Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia

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(With 9 plates and 45 figures in the text)

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Synopsis

During the past decade the Nile Crocodile has been greatly reduced in numbers. Scientific information on the general and breeding biology was deficient and research urgently required to ascertain the possible effects on fisheries of further drastic reduction by commercial exploitation. The results reported are based upon observations made in Uganda, Northern Rhodesia, Barotseland and Zululand during 1952, 1956 and 1957.

The diurnal rhythm of activity is related to feeding and thermal requirements. Thermoregulation, at about 25·5° C., is effected by habitat selection and behavioural adaptation. Information is given on terrestrial and aquatic locomotion, respiration and diving times. Evidence is presented that stomach stones, always present in the adult, are deliberately swallowed and subserve hydrostatic functions. Rate of growth is most rapid, about 265 mm. per annum, in early life : it decreases progressively to about 35 mm. per annum or less. The sexes are equal in numbers : the males grow more rapidly and attain larger size than the females.

Sexual maturity is attained at a length of about 2·9 to 3·3 metres in the male, and about 2·4 to 2·8 metres in the female, and at an estimated age of not less than nineteen years. The breeding season, which differs with locality, coincides with the period of low water levels. Aspects of breeding behaviour in the male, including territorial defence, combat and vocalization are discussed. A pre-nuptial display in the female and inititial stages of copulation have been observed. An account is given of colonial nesting grounds, nest sites, clutch sizes and parental care by the female. Juveniles are ecologically separated from the adults.

A detailed survey is made of the food and feeding habits : the diet is extremely varied ; it changes progressively with the crocodile's age ; and differs according to locality. Data relating to predatory enemies, parasites and injuries, and an account of commensal relations with three species of birds, are given. Attention is drawn to the complex web of relationships in which the species plays a part as master predator, cannibal and scavenger : its status in relation to man and to commercial fisheries is reassessed. It is concluded that *C. niloticus* is a valuable member of the African fauna ; and recommendations are made for its conservation.

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INTRODUCTION

The trade in crocodile leather has in recent years grown to the proportions of almost a major industry in various East and Central African territories, from which thousands of skins are exported each month. As a result of this commercial exploitation, the Nile crocodile is being rapidly reduced and in some localities its continued existence is threatened.

Meanwhile surprisingly little scientific information has been published on its general biology and economic status. Further research was clearly needed in order to assess the probable effect which extermination or drastic reduction of crocodiles may have in the economy of inland waters and in particular on commercial fisheries.

At the invitation of the Government of Northern Rhodesia, and with this problem in view, a survey was undertaken in 1956 in the swamps of Bangweulu and Mweru Wa Ntipa in the Northern Province. The following year the investigation was continued in the riverine habitats of the Luangwa, Kafue and Upper Zambesi valleys in the Central and Southern Provinces, and Barotseland. Previous work had already been carried out in Uganda in 1952, and was continued during subsequent visits to Uganda, and in Zululand.

LOCALITIES AND MATERIAL

The results to be discussed in the following pages rest upon two types of information, namely : that derived from observation of free-living crocodiles ; and that from the examination of freshly-killed material.

Observations on crocodiles in the natural state were mostly made along the eighteen-mile reach of the Victoria Nile from Murchison Falls to the Lake Albert delta. These waters support a concentration of crocodiles which, in number and size, is probably unrivalled today anywhere in Africa. The area thus provided an ideal base for ecological studies and photography. The work was carried out during four visits: in July and December, 1952 ; June to August, 1956 ; and December to January, 1957. Camps and nearby observation posts were established at various points below the Falls and above Magungu in specially favoured localities where large concentrations of the reptiles were available for undisturbed, close-range study from hides. Further observations were made in the Hluhluwe, Umfolozi, Ndumu and St. Lucia Game Reserves of Zululand. A detailed photographic record was obtained. Some of the results (of which only a few appear here) showing crocodiles in their pristine state, are of special interest because—as a result of hunting, poaching and general disturbance—the scenes they depict are rapidly disappearing.

