crocodiles in the section on population dynamics. Since it is apparent (see section 4b) that growth in crocodiles elsewhere is more rapid, the age/size relationships in Figure. 7 should only be applied to Rudolf crocodiles and until confirmatory evidence from other sources is available the conclusion drawn from dentary layering should be treated with caution.

4 b Growth

Size and shape

The more rapid growth of male crocodiles results in a size differential between the sexes so that on Rudolf the longest males (470 cm) are 3.5 times as heavy as the longest females (320 cm). This condition also exists in alligators and other crocodilians (Schmidt and Inger 1957) During this survey 27 standard body measurements were taken from all animals examined to establish: whether any change in proportions that occurred with growth could assist in ageing; and to determine whether animals could be sexed by external examination. Although a full analysis of these data is not complete, preliminary results suggest that any differences are too slight to use as age or sex indicators.

In Table 17 are listed the mean weights in kg for males and females in 437 Rudolf crocodiles, and 42 Ugandan and Zambian crocodiles (Cott 1961), for each of 15 size groups rising in 30-cm cm intervals. Also shown is the combined mean weight for males and females. In Table 18 are listed male and female weights for 49 crocodiles from the Galana river (Parker: unpublished data).

No difference is apparent between the mean male and female weight for each length group in the 3 samples. The conclusion of Cott (1961) p. 255 that females are heavier than males of the same length is not borne out by his data. Further, no difference among the 3 samples is apparent. The data in Table 17 have been plotted in Figure.9 as the cube root of the mean combined weight against length and the regression of weight (y) on length (x) calculated for the Rudolf sample.

			Rudolf			Uganda and Zambia		
			Males	Females	Males & Females	Males	Females	Males & Females
Length group	Length range cm	Mean length cm	Mean weight kg	Mean weight kg	Mean combined weight	Mean weight kg	Mean weight kg	Mean combined weight
1	26- 55	40	-	-	-	-	-	-
2	56- 85	70	1.5	-	1.5	-	-	-
3	86-115	100	4.1	3.5	3.8	-	-	-
4	116-145	130	9.5	9.5	9.5	-	-	-
5	146-175	160	16.2	15.8	16.0	-	-	-
6	176-205	190	27	27.4	27.2	-	-	-
7	206-235	220	38	36.9	37.5	-	-	-
8	236-265	250	65	62	63.5	-	70	70
9	266-295	280	89	87	88	70	94.1	82.5
10	296-325	310	109.5	110.5	110	120	124.5	122.3
11	326-355	340	149		149	160.8	168.8	164.8
12	356-385	370	-		-	225		225
13	386-415	400	280		280	220		220
14	416-445	430	398		398	368.3		368.3
15	446-475	460	451		451	-		-

Table 17. Lists the mean weight in kg (where available) for each of 15 length groups of 30 cm intervals in 437 Rudolf crocodiles and 42 Ugandan and Zambian crocodiles (data derived from Cott 1961)

Length group as for Table 16	Males mean weight (kg)	Females mean weight (kg)	Males and Females mean combined weight (kg)
1	-	-	-
2	2	2.2	2.1
3	4	4.1	4.0
4	8.5	7.7	8.1
5	16.3	15	15.7
6	25.7	24.6	25.1
7	46.4	42.8	44.6
8	-	62.7	62.7

Table 18. Shows the mean weight in kg for males and females in each of 8 length groups in 49 crocodiles from the Galana river, Kenya (Parker: unpublished data)

The regression coefficient was 0.01684. The regressions for the Uganda and Galana samples have not been calculated, but the points for both these samples are found to lie close to the regression line for the Rudolf sample. Thus, no difference in the body weight to body length relationship between animals of the 3 samples is apparent.

Because of its importance in fundamental considerations of the size/time relationship it is useful to determine how large crocodiles may grow. Casual observation suggests that few individuals in a population exceed certain sizes and this is borne out by examination of killed samples.

Size of Males

In the Rudolf population 50% or more males are sexually mature at about 270 cm long. There is however, considerable variation, with some animals mature at

189 cm and others not mature until 338 cm. Growth evidently still continues after sexual maturity, so that the largest males of 470 cm are nearly twice as long and weigh ten times as much as those of 270 cm. The largest of 202 males examined during the survey was 472 cm long, with 11 animals in the range 430-470 cm. Of several hundred animals shot by the Kenya Game Department in Ferguson's Gulf, none were larger than this. The largest of 324 males examined by Cott (1961) p. 251 in Uganda and Zambia were 7 animals 430-475 cm long. Cott does however quote several, apparently authentic, records of animals up to 600 cm long. The author has two records (Turner and Bell, pers. comm.) of animals more than 500 cm long from the Grumeti River, Tanzania. There thus appears to be a size that very few individuals exceed. There is no suggestion that growth ceases altogether at a particular size and in fact is probably continuous, but a limit on the average size of the oldest individuals in any population will be imposed by the complex of mortality factors that govern the maximum age attained. Occasional very large animals would be the result of unusually rapid growth and long life.

Size of females

Sexual maturity in females of the Rudolf population is reached at about 190 cm, when 43% or more are mature. But, as with males, considerable variation exists, with some mature at 170 cm and others not mature until 300 cm. This variation in the size at maturity could result from differing growth rates, so that individuals maturing at the same age vary in size; or it could reflect differences in the age at which various individuals mature, assuming relatively constant growth rates. In practice it is probably a combination of both effects.

Of 278 females examined during the survey the largest were 9 animals in the range 310-320 cm. The largest of 327 females examined by Cott in Uganda and Zambia were 11 in the range 325-350 cm. Cott also quotes unpublished data of Pitman's in which the 16 largest of 855 females from Lake Victoria were 380-470 cm long, and another 74 of 350-380 cm. This sample was shot while presumed to be lying near nests, and it is possible that the very large animals were erroneously assumed to be females because of their presence near nests.

The largest females on Rudolf are about 320 cm long while in Uganda they may grow larger. Preliminary results of a survey of the Murchison Falls population suggest that the size limits for both sexes there may be considerably greater than on Rudolf.

Lifespan

Neither the potential nor actual lifespan for any crocodilian is known. Information is confined to records of captive animals and such data do not indicate average longevities. To obtain some idea of lifespan, 110 zoos comprising all the larger ones in the world were consulted for information on growth and age. The records obtained are shown in Table 19, to which have been added similar records from Flower (1937) and the International Zoo Year Book (1966).

	Age (years)			
	20-30	31-40	41-50	51-60
Alligator mississipiensis	10	8	4	2
Crocodylus niloticus	3	3	1	
Alligator sinensis	3			1
Caiman niger	1			
Caiman crocodilus	2			
Crooodylus oataphractus	3	2		
Crooodylus intermedius	1			
Crocodylus palustris	1			
Crocodylus porosus	1			
Crooodylus siamensis	1			
Gavialis gangeticus	4			
Osteolaemus spp.	2			
Tomistoma tetraspis	1			

Table 19. Recorded longevities in 30 individuals of 13 species of crocodylians. From Flower (1937), International Zoo Year Book (1966) and present study.

Reptiles are widely considered to be very long-lived and Flower discusses several claimed instances of tortoises living more than 100 years, but none of these are recorded in a very convincing manner. Only in the case of the chelonian *Emys orbicularis* has an age of over 70 years been authentically recorded. For crocodilians, only two ages of more than 50 years have been recorded, both in *A. mississipiensis*. One of 53 years is alive at the time of writing (South Australia Zoological Gardens) and the other of 56 years was alive when recorded by Flower (1937). 20 years have been recorded for at least 13 species of crocodilian (Table 19): but ages of more than 30 years are uncommon and more than 60 years unknown. It appears that 60 years can be considered an exceptional age in captive animals. To what extent these ages reflect ages in wild animals is unknown, but there is no reason to suppose that a healthy captive animal should differ greatly from a healthy wild animal. The age scale in Figure. 7 suggests that crocodiles on Rudolf do not survive for more than 70 years.

That various species of crocodilians may live for many years without growing is well-known to zoo keepers. Three alligators in the Berlin Zoo (in litt.) all about 335 cm long (30 cm shorter than the usual size limit for males) lived 25 years without growing. A caiman in the Munster Zoo (in litt.) lived 28 years without growing. This phenomenon occurs in the wild (see section on "growth in known age crocodiles") and while the causes are unknown it is likely to be in response to conditions such as overcrowding or insufficient food.
The causes of mortality in older animals are discussed in the section on Population dynamics.

Growth in *Alligator mississipiensis*

Because of the general similarity between *A. mississipiensis* and *C. niloticus* it is of interest to consider growth in the former species since more is known about it, and see how far it compares with growth in crocodiles. Some information on growth in wild alligators comes from observations by McIhlenny (1934) who released 38 marked hatchlings on Avery Island, Louisiana, recovering a number of individuals at intervals during the next 11 years. By 5

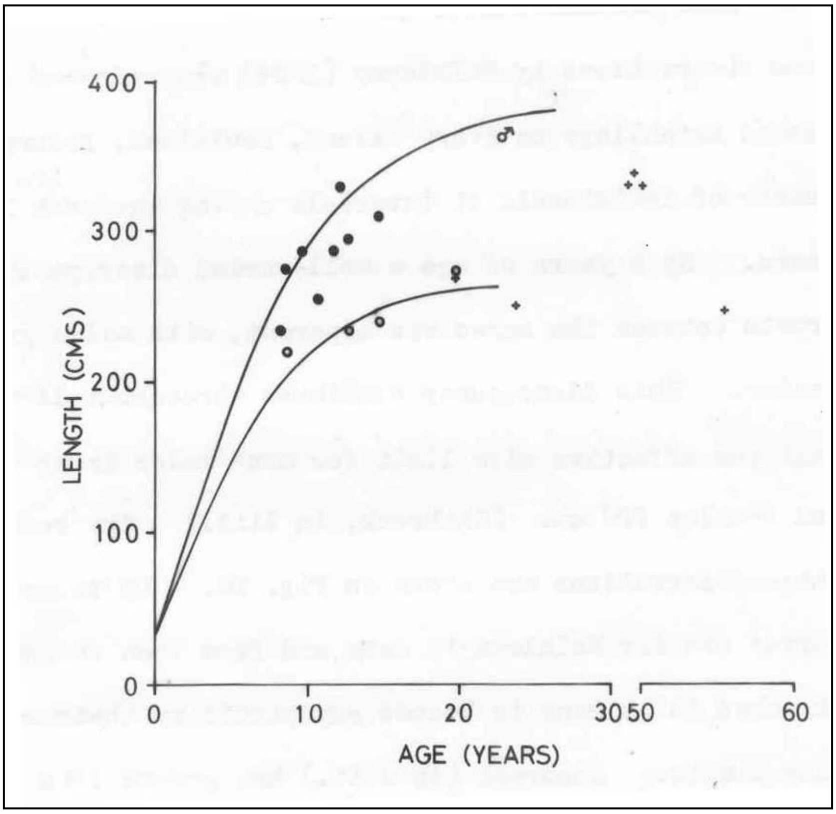


Figure 19. The age/length relationship in Alligator mississipiensis. Suggested curves for adult growth have been sketched in by hand to become asymptotic at their respective size limits. Closed circles: males. Open circles: females. + are known-age, unsexed animals.

years of age a well-marked discrepancy in growth between the sexes was apparent, with males growing faster. This discrepancy continues throughout life, so that the effective size limit for most males is 370 cm and females 250 cm. (Chabreck, in litt.) The results of these observations are shown in Figure. 10. Up to age 11 the curves are for McIhlenny's data and from then on have been sketched in by hand to become asymptotic by their respective size limits. Chabreck (in litt.) has growth data from a large sample of wild alligators, as yet unpublished, which confirm that normal adult size is reached at about age 20-25 years.