These studies were supplemented by the examination of a large series of specimens in Uganda, Rhodesia and Barotseland. A standard routine was developed for the examination of material—it being necessary to systematize procedure since in the heat of the tropics crocodiles had to be skinned with the least possible delay. Each specimen of the night's catch was first toe-marked, and a serial number assigned to it. All data were set down on printed Record Sheets, one for each crocodile examined. Prior to skinning, about forty measurements of various parts of the body were taken with steel-tape and calipers. (Such measurements were required for studies of relative growth and—apart from the key-measurement of total length from snout to tail-tip—will not be considered in the present paper). Other information recorded at this stage included notes on external characters, scute- and tooth-counts, abnormalities, injuries, the location and density of leeches; and specimens small enough were weighed entire on a spring-balance or yard-arm. In the case of large crocodiles the skin was weighed separately and the carcass dismembered and weighed in parts. After the skinners had completed their task, the stomach was removed, opened in a basin, and flushed with water prior to examination of its contents. The weight of stomach stones was recorded; and the sex and state of the reproductive organs and the presence of parasites noted. A complete examination of every crocodile was not always possible: in particular, information on internal parasites and on the condition of the gonads is often wanting. On the other hand, in all cases full information was recorded for stomach contents; and the above-mentioned pre-skinning routine was nearly always carried out in full.

Five hundred and seventy-six crocodiles were examined by the writer in the course of the investigation. Serial numbers, with dates and localities for this material, are listed below. The information thus obtained, together with some additional records on stomach stones and prey organisms received from other sources (see pp. 236, 278) is set out and discussed in the relevant sections of the report.

UGANDA

Lake Victoria:	Sese Is.: 2 (16 Jan.), 101 (10 Nov. 1952).
	Damba Channel: 70–73 (2–4 Sept. 1952).
	Bukafu Bay: 64–67 (28–29 Aug. 1952).
	Nsadsi: 68 (1 Sept. 1952).
	Bulago: 69 (2 Sept. 1952).
	Buka Bay: 75–79 (4 Sept. 1952).
	Masovwe: 74, 80 (4–5 Sept. 1952).
	Buvu: 100 (9 Nov. 1952).
	Buluba Bay: 43–63 (22–25 Aug. 1952).
	Napoleon Gulf: 1 (9 Jan.), 8 (27 Mar.), 9 (2 April), 11 (8 April), 42 (22 Aug.), 82–94 (6–8 Oct.), 103 (7 Dec. 1952).
Lake Kioga:	Kigi Is.: 4–7 (4–7 Mar. 1952).
Victoria Nile:	Jinja: 3 (5 Feb.), 27 (8 July), 38–41 (7–22 Aug.), 81 (12 Sept. 1952).
	Namasagale: 10 (5 April), 95–99 (29–30 Oct. 1952).
	Fajao: 32–37 (21–24 July 1952).
	Magungu: 28–31 (17–19 July 1952), 106–109 (1–6 Aug.), 222 (29 Dec. 1956), 223 (2 Jan. 1957).
Lake Albert:	Butiaba: 102 (22 Nov.), 104, 105 (17 Dec. 1952).
	Kaiso: 20–26 (22–23 June, 1952).
	Ntoroko: 14–19 (15–21 June 1952).
Semliki River:	Bweramule: 12, 13 (15–23 April 1952).

NORTHERN RHODESIA	
Bangweulu Swamp :	L. Kinweshewa : 110 (17 Aug. 1956).
	Panta Point to Chilubi : 111–115 (19 Aug.), 157 (6 Sept. 1956).
	Lake Chali : 116–119 (21 Aug.), 156 (30 Aug. 1956).
	Kansenga : 120 (21 Aug. 1956).
	Miloki : 121–123 (22 Aug. 1956).
	Bwalya Mponde : 124–135 (23–25 Aug. 1956).
	Mutwamina : 136–146 (26 Aug. 1956).
	Matongo : 147–155 (27 Aug. 1956).
Mweru Wa Ntipa :	158–208 (12–15 Sept. 1956).
Kalungwishi River :	Ollandi : 209–220 (18–19 Sept. 1956).
Luangwa Valley :	Lunsemfwa R. west of Rufunsa : 224–243 (2–3 Aug. 1957).
	Lunsemfwa R. east of Rufunsa : 244–257 (4–5 Aug. 1957).
	Musukwe Lagoon : 258 (5 Aug. 1957).
	Lower Lunsemfwa R.: 273–282 (9 Aug. 1957).
	Luangwa R., Beit Bridge : 259–272 (7 Aug. 1957).
	Luangwa R., Nytande : 283–301 (11 Aug. 1957).
	Luangwa R., Ndevu : 302–320 (13–14 Aug. 1957).
Kafue Flats :	Chembe : 321–322 (22 Aug. 1957).
	Nampongwe R.: 323–336 (23 Aug. 1957).
	Luwato R.: 337–339 (24 Aug. 1957).
	Lochinvar Swamp : 340–363 (25 Aug. 1957).
	Chimwajila : 364–373 (26 Aug. 1957).
	Iyeshya : 374–412 (29 Aug. to 1 Sept. 1957).
BAROTSELAND	
Upper Zambesi :	Mongu to Lukulu : 413–428 (10 Sept.), 437–448 (12 Sept.), 481–499 (15 Sept. 1957).
	Mongu to Senanga : 429–436 (11 Sept.), 449–480 (13–14 Sept.), 500–576 (16–20 Sept. 1957).
ZULULAND	
St. Lucia :	221 (24 Oct. 1956).