The known age animals plotted in Figure. 10 are McIhlenny’s (up to age 11) and 2 animals in the New York Zoological Park (Downing and Brazaitis, 1966). Also shown are 5 unsexed animals from the Berlin Zoo and the South Australian Zoological Society (in litt.).

Sexual maturity in the female alligator is reached at about 5 years and 190 cm length (Chabreck 1967, p. 8) and inspection of the curves in Figure. 10 show that growth begins to fall off gradually after maturity, becoming negligible by the time males are 370 cm long and females 250 cm. As with crocodiles, captive alligators may live for many years without apparent growth.

Growth in known age crocodiles

In an attempt to collect information on growth in captive animals all the major zoos of the world, 110 in all, were consulted for records. Data covering various stages of the first 7 years of life (juvenile life) were obtained for 14 unsexed immatures from a variety of zoos. The growth of 3 Rudolf hatchlings kept in artificial conditions in Nairobi was recorded during the survey. Pooley (1962) has data on 10 hatchlings for the first 2 years of life. Cott (1961) quotes records of 5 immatures. Records of 8 known age adults were obtained but none were accompanied by growth rates for any part of adult life. Davison (in litt.) has records for a single, unsexed wild animal covering 31 years of life. Since growth in juveniles and adults is different the two stages have been considered separately.

These 32 known age immatures are shown in Table 20, where their growth rates, expressed as annual length increments, are grouped into categories at 3

Length increment (cm/y)	**10-12**	**13-15**	**16-18**	**19-21**	**22-24**	**25-27**	**28-30**	**31-33**	**34-36**	**37-39**	**40-42**
Increment group	1	2	3	4	5	6	7	8	9	10	11
Sample	0	1	3	3	5	2	4	4	8	2	0
Percentage	0	3.1	9.4	9.4	15.5	6.3	12.5	12.5	25	6.3	0
Accumulating percentage	0	3.1	12.5	21.9	37.5	43.8	56.3	68.8	93.8	100.1	0

Table 20. Annual length increments in 32 immature crocodiles grouped at 11 categories at 3-cm intervals.

cm intervals. These growth rates have been analysed as follows, using the method of Cassie (1954). The frequency of occurrence of each growth rate was plotted on arithmetical probability paper (Figure. 11). A normal distribution of growth rates would give a straight line but the plot showed 2 modes of growth rate. Furthermore, the point of inflexion occurs at the 50% level, which is what would be predicted if the sample comprised equal numbers of males and females with different mean growth rates. The two component normal distributions have been plotted and the best straight lines fitted by eye. The mean growth rates and standard deviations are given by the ordinate value when the straight lines cut the 50% and the 15.8% and 84.13% verticals respectively. The 2 means were 31-33 cm and 19-21 cm per year and compare favourably with Pooley's male and female growth rates of 34 and 26 cm per year respectively. Although other interpretations of these growth rate frequencies can be made this constitutes the simplest reasonable explanation and the values so obtained have been used to draw the curves for immature growth shown in Figure. 12. Male and female growth curves up to 300 cm and 200 cm respectively have been drawn from the growth rates derived in the preceding paragraph (Table 20 and Figure 11). These assume a nearly constant rate of growth up to sexual maturity, as in alligators. What is known of

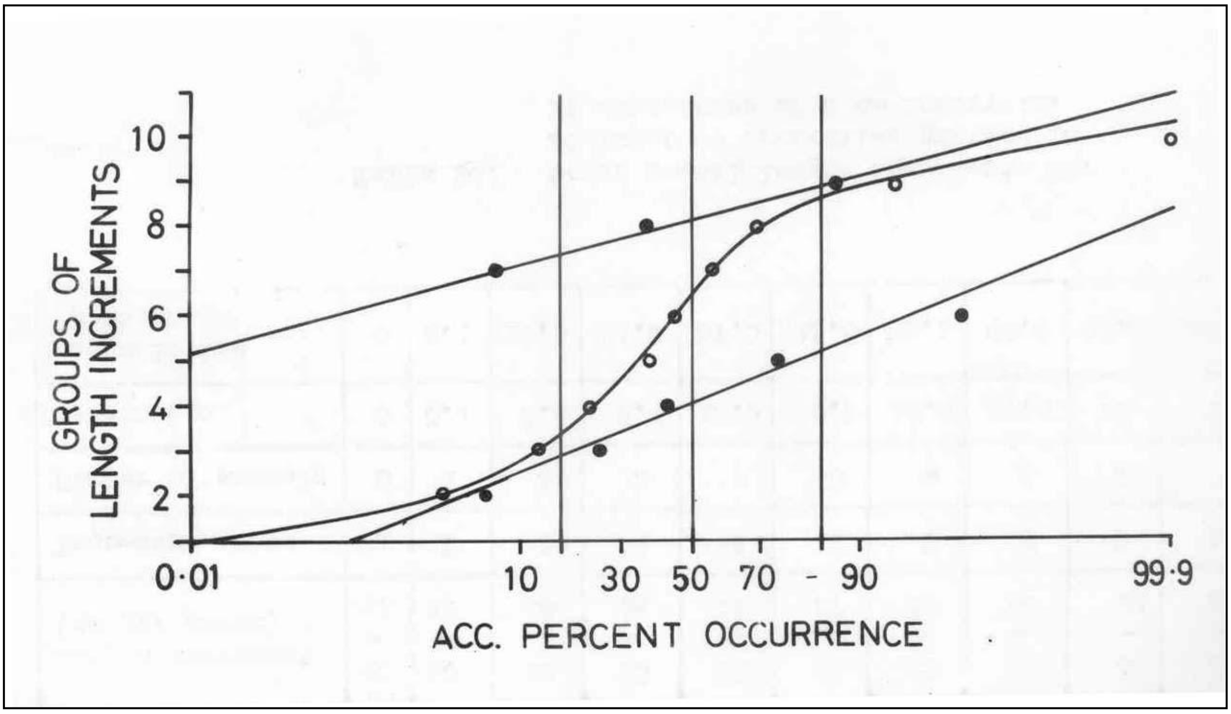


Figure 11. Analysis of growth rate in 32 immature crocodiles. Accumulating frequencies of 9 incremental rates are plotted on arithmetical probability paper indicating 2 modes. The 2 component normal distributions are derived and the means and standard deviations are given by the ordinate value where the straight lines cut the 50%, 15.8% and 84.13% verticals.

growth in crocodiles suggests that maturity is attained in approximately 7-8 years, assuming a mean length at this point of 300 cm in the faster growing males and 200 cm in females. Thereafter, growth in length falls off with age and purely speculative curves have been sketched in to follow the sort of slope observed for alligators (Figure. 10), becoming asymptotic at an arbitrary 500 cm (males) and 350 cm (females). These represent the maximum sizes reached by the majority of older animals in a population; obviously some individuals will grow larger and some never reach these sizes. There is no information to say whether growth ever ceases or whether it becomes as slow as indicated in Figure. 12; nor are there any data on mean life spans in any population and these curves must be regarded as hypothetical curves for "normal” wild crocodiles. As indicated in Figure. 7 this consideration of growth does not apply to Rudolf animals where growth is very much slower and in which animals appear to be stunted.

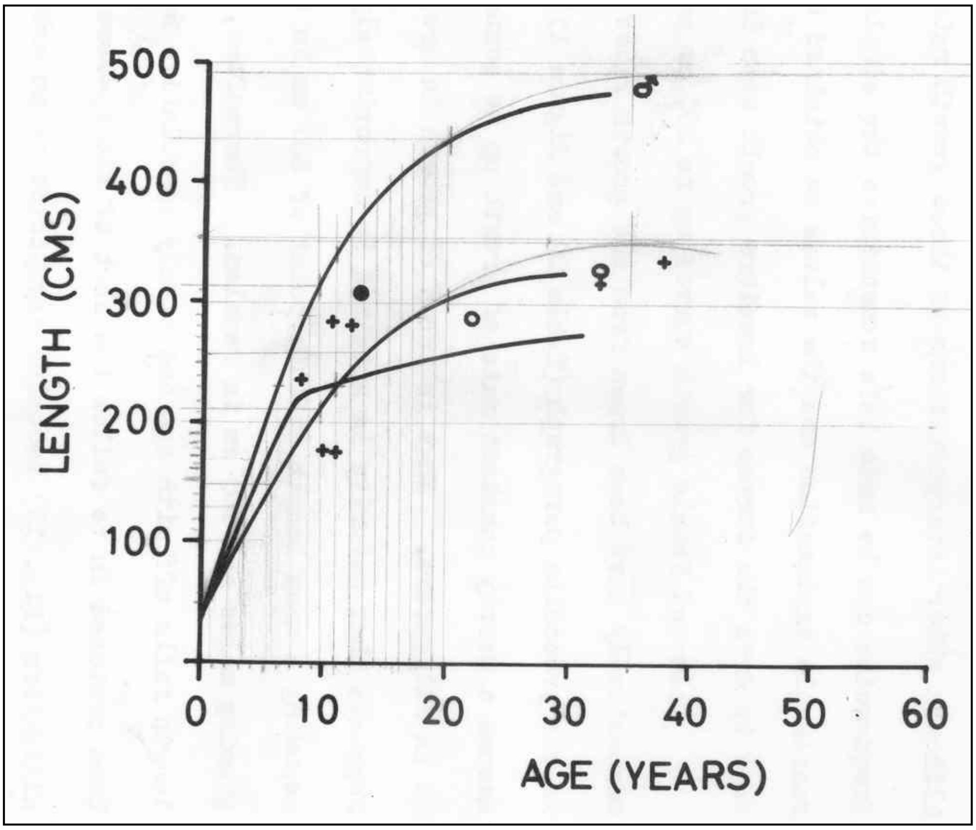


Figure 12. Growth curves for male and female immature crocodiles (values from Figure. 11) up to 300 cm and 200 cm respectively. Suggested curves for adult growth have been sketched in by hand, becoming asymptotic at 500 cm (males) and 330 cm (females). Also shown is the actual growth for Davison's animal (see text). Eight known age animals are shown. Closed circles: males. Open circles: females. + are unsexed animals.

Also shown in Figure. 12 is a wild crocodile in the Wankie National Park, Zimbabwe, for which data are available covering the first 31 years of life (Davison in Cott 1961, and in litt). Growth in this animal was continuous until age 7 and a length of 213 cm, thereafter falling sharply so that by age 31 growth was only 1 cm per annum, or may even have ceased. The curve for this animal fits fairly well the female curve and suggests that growth in older animals slows, possibly after sexual maturity.

At the start of this survey attempts were made to capture and mark animals for release and subsequent recapture to obtain growth data on wild animals. Initially efforts were concentrated on adults, as they were of more interest, using a 10" nylon shark net and snares. Neither technique was successful enough to catch sufficient animals in the limited time available, so activity was confined to capturing small animals by hand at night while dazzling them with a torch. 152 animals were caught and marked by clipping off a combination of the vertical caudal scutes and fastening self-locking, plastic tags through a similar scute. The recovered animals showed that both techniques were satisfactory and could be expected to last for years.

Recapture effort was combined with the routine collection or specimens and totaled 61 nights plus various times during a greater number of days. Only 3 animals (of 78-88 cm total length) were subsequently recovered, after an interval of 8-9 months, during which they grew respectively 0.4; 0.75 and 2.6 cm, or an average of 1.7 cm per annum. It is unlikely that such low growth rates reflect normal growth in Rudolf. animals as the slower growing animal would, at this rate, take 900 years to reach 470 cm. The importance of these observations lies in demonstrating the extent to which growth in crocodiles may vary although the causes of this variation remain largely speculative.

Growth in Rudolf crocodiles

It can be seen (Figure. 7) that up to a length of 190 cm there is a mean immature growth rate of 10 cm a year (body length). This is less than half the growth rate Shown in Figure. 12 and is continued through adult life. That considerable depressions in crocodile growth can and do occur is demonstrated by the 3 marked animals mentioned in the preceding paragraph. These animals, although appearing to be in "good condition" grew, in 9 months, an average of only 1.7 cm per annum. 3 hatchlings captured from the same locality and kept in Nairobi in a tank where the water temperature was maintained at approximately the same level as in Rudolf (26°C), but with an optimal food supply of live fish, averaged 30 cm per annum. The slow growth rate observed on Rudolf is clearly not intrinsic, but determined by some environmental factor or factors. The most obvious one for which there is any evidence is a poor food supply. An exceptionally high incidence of empty stomachs (48.4%) is observed in Rudolf animals and this could result from an inadequate food supply. It would be expected that such an inadequacy would be compensated for by a depression in growth rate, which, other things being equal, is proportional to the rate of food intake. Another factor known to influence crocodile growth is the temperature of

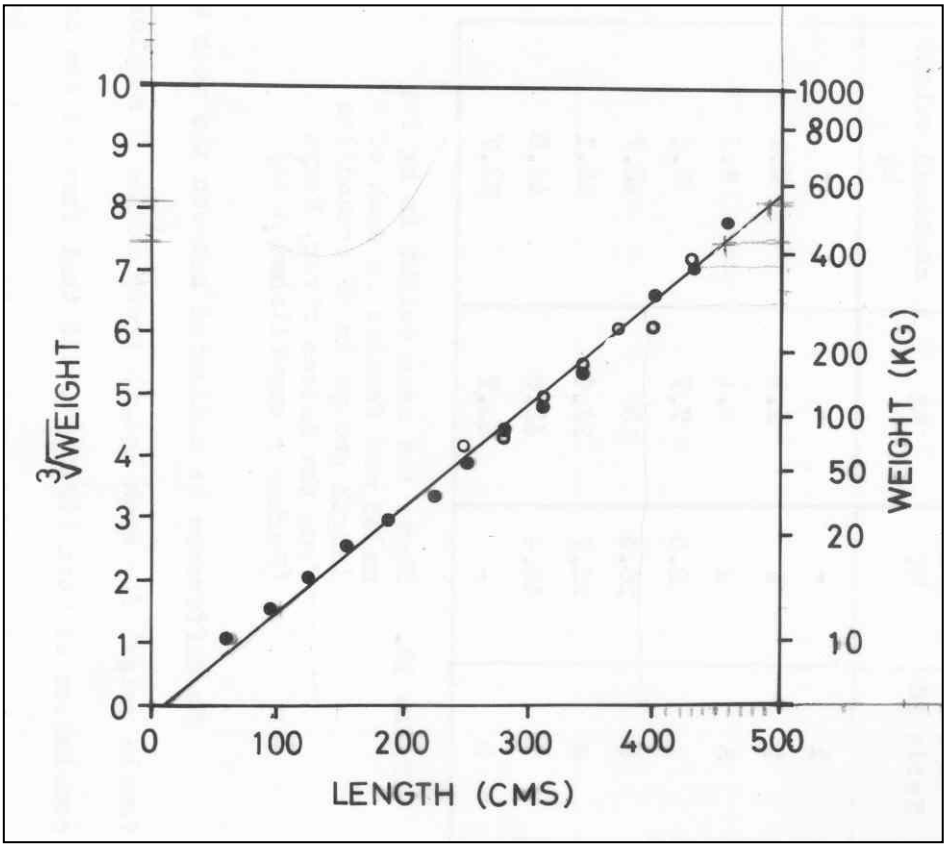


Figure 9. Shows the cube root of body weight plotted against length in 437 Rudolf crocodiles. Male and female weights have been lumped and the mean weight of each size group calculated. The regression coefficient was 0.01684. Also shown (open circles) are the weights of 42 Ugandan and Zambian crocodiles.

their environment. Pooley 1962 found that growth in captive animals bore a close relationship to environmental temperature. Growth slowed with falling temperature and ceased altogether for a period during winter. Since the high air and water temperatures on Rudolf vary little over a 12 month period, or during the 24 hour cycle, this cannot be the inhibiting factor there.

There is also the possibility that some direct, density-dependent effect is exerting an inhibitory influence on growth. Although, in the overall sense, crocodile numbers on Rudolf are surprisingly low compared to localities like Murchison Falls National Park, this is not a valid observation on real density. Using the age structure indicated in Figure. 13 (assuming a similar curve for males) and the weight/length relationship in Figure. 9, the total biomass of crocodiles on Rudolf is estimated as 325,000 kg. This represents, in Section 2 on the east shore, densities of 9,000-39,000 kg per square mile. While our knowledge of crocodile biology is insufficient to judge whether such densities are "high" or "low", it seems possible that they are in fact high when compared to terrestrial situations such as those summarized in Lamprey (1964). Occupance, in the sense used by Watson (1967), of favoured areas in continuous and local densities may be at a maximum with no opportunities for dispersal. Emigration is also impossible in Rudolf crocodiles since the only possible route, the Omo river, already contains large numbers of crocodile.

Section 5 Population dynamics

The object of this section has been to determine some population parameters of the Rudolf population. Recruitment, in this instance the addition of fertile off-spring to the breeding population, is considered first, followed by a discussion on mortality. The age structure of the population is speculated on and some theoretical aspects of the female life Table and the net reproductive rate considered.

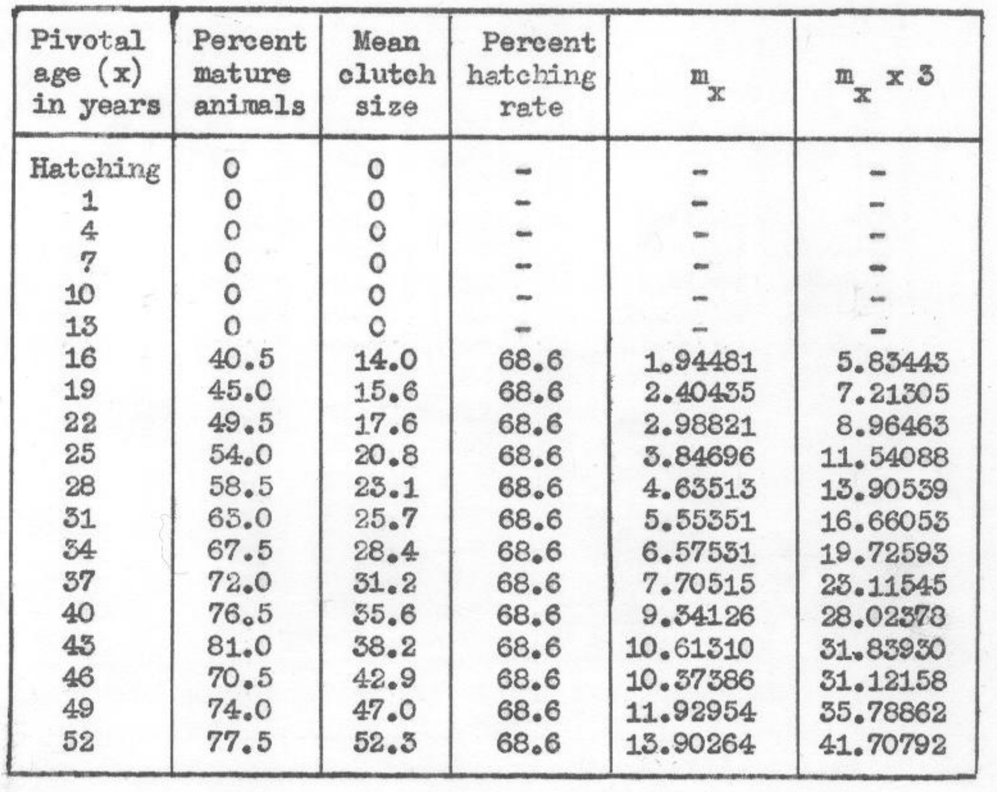
5 a. Recruitment

Reproduction

This section considers those aspects of reproduction that are influencing the age-specific fecundity, or the number of hatching eggs produced per year by each age class of breeding female. Several factors, considered below, contribute to this value.

The ill-defined reproduction cycle prevented accurate assessment of the proportion of mature females that reproduce every season (1 year). In the absence of this data all mature animals have been assumed to breed each year and examination of Table 12 would suggest that the proportion is high. The proportion of females in each age class that are mature (and assumed to breed) has been determined (Table 10, Figure. 4) and these values incorporated. The proportion of older females that have ceased reproducing has also been taken into account (Table 12.). Values for age specific clutch size were read off Figure. 5 and have been included in the calculation.

Modha (1967) gives some data on hatching success on Central Island in 1965/66 and from this an estimate of the hatching rate has been calculated. Modha lists a total of 152 nests made on the island in 1965/66. 126 (82.9%) of these hatched. He does not state what his criteria for assuming 152 to be the total were, but since the nests are easy to locate once they have hatched we can accept these data as fairly accurate, since the number of unknown nests that failed to hatch is likely to have been negligible.



Pivotal age (x) in years	Percent mature animals	Mean clutch size	Percent hatching rate	m_x	m_x x 3
Hatching	0	0	-	-	-
1	0	0	-	-	-
4	0	0	-	-	-
7	0	0	-	-	-
10	0	0	-	-	-
13	0	0	-	-	-
16	40.5	14.0	68.6	1.94481	5.83443
19	45.0	15.6	68.6	2.40435	7.21305
22	49.5	17.6	68.6	2.98821	8.96463
25	54.0	20.8	68.6	3.84696	11.54088
28	58.5	23.1	68.6	4.63513	13.90539
31	63.0	25.7	68.6	5.55351	16.66053
34	67.5	28.4	68.6	6.57531	19.72593
37	72.0	31.2	68.6	7.70515	23.11545
40	76.5	35.6	68.6	9.34126	28.02378
43	81.0	38.2	68.6	10.61310	31.83930
46	70.5	42.9	68.6	10.37386	31.12158
49	74.0	47.0	68.6	11.92954	35.78862
52	77.5	52.3	68.6	13.90264	41.70792

Table 21. Age specific fecundity in female crocodiles from Rudolf. Proportion of mature animals from figure 4, mean clutch size from figure 5 and hatching rate calculated from data given in Modha (1967) (see text). m_x is the mean number of female offspring produced per female in the period of time x, assuming a generation interval of a year. Since a pivotal age interval of 3 years was adopted the calculated m_x values have been multiplied by 3.