PART I. GENERAL BIOLOGY

Diurnal activity rhythm

The diurnal movements of the Nile Crocodile have been remarked upon since ancient times. Thus, Pliny (Holland, 1601) observed : "All the day time the Crocodile keepeth the land, but he passeth the night in the water." But information of a more than anecdotal character on behaviour in relation to the diurnal cycle is extremely scanty. The observations here described are of two kinds—general, and counts made from observation posts.

General observations

Numerous observations made at different hours of the day and night, along the Murchison reach of the Nile between Fajao and Magungu, in the Lower Semliki, and Lakes Albert, Kioga and Victoria, provide a general picture of the activity rhythm in tropical waters. The combined data, for crocodiles lying (i) on land, (ii) with part of the body in the water, and (iii) in water, are given in Table 1, and expressed graphically in Fig. 1.

The crocodile is nocturnally aquatic. Movement to the water has already begun before sunset, and during the hours of darkness virtually the whole population is afloat. My Uganda records for the hours between midnight and dawn are few; but the results are fully confirmed from Northern Rhodesian specimens—almost

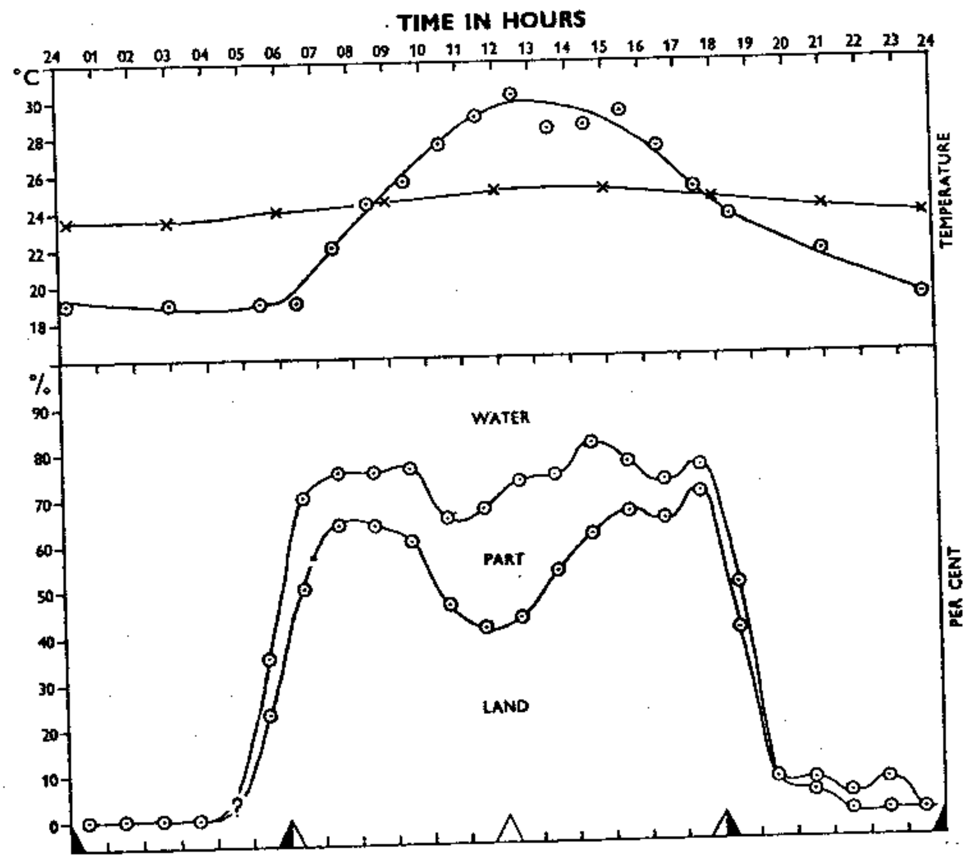