For the nests that hatched Modha estimated the hatching rate by counting egg-shells and unhatched eggs from each nest, and assuming a mean clutch size of 33 (where the clutch size was unknown) computed the hatching success. From an examination of this data (given in Tables A 10 and A 11) a hatching rate of 82.8% is apparent. Thus for the total of 152 nests, representing 5,016 eggs, an overall hatching rate of 68.6% (3,441 eggs) is calculated.

The calculation of age specific fecundity, expressed as an m_x value where this is the mean number of female offspring produced per female in a period of time x, is summarized in Table 21, for each age class of mature females. Since a pivotal age of 3 years has been adopted the m_x values have been multiplied by 3, since the length of each generation is one year.

Mortality up to sexual maturity

Where it occurs, the Nile monitor lizard (*Varanus niloticus*) may be an important agent in egg mortality as suggested by the numerous observations of predation by this animal (Cott 1961, p. 304.). However, during this survey no evidence was found for the existence of monitors on the mainland of Rudolf (although they occur on North and Central Islands) and it is not, therefore a significant agent of egg mortality on the lake as a whole. Cott (ibid.) records a variety of animals that have been observed to prey on crocodile eggs, but of these the only ones present on Rudolf in any numbers are hyaenas (*Crocuta crocuta* Erxleben and *Hyaena hyaena* Meyer). Both species are common along the shores of the east side, but during the 14 months of the survey only one nest was found destroyed by hyaenas in an area where an estimated 100 or more nests were made.

The human populations of the south-east and west shores destroy a high proportion of nests made there and although these are low density areas (for crocodile) man is almost certainly the most important egg predator on Rudolf.
A form of catastrophic mortality which must take place occasionally is inundation by early, exceptionally high floods. In East Africa where deterioration of the catchment areas of many rivers is resulting in increased run-off the chances of this sort of mortality are increasing. Modha (1967) records 3 nests on Central Island destroyed by waves during a storm.

Many other factors will contribute towards egg mortality. Disease, adverse environmental conditions, infertility and failure of the parent animal to unearth the hatching eggs have all been known to occur (Modha 1967), but unfortunately no quantitative assessment of any of these exists. Of 26 nests that Modha recorded as failing to hatch the fates of 9 are described while for the remaining 17 no information is given.

Mortality in immature crocodiles

The small size of hatchlings could be expected to make them available to a wide spectrum of predators and a variety of animals have in fact been recorded feeding on young crocodiles (Cott 1961, p. 304). While predation on hatchlings at Rudolf may be high no actual instances are on record and the extent to which it occurs remains speculative. The finding of a hatchling in the stomach of a catfish (*Clarias lazera* Val) on Central Island (Modha 1967) is of interest. While it may have been scavenged it could represent active predation by a fish which, in the extensive unsheltered water of Rudolf, might be significant. Modha (1967) p. 92 concluded that most hatching took place at night which may favour survival at a particularly vulnerable stage, since a nocturnal predator would have to be near a hatching nest to detect it while a diurnal avian predator such as a marabou (*Leptoptilos crumeniferus* Lesson) could see a nest hatching from some distance. The appearance in a given habitat of a large number of hatchlings in a relatively short space of time, a concomitant of a breeding season tied to climatic cycles, may or may not favour survival. As has been suggested by Darling (1938), this will prevent predators from building up to densities that could exploit hatchling crocodiles maximally. It would also preclude the evolution of predators exclusively dependent on very small crocodiles. Conversely, "specific search images" might develop, resulting in a high level of exploitation by some predators. The nature of the habitat could also be expected to influence the level of predation since very shallow water and dense cover would make crocodiles less vulnerable to predators than in habitats with scant cover like much of Rudolf.

Food supply would be important in that low availability might, apart from direct starvation, depress growth rates, seems to be the case on Rudolf, leaving immature animals susceptible to hazard for a longer time.

There is evidence that in localities without shelter mortality may be very high. 15 nests were found on various occasions up to 3 days after hatching, on 2 small islands 1-2 miles offshore in Allia Bay. There is no shelter of any sort on either island and frequent close examination, both by day and night, failed to reveal any of the hatched animals. An appreciable current flowing away from land in a north westerly direction combined with the nearly continuous easterly wind makes it very unlikely that these animals swam to shore and it seems that nesting here resulted in, perhaps, 100% mortality to the hatchlings. There is circumstantial evidence that a similar state of affairs exists on the larger North and Central Islands. (Only one visit was made to South Island during the survey and no relevant information was recorded.) 14 days were spent on North Island in August 1965 during which considerable effort was spent on locating crocodiles. Despite the fact that at least 18 nests, representing about 400 hatchlings, had hatched the previous season, only 1 animal < 90 cm long was observed on the island. Modha (pers. comm.) has remarked on the scarcity of small crocodiles <100 cm on Central Island prior to the onset of the 1965/66 breeding season. In 1966 he observed 126 nests to hatch on the island, which represents approximately 3,500 hatchlings. Assuming a similar number the previous season his observation would suggest a massive mortality among hatchlings. (This ignores the unlikely possibility that the young animals dispersed by swimming the 6 miles to the mainland). North and Central Islands are noteworthy for the complete absence of any swampy habitat which is where, on the mainland, young crocodiles tend to accumulate. What sheltered water that does exist on Central Island is occupied, at times, by high densities of large crocodiles. It is therefore possible that these islands are unsuitable as habitats for young crocodiles and mortality on them may approach 100%. Nesting there may be a response to some disturbing influence on the mainland such as harassment by man at the expense of survival in the young. The implications of this are discussed further in Section 6 b on "Exploitation".

Some idea of the order of magnitude of mortality in young crocodiles is given in Section 5 c.

5b Mortality in older animals

As crocodiles grow larger they presumably become susceptible to fewer predator species so that in the case of a full-grown male the only one remaining is man. Two lions (the most powerful potential predators) were observed to kill a crocodile of 320 cm at Allia bay during the survey, but individuals larger than this have not been recorded killed by lion (Cott 1961). The entire shoreline of Rudolf is subject to illegal hunting by man, but it is unlikely that the numbers of animals taken is large, since, with the exception of Merrille hunting sorties from Ethiopia and a few in Kenya, firearms are not used, and traditional weapons are relatively inefficient. Also, until recently crocodile hunting was for food only and animals were only killed occasionally. Predators, apart from man, are therefore unlikely to be causing much mortality in older crocodiles. Catastrophic mortality may occur from such agencies as lightening strikes, which, in the shallow, saline littoral of Rudolf could eliminate considerable numbers of individuals. A volcanic area like Rudolf might suffer occasional underwater eruptions causing a local and rapid rise in water temperature to lethal levels. Although riverine crocodiles are known to aestivate in response to drying rivers, (Cott 1961, p.231) drying up of entire lakes, such as happened to Lake Rukwa (Tanzania) in recent years, can result in heavy mortality. Hippopotamus have been known to kill full grown male crocodiles (Cott, ibid.), but, while the frequency of such conflicts is unknown, it is unlikely to be high. Apart from disease, about which nothing is known, the other possible cause of mortality is the complex of conditions associated with "senescence." Whether senescent processes occur is not clear, but the finding of evidently non-functional ovaries in large females (see section on female reproduction), and one male with possibly non-functional testes, does suggest senescence. This latter animal measured 445 cm with testis weights of 52g and 59g (about 300 g in an active male this length). No spermatogenesis was present, although it was at the height of the breeding season, and the testes were enclosed in a thick, fibrous sheath. Histologically, the testis was superficially similar to a mature, quiescent animal with large tubules and relatively little interstitial tissue. But the epithelium of the tubules (Figure. 2) was seen to be very thin and showed a tendency to break away from the underlying tissue. The interstitial tissue contained fewer stained nuclei than in an active animal. Although possibly a pathological condition, it may have been a manifestation of senescence. Pitman, in Cott (1961) comments that several exceptionally large females examined by him on Lake Victoria had ceased breeding, although he does not state what the criteria for determining this were. Old animals with inactive gonads have been described by Legler (1960) in the turtle *Terrapene ornata ornata*, and in *Pseudemys scripta elegans* by Cagle (1944).

There is then some evidence for supposing that senescent processes occur in crocodiles and this may account for ultimate mortality in very old animals.

5c Survivorship in Crocodiles

No assessment of the age structure of the Rudolf crocodile population was made during the survey and this section is confined to theoretical considerations only. (But see Table 23.)

In a crocodile population with a stable age distribution mortality from hatching to the onset of reproduction must be very high since relatively large numbers of offspring are produced per breeding female. The order of magnitude of this mortality is indicated in the following argument.

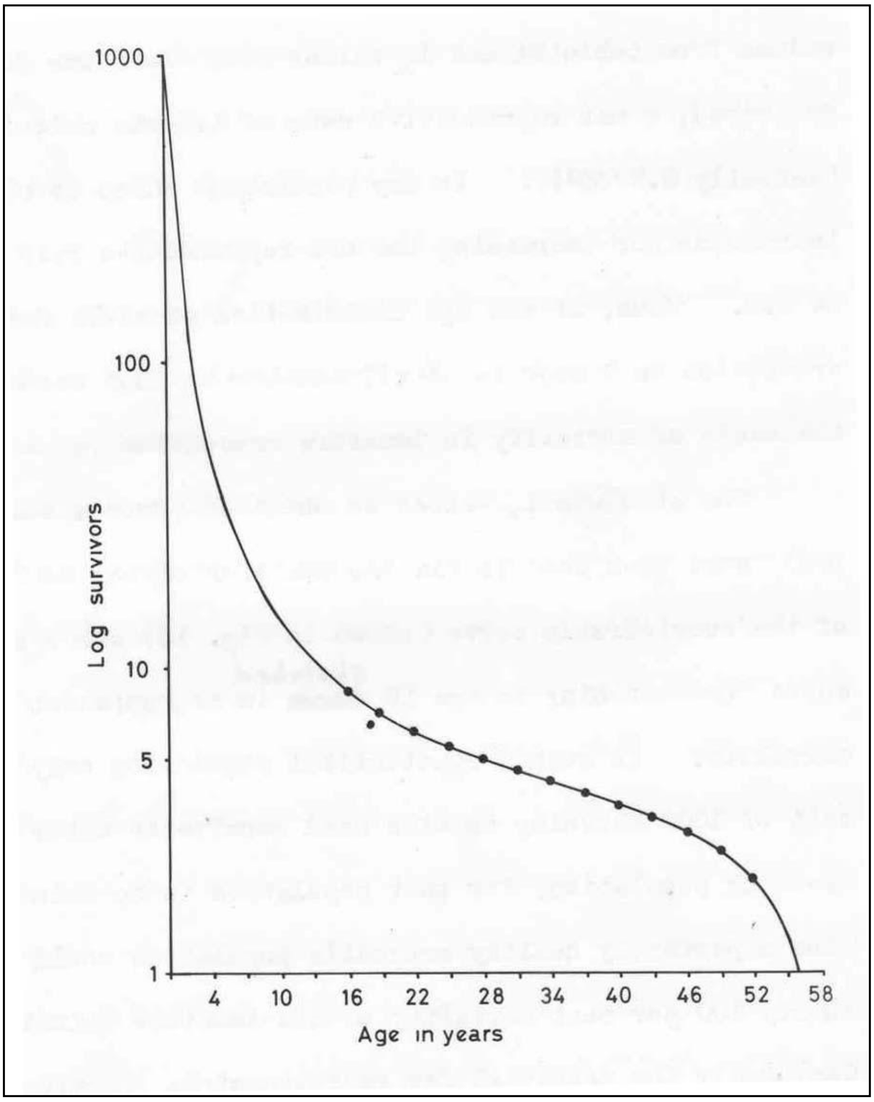
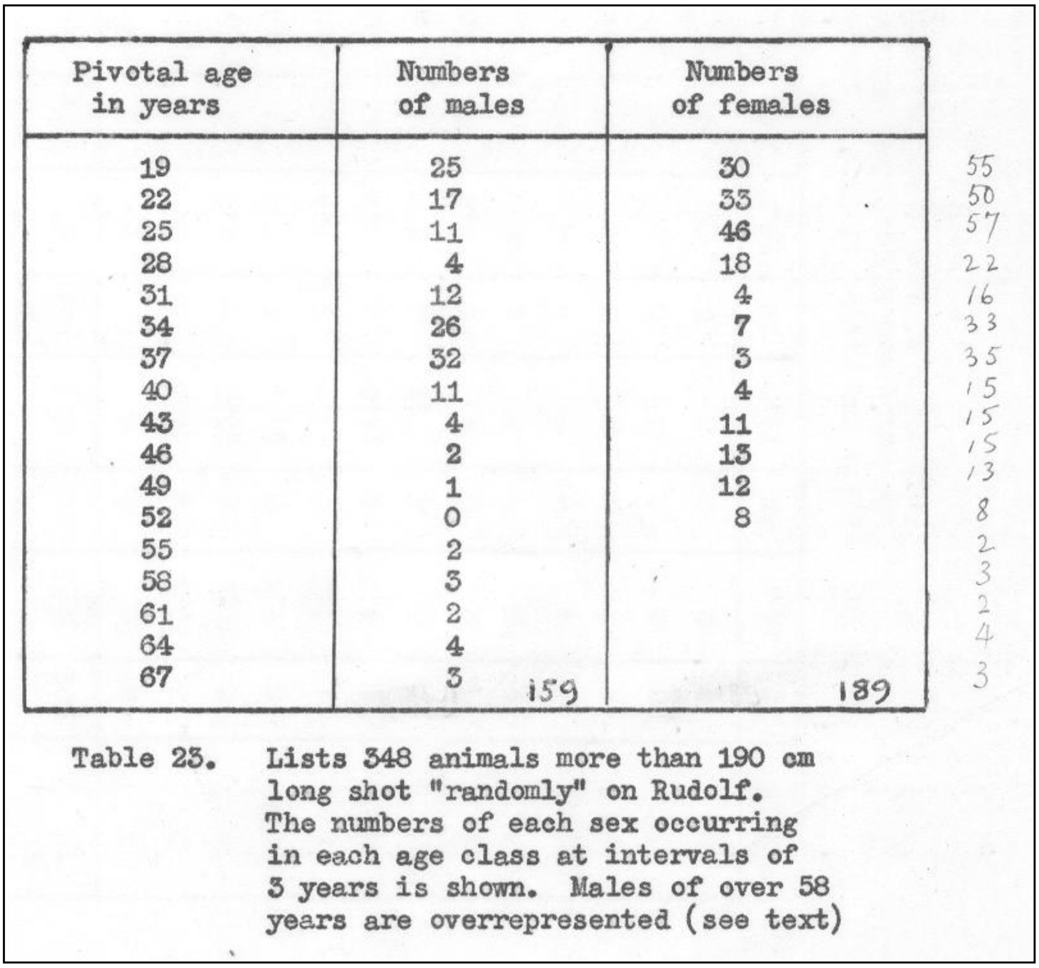


Figure 13. Hypothetical female survivorship curve for Rudolf crocodiles. The adult portion from age 16 was fixed by trial and error to give a value for R_0 of 1.0 (see text and Table 22). The curve from hatching to age 16 was sketched in by hand to represent total immature mortality (see text).

Although no data exist there is no reason to suspect that any major change has taken place in the Rudolf crocodile population over the last 20 years. Assuming for the purposes of this argument that there has been a stable age distribution over that time the following speculation on survivorship has been made. First, a purely arbitrary survivorship curve, for females, was drawn, incorporating the following features. Beginning at age 16 (onset of maturity) a decrease in mortality rate until age 35 was followed by an increasing mortality rate to the maximum age of 53. This curve, drawn as symmetrically as possible, is similar to type IV of Slobodkin (1964) in which a high rate of mortality in immatures is followed by a relatively good expectancy of further life in adults. The increase in mortality rate of very old animals is implied by the presence of senescent processes which will decrease the expectancy of further life in such individuals. The actual shape of the curve at this stage had no meaning and was drawn purely to provide a relative scale of survivors in each age class from 16-53 years. Then, by trial and error, using m_x values from Table 21 and l_x values from the curve just described, a net reproductive rate of 1.0 was calculated (actually 0.999894). In any population which is neither increasing nor decreasing the net reproductive rate will be 1.0. Thus, if the age distribution of adult female crocodiles on Rudolf is at all similar to that assumed above, the scale of mortality in immature crocodiles can be gauged.

The absolute l_x values so obtained (from a cohort of 1000) were then used to fix the position of the adult portion of the survivorship curve (shown in Figure. 13) and a smooth curve from hatching to age 16 sketched in to represent immature mortality. In such a hypothetical population only 0.8% of 1000 hatching females need survive to enter the breeding population, for that population to be maintained. Thus a perfectly healthy crocodile population could experience nearly 100% mortality of its immature animals. Conversely the potential for recruitment is enormous. To what extent this immature mortality is density-dependent is impossible to decide, but it is highly likely that it is sensitive to population density since a certain range of survivorship must be intrinsic to permit the animal to recover from catastrophe or exploit new situations. A certain level of mortality may be inevitable regardless of the suitability of an environment for young crocodile survival. Lack (1954) discusses the question of survival in young birds and concludes that a high reproductive rate is a result of selection and an inevitable consequence will be a high mortality in young animals. It is variations to their mortality that provide the animal with the flexibility in recruitment it needs to survive as a species. This range in recruitment rate is the phenomenon of most concern to this survey since it is from this that the productivity and hence the degree of exploitation by man can be judged. A life Table drawn up on the basis of the l_x values in Figure. 13 is shown in Table 22.

Of interest is the age structure of the 500 animals shot during the survey, since it reveals the sort of result that can be expected from "random” shooting. These animals were collected in such a way that the larger individuals constituted a quasi-random sample of those age groups at Moite and Allia Bay. Animals judged to be less than 190 cm long were avoided because most of them would be immature and consequently of little scientific value to this survey. Altogether 152 animals less than 190 cm long were collected, being mostly the result of misjudged size or to make up numbers when occasion demanded. But over this size no conscious selection was exercised since the time required for one person to hunt, recover and process the animals was so great that selection was impossible and any available animal was taken. Nevertheless, some bias towards larger animals was probably present since these were of much more interest than smaller ones. On at least 4 occasions smaller animals were passed up in favour of exceptionally large males, selected because of their relative scarcity. No difference in the ease with which animals of different sizes or sexes could be hunted was noticed. The 348 animals concerned were all collected from Moite and Allia Bay (excepting 5 from North Island) and although this involved hunting 30-40 miles of shore they are not necessarily representative of other parts of the lake. The sex ratio in the sample was 54.3% in favour of females. 651 crocodiles from a variety of localities examined by Cott (1961) showed a ratio of 50.2% in favour of females. It thus appears that the sex ratio in crocodiles can be taken as 1:1. The 348 animals are listed in Table 23. Although the sample may represent the age structure of the population as a whole, the erratic distribution of relative numbers remains unexplained and attempts to use the sample to construct survivorship curves were discarded in favour of the theoretical treatment discussed in the previous section.



Pivotal age in years	Numbers of males	Numbers of females	
19	25	30	55
22	17	33	50
25	11	46	57
28	4	18	22
31	12	4	16
34	26	7	33
37	32	3	35
40	11	4	15
43	4	11	15
46	2	13	15
49	1	12	13
52	0	8	8
55	2		2
58	3		3
61	2		2
64	4		4
67	3		3
	159	189	

Table 23. Lists 348 animals more than 190 cm long shot "randomly" on Rudolf. The numbers of each sex occurring in each age class at intervals of 3 years is shown. Males of over 58 years are overrepresented (see text)

Section 6. Exploitation

To date, crocodile exploitation has consisted of sport hunting, and collection of eggs for food by man (probably involving only small numbers on Rudolf) and hunting for skins. It is important to consider the value of crocodile skin and the factors influencing it since any management program must relate directly to this, particularly in a species where fairly precise selection of individuals is both feasible and desirable.

6a Value of crocodile skins

The skins of all 500 animals killed during the survey were collected and sold. Records of size and "grade" were kept, but the accidental loss of some records resulted in data being available for only 393 skins (78.6%).

Grading

The commercial grading of crocodile skins is governed by several factors, the most important of which is the incidence of structures known as "buttons". These are hard, flat discs of a bone-like substance that form inside the commercially valuable ventral scales. They begin in the centre and grow out radially, eventually occupying the entire scale and their effect is to render the normally pliable scute hard and brittle and unsuitable for leather work. A tendency for buttons to appear first in the pectoral region is observed. The nature and cause of buttons is unknown and although they occur in most if not all populations they are usually not found in animals less than 300 cm long. But lakes Rudolf and Baringo are peculiar in producing an exceptionally high incidence of buttoned skins even in small animals, which is unexplained. The other factors governing skin grade are natural blemishes or injuries caused during skinning, and decomposition. Three basic grades are recognised with occasionally a fourth for "reject" skins. No "fourth" grades were produced during the survey. "First" grades are those skins with no buttons, damage or decomposition. "Second" grades are those with buttons confined to the pectoral region or with minor injuries or damage. "Third" grades include skins with a high incidence of buttons, or with relatively severe damage or patches of decomposed skin. Although this system of grading is arbitrary it was found to be consistent among different commercial firms. The value of a skin also varies according to size; the larger the skin the more valuable it is within each grade range. The size of a skin is commonly determined by measuring across the widest point on the ventral surface, starting and ending at the first line of rigid scales (which are useless as leather).

Grade and value of Rudolf skins

The 595 skins are listed in Table 24 as the number of first, second and third grade male and female Skins, occurring in each of 15 size groups (groups as in Table 17).

As can be seen, the incidence of first grades is highest in the smallest animals, decreasing to zero in animals over ~1 am. The incidence of second grades is similar to first: being higher in small animals and nil in animals over 541 cm The incidence of thirds is conversely lowest in the smaller animals, becoming 100% in animals more than 341 cm long. Firsts comprised 17% of the total, seconds 17% and thirds 66%: these proportions will obviously vary according to the size distribution of animals taken.

Although the data suggests that females produce more high grade skins than males the samples are too small for critical comparison and the sexes will therefore be considered together. The grade/length relationship is illustrated in Figure. 14 where the percentage occurrence of each grade is plotted against length and suggested curves sketched in.

Although comparable data for skins elsewhere does not exist (commercial firms' records give only grades with no accompanying data) it is well known that the

Length group from Table 17	Firsts				Seconds				Thirds				Sample
	Males		Females		Males		Females		Males		Females		
	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	Nos	%	
4	3	60	0	0	0	0	2	40	0	0	0	0	5
5	3	33.3	4	44.4	0	0	2	22.2	0	0	0	0	9
6	8	12.9	16	25.8	5	8.0	14	22.6	4	6.5	15	24.2	62
7	5	6.3	9	11.2	6	7.5	5	6.3	18	22.5	37	46.3	80
8	4	4.5	6	6.7	7	7.9	11	12.3	17	19.1	44	49.4	89
9	1	4.0	3	12.0	1	4.0	2	8.0	10	40.0	8	32.0	25
10	0	0	4	7.8	0	0	6	11.8	31	60.8	10	19.6	51
11	0	0	0	0	2	3.8	3	5.8	24	46.1	23	44.2	52
12	1	20	0	0	1	20	0	0	3	60.0	0	0	5
13	-	-	-	-	-	-	-	-	-	-	-	-	-
14	0	0	0	0	0	0	0	0	2	100	0	0	2
15	0	0	0	0	0	0	0	0	6	100	0	0	6
16	0	0	0	0	0	0	0	0	7	100	0	0	7
Totals	25	14.8	42	18.7	22	13.0	45	20.1	122	72.2	137	61.2	

Table 24. Lists the number of first, second and third grade skins in 169 males and 224 females from Rudolf, shown as the proportion of each grade occurring in each of 13 size groups.

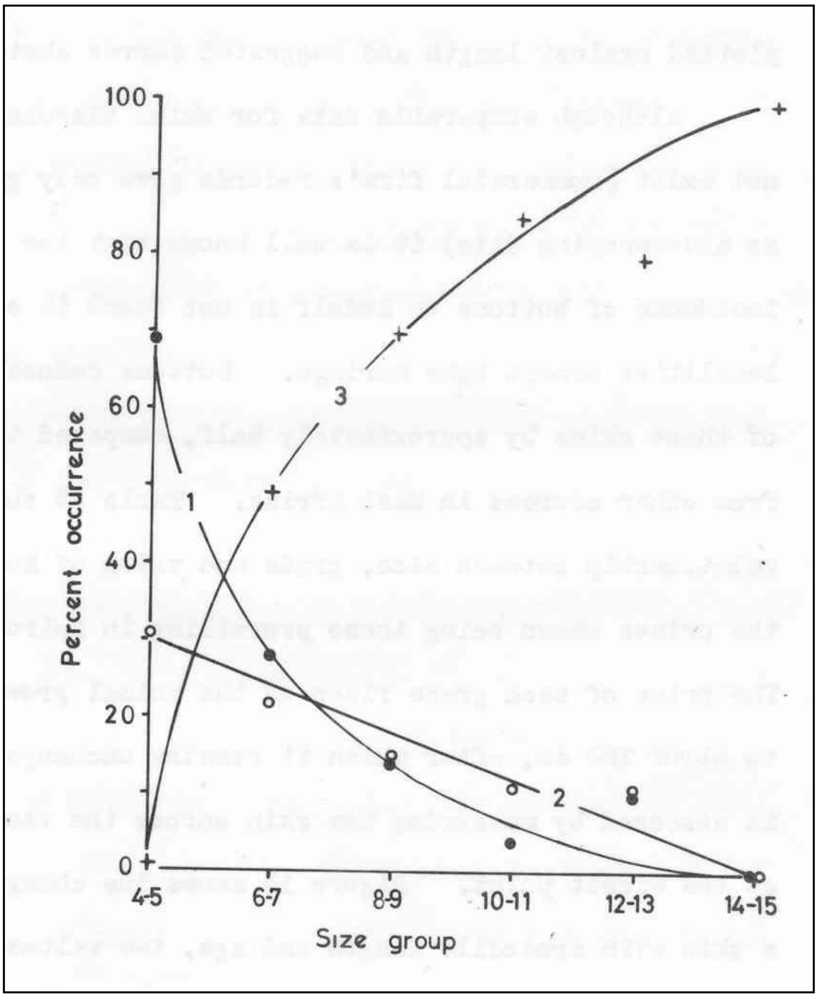


Figure 14. Percent occurrence of “first” (1), “second” (2) and “third” (3) grade skin in each of 12 length groups of Rudolf crocodiles. Data from Table 24 with males and females lumped and the mean for wach successive pair of size groups plotted. Closed circles: firsts. Open circles: seconds. + thirds.

high incidence of buttons on Rudolf is not found in other localities except Lake Baringo. Buttons reduce the value of these skins by approximately half, compared to skins from other sources in East Africa. Table 25 shows the relationship between size, grade and value of Rudolf skins, the prices shown being those prevailing in Nairobi in 1966. The price of each grade rises as the animal grows longer, up to about 190 cm, after which it remains unchanged. The size is assessed by measuring the skin across the ventral surface at the widest point. Figure 15 shows the change in value of a skin with crocodile length and age, the values being the average for each length class considered.

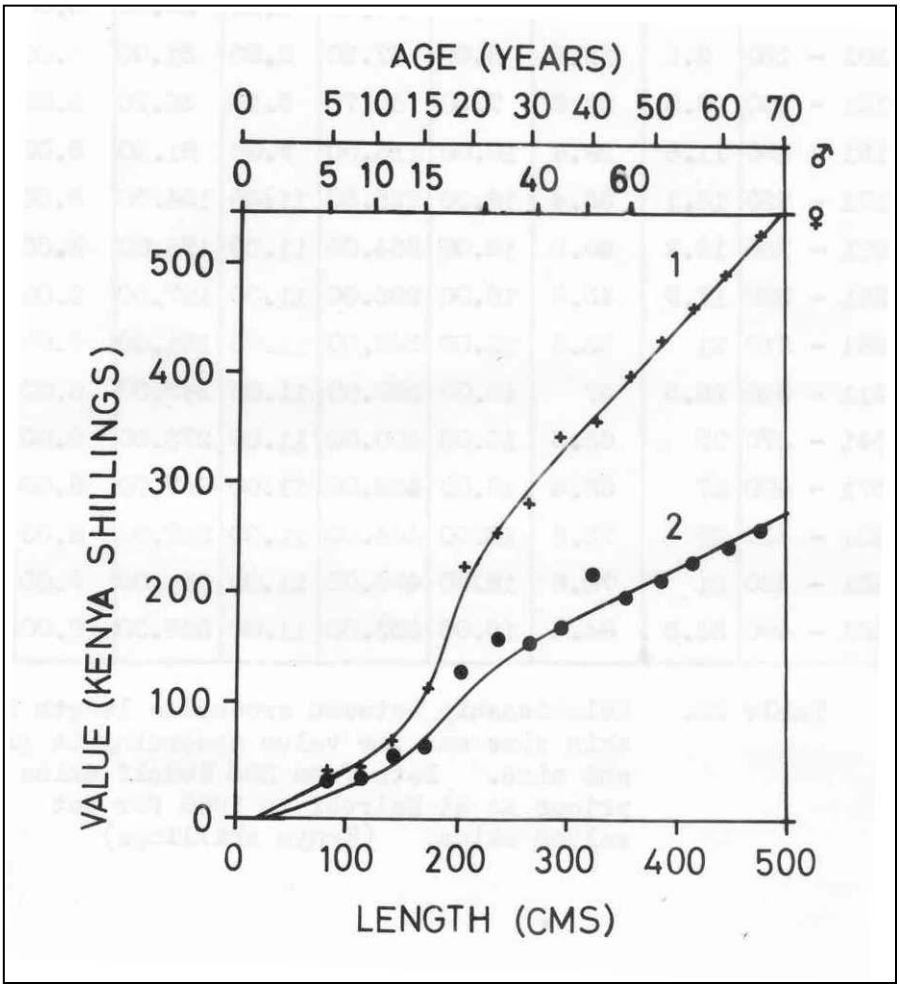
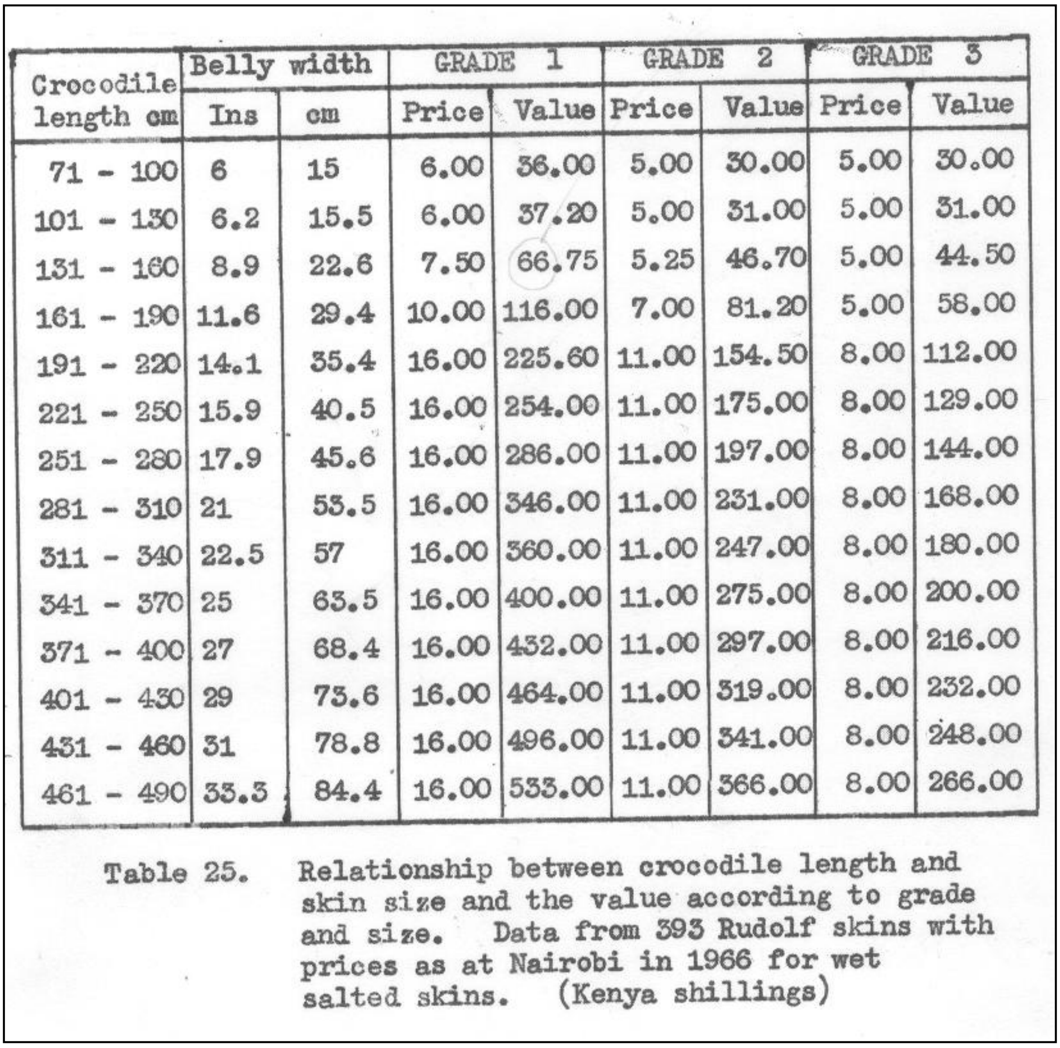


Figure 15. the increase in average value of Rudolf crocodile skin (2) with length and age, and the value of the same skin if all were first grade (1).

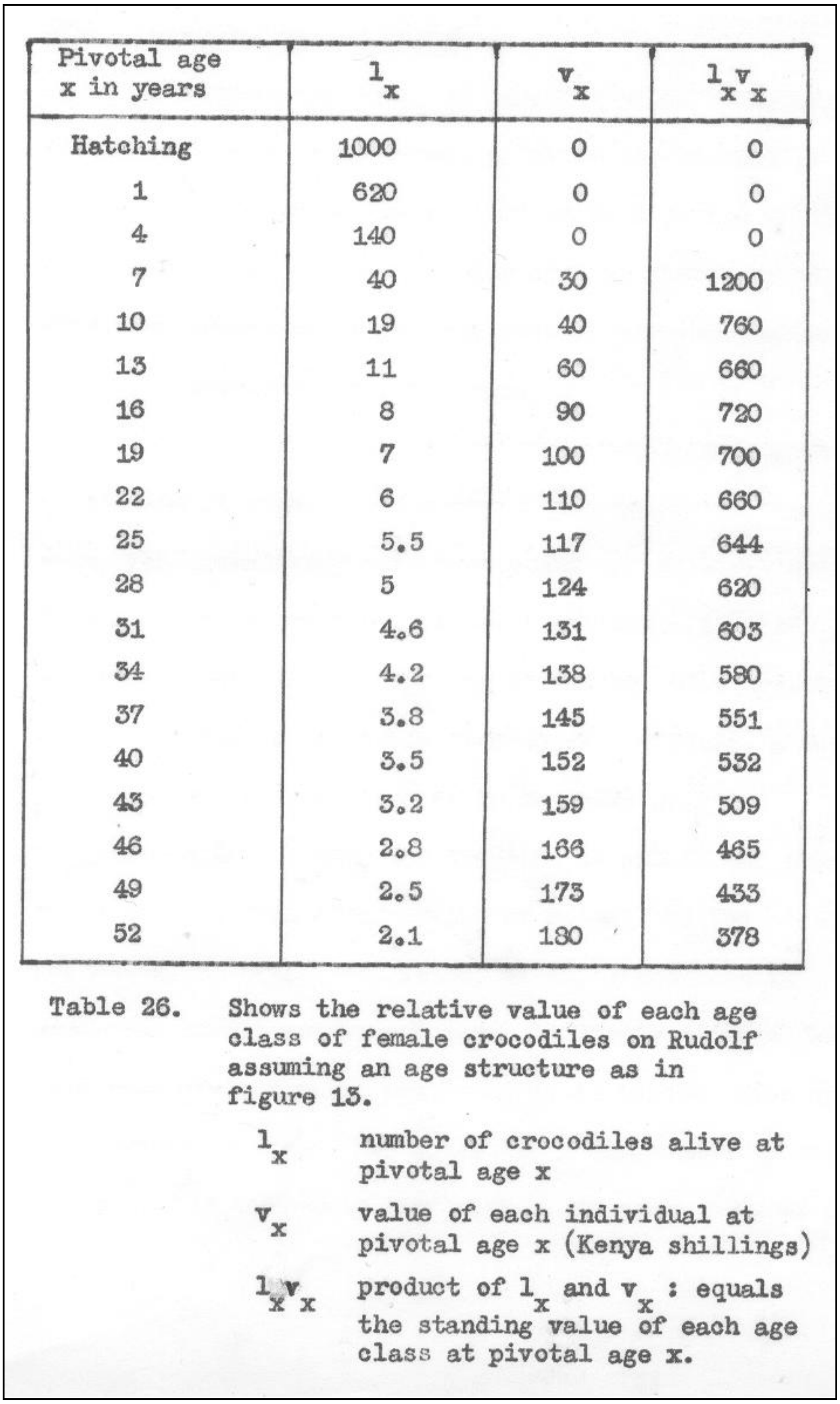
Also shown for comparison, are the values of the same skins assuming 100% first grades, which would more nearly approximate the position with most other East African skins, at least in the younger animals. It must be borne in mind that these values depend entirely on the prices paid by commercial buyers, which are a matter of negotiation between the parties concerned. The prices incorporated into the above analyses were those prevailing in Nairobi during 1966 and while probably higher than any previously offered will fluctuate according to demand.

Shown in Table 26 is the relative value of each age class of female crocodiles, assuming an age structure as in Figure. 13 and values as for Rudolf animals. Assuming a similar age structure for males it is interesting to find that the most valuable age classes are the young animals just before and just after the onset of sexual maturity, of 7-19 years age. This is due to increasing mortality cancelling out the rise in value with size and age. This has very important implications in crocodile management since it suggests that the most valuable crop would consist largely of very young animals. There are many other reasons why cropping young crocodiles may be desirable, discussed in the next section.



Crocodile length cm	Belly width		GRADE 1		GRADE 2		GRADE 3	
	Ins	cm	Price	Value	Price	Value	Price	Value
71 - 100	6	15	6.00	36.00	5.00	30.00	5.00	30.00
101 - 130	6.2	15.5	6.00	37.20	5.00	31.00	5.00	31.00
131 - 160	8.9	22.6	7.50	66.75	5.25	46.70	5.00	44.50
161 - 190	11.6	29.4	10.00	116.00	7.00	81.20	5.00	58.00
191 - 220	14.1	35.4	16.00	225.60	11.00	154.50	8.00	112.00
221 - 250	15.9	40.5	16.00	254.00	11.00	175.00	8.00	129.00
251 - 280	17.9	45.6	16.00	286.00	11.00	197.00	8.00	144.00
281 - 310	21	53.5	16.00	346.00	11.00	231.00	8.00	168.00
311 - 340	22.5	57	16.00	360.00	11.00	247.00	8.00	180.00
341 - 370	25	63.5	16.00	400.00	11.00	275.00	8.00	200.00
371 - 400	27	68.4	16.00	432.00	11.00	297.00	8.00	216.00
401 - 430	29	73.6	16.00	464.00	11.00	319.00	8.00	232.00
431 - 460	31	78.8	16.00	496.00	11.00	341.00	8.00	248.00
461 - 490	33.3	84.4	16.00	533.00	11.00	366.00	8.00	266.00

Table 25. Relationship between crocodile length and skin size and the value according to grade and size. Data from 393 Rudolf skins with prices as at Nairobi in 1966 for wet salted skins. (Kenya shillings)



Pivotal age x in years	l_x	v_x	l_xv_x
Hatching	1000	0	0
1	620	0	0
4	140	0	0
7	40	30	1200
10	19	40	760
13	11	60	660
16	8	90	720
19	7	100	700
22	6	110	660
25	5.5	117	644
28	5	124	620
31	4.6	131	603
34	4.2	138	580
37	3.8	145	551
40	3.5	152	532
43	3.2	159	509
46	2.8	166	465
49	2.5	173	433
52	2.1	180	378

Table 26. Shows the relative value of each age class of female crocodiles on Rudolf assuming an age structure as in figure 13.

l_x	number of crocodiles alive at pivotal age x
v_x	value of each individual at pivotal age x (Kenya shillings)
l_xv_x	product of l_x and v_x : equals the standing value of each age class at pivotal age x.

Productivity and Yield

To compute the crop, or possible yield to man, the "productivity" must be known, which is the biomass of crocodile produced by the population in a period of time, for convenience, one year. The crop is that part of the gross production which man may remove, per year, without depleting the stock or production. Calculation of productivity requires knowledge of population size and age structure, the potential recruitment rate, the actual recruitment rate and age specific mortality rates. The information presently available does not permit accurate prediction of cropping levels but some hypothetical considerations are possible from which, at least, a management plan for Rudolf crocodiles could be drawn up.

There is a widespread tendency to relate the possible yield or crop from a population of animals to the size of the stock, or total population, at any given moment. But as Macfadyen (1963) points out there is little relation between stock and productivity, particularly in species with high reproductive rates. The potential production of a crocodile population is obviously very high. From the data in Table 22 the total annual egg production on Rudolf has been estimated as 18,000-30,000 eggs, and may be much greater, depending on the actual size of the breeding population. Taking, for the sake of argument, a mean of 24,000 eggs this represents 14,000 hatchlings (68.6% hatching rate). At the growth rate indicated in Figure. 7 this would represent a gross production of 323,000 kg of crocodile at 15 years of age. The value, at this age, of Rudolf crocodiles is Kenya shillings 3.24 per kg (Figure. 14), giving a total value of Shs. 1,046,520 (£50,000). If the growth rate were raised to that shown in Figure. 12 then this same amount would be produced in 6 years.

It is interesting to compare this with the value of elephant, the only other East African wild animal apart from hippopotamus and some fish for which a realistic value has been created, although this value is not always realisable due to marketing problems. At 15 years an elephant is worth up to Shs. 2.70 per kg (Wildlife Services Ltd., unpublished data), but the overall value of this species is greater due to its more rapid growth (Laws 1966).

The actual crocodile crop realisable by man is the proportion of gross productivity remaining after recruitment the breeding population has been satisfied (which may be as little as 0.8% of those hatching), and natural mortality up to the age of cropping. Maximising the crop thus consists of reducing the high immature mortality. Le Cren (1962) bas shown that in some freshwater fishes recruitment tends to be the same regardless of the numbers of eggs produced, and that the efficiency of the reproductive and recruitment process in fish is inversely related to population density so that cropping at the correct level results in an increased yield, by relieving the pressure of density. A certain amount of immature mortality in the wild state is probably inevitable and has to be taken into account. There is also the possibility that survival from year to year is very variable as has been demonstrated in a variety of other animals. On Rudolf there may be increased survival in very young animals in years when there is an unusual rise in lake level, resulting in large areas of inundated bush and grass providing shelter and good feeding conditions for small crocodiles (see plates at end).

There are several ways in which immature mortality might be reduced. In Figure. 13 a high rate of mortality from hatching right up to maturity is shown, but it is likely that in reality mortality soon after hatching is much higher and conversely much lower thereafter, as has been observed in birds (Lack 1954) and in many fish and invertebrates with high reproductive rates. A possible way of reducing this sort of mortality is to collect and hatch eggs artificially and only release the young animals after a period of growth that could be expected to leave them less available to predators and more experienced in movement and feeding. Simply ensuring that the young animals are released into a favourable environment would improve survival in those animals that would, under natural conditions, have hatched into unsuitable situations such as most of the west shore of Rudolf, or the large, isolated islands. There is also the alternative of maintaining the animals in captivity right up to the point at which they are harvested, although there are indications that such crocodile "farming" may be economically unfeasible (Parker 1967, unpub. report to the Kenya Game Department). As already mentioned, cropping, will in it itself, relieve pressure on density-dependent mortality, particularly if young animals are cropped.

6c Crocodile management on Rudolf

Since the continued survival of crocodiles on Rudolf may depend upon their competing with other forms of utilization of the lake, such as the growing fishing industry, it is necessary to consider how their exploitation might best be carried out.

Cropping

Some of the reasons for cropping those age classes approaching maturity have been considered. There are other reasons why this may be desirable. If adult animals are cropped then an essential requirement is that cropping operations be confined to the quiescent phase of the reproductive cycle, or serious interference with the reproductive rate is likely to result. This means that the 8-month period October-May, which includes most laying, incubation and hatching, must be a closed season. Cropping of immature animals on the other hand would interfere little with reproduction, although the 4 months February-May when the females are unearthing their nests is probably best kept a closed season at all times, particularly since some of the animals cropped will include recently matured females, even if the maximum length is kept below 200 cm.

Cropping young animals takes maximum advantage of the high rate of immature growth, and the still-rising skin values which stabilize after a length of 190 cm.

The imposition of an upper size limit in the vicinity of 200 cm will introduce the danger of over-cropping females since the faster growth rate of males will leave them underrepresented in these size (as distinct from age) groups. This would have to be carefully monitored. There are important practical advantages in cropping young animals related to the fact that the conduct of a cropping operation is facilitated by both a constant size of product, and small unit size. In the field it is easier to train hunters to pick a consistent size group of animals than to select precise numbers of certain different sizes. Large animals are disproportionately difficult to handle and skin and are awkward to pack and transport.

Although the basis of the crop would consist of young animals analysis of the adult age structure might indicate some initial adjustment to maximise production. Some cropping of adults will be inevitable. The "control" of crocodiles by the Game Department in response to the danger to human life and damage to fishing gear that crocodiles cause, presently involves the killing of several hundred animals a year, many of them adults. Illegal hunting removes an unknown but possibly significant number of adults per year. A certain quota of large males should be set aside for sport hunting since this is an important element in the tourist use of the lake. Removal of these animals probably has little effect on the stock since their expectancy of further life is short. All these activities may combine to remove all the permissible adults of the crop, leaving the specifically commercial operation confined to young animals.

A practical consideration which must be included is that 70.9% of the lake‘s crocodiles occur on the east shore where the present political uncertainties may inhibit operations. The extreme north end of the lake is in Ethiopia with about 8% of the population. The rest of the lake falls under two different administrative areas, Marsabit and Turkana.

Egg production

The other obvious form of exploitation is to consider the lake as a potential source of eggs, either to support a crocodile farming industry, or for export to other areas to augment depleted stocks. The estimated annual production of 26,000 eggs makes this a potentially sizeable prospect. The very strong possibility that crocodile breeding on North, Central and South Islands contributes nothing to recruitment makes them an ideal source of easily found eggs.

Section 7. Conclusions

Although further information is required, the results of this work strongly suggest that Rudolf crocodiles presently exist at maximal densities, evidenced by a depressed growth rate, stunted size, small size of breeding females and small size at maturity.

Within Lake Rudolf distribution is seen to relate closely to environmental conditions. "Shelter”, in the form of shallow water, undisturbed by wind and with some cover provided by vegetation is essential. Such localities invariably contain relatively high densities whereas exposed shorelines, or those subject to the effects *of* wind, invariably support low densities. This results in an accumulation of animals in the more favourable situations, producing the situation on Rudolf where 70.9% of the population inhabits the east shore, the whole west side being exposed to the persistent easterly wind. Although considerable movement of individuals is thought to take place, occupance of favoured areas is at continuous high levels. The dependence of crocodiles on the shore and the shallow water near it effectively limits them to a relatively small area of habitat, on Rudolf approximately 2% of the lake’s surface area. Thus density in terms of biomass per unit area may be high with apparently low numbers of individuals.

The observed low incidence of food-containing stomachs suggest that a primary agent limiting density is food availability, although it may be that when overcrowded crocodiles feed less frequently, thus depressing individual growth. Whatever the causes, it seems that Rudolf crocodile numbers have exceeded that which can exploit the food source optimally, which has been compensated for by depressed growth that in turn has led to a lowered reproductive rate.

In planning the future of the population an important consideration is that in a rapidly developing environment, management priorities cannot always wait for the completion of ideal long-term research programs. The solution may be a compromise in which carefully planned exploitation, based on the indications of this initial survey, is accompanied by research aimed at monitoring the effects of exploitation and finding ways of maximising it. It is certain that unplanned, uncontrolled exploitation will produce the same result as it has in other East African waters where something close to total extinction was achieved in a very short space of time. Examples are Lake Rukwa in Tanzania, Lakes Victoria, Kioga and Albert in Uganda, the Semiliki River and much of the Nile: the Tana and Athi rivers in Kenya and more recently Lake Baringo. Thus, sustained cropping of adult animals offers little economic prospect due to slow growth and relatively small population size. But cropping young animals, supplemented by artificial reduction of immature mortality, shows promise. Enough information is available to draw up a management program based on these indications, and which could be, at least in part, self-financing.

Proper cropping in a wider sense may be a highly desirable adjunct to any conservation policy aimed at maintaining viable animal communities, by adjusting the age structure and density so that reproductive and growth rates are maximised. This results in a more vigorous population better able to withstand catastrophe or unfavourable conditions and to respond to favourable conditions.

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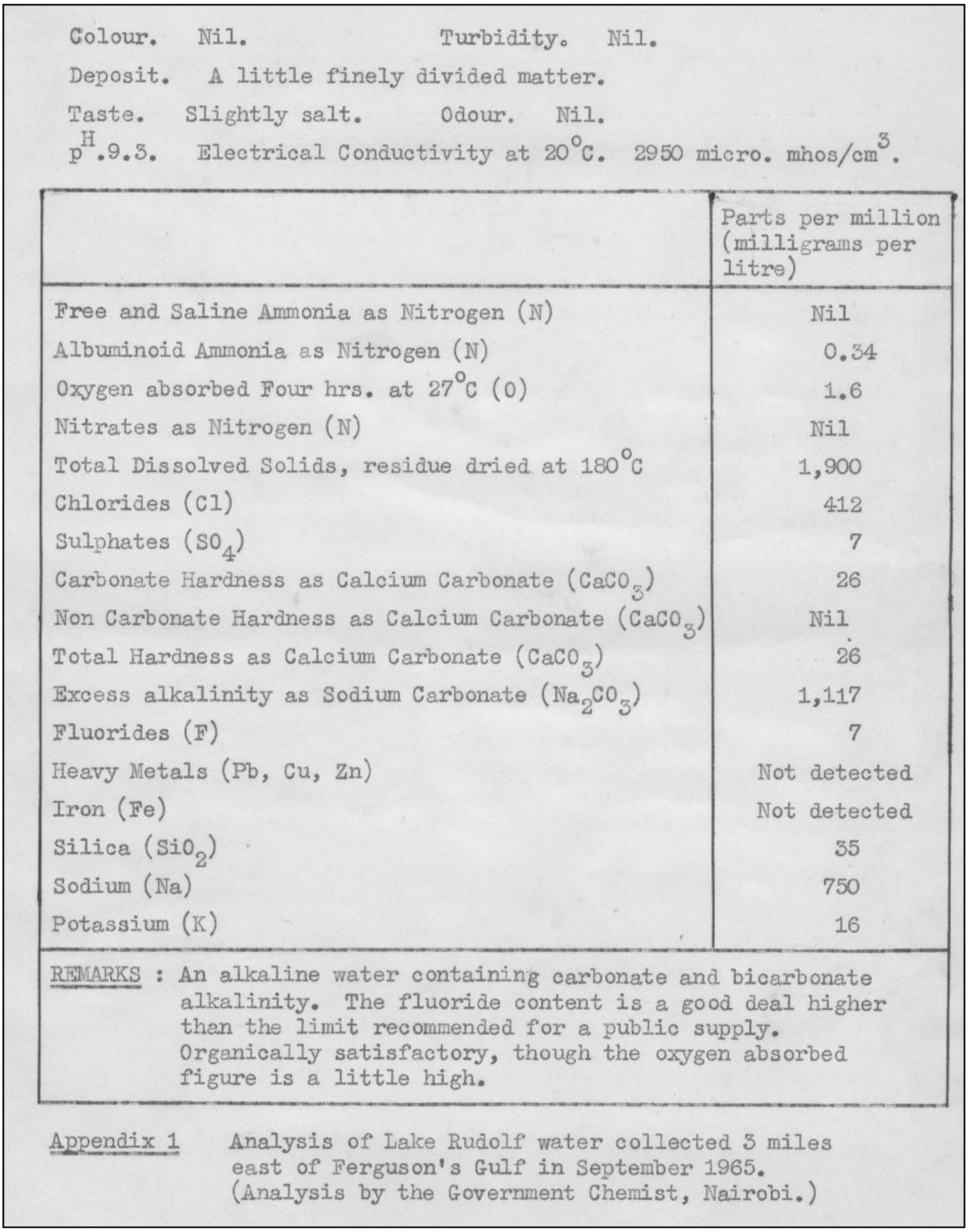
Appendix 1. Water analysis



Colour. Nil. Turbidity. Nil.

Deposit. A little finely divided matter.

Taste. Slightly salt. Odour. Nil.

p^H.9.3. Electrical Conductivity at 20°C. 2950 micro. mhos/cm^3.

	Parts per million (milligrams per litre)
Free and Saline Ammonia as Nitrogen (N)	Nil
Albuminoid Ammonia as Nitrogen (N)	0.34
Oxygen absorbed Four hrs. at 27°C (0)	1.6
Nitrates as Nitrogen (N)	Nil
Total Dissolved Solids, residue dried at 180°C	1,900
Chlorides (Cl)	412
Sulphates (SO_4)	7
Carbonate Hardness as Calcium Carbonate ($CaCO_3$)	26
Non Carbonate Hardness as Calcium Carbonate ($CaCO_3$)	Nil
Total Hardness as Calcium Carbonate ($CaCO_3$)	26
Excess alkalinity as Sodium Carbonate (Na_2CO_3)	1,117
Fluorides (F)	7
Heavy Metals (Pb, Cu, Zn)	Not detected
Iron (Fe)	Not detected
Silica (SiO_2)	35
Sodium (Na)	750
Potassium (K)	16

REMARKS : An alkaline water containing carbonate and bicarbonate alkalinity. The fluoride content is a good deal higher than the limit recommended for a public supply. Organically satisfactory, though the oxygen absorbed figure is a little high.

Appendix 1 Analysis of Lake Rudolf water collected 3 miles east of Ferguson's Gulf in September 1965. (Analysis by the Government Chemist, Nairobi.)

Appendix 2.

Two counts made to illustrate the high density of small crocodiles on Lake Rudolf.

Count 1. Allia Bay, mid-March 1966 at 2020 hours. Swamp east of sandbank.
A single 180° sweep of a Hunter 6V torch from the water's edge, dark night, no wind i.e. calm water & good conditions for seeing crocodiles. 126 crocodiles, mostly small, but no hatchlings.

Count 2. A quarter of a mile further along the shore same evening a 90° sweep returned 94 crocodiles.

The maximum distance a Hunter lantern with new battery can get a reflection off a crocodile's retina is 180 yards. Effective distance (not all animals will be perfectly positioned to reflect) is less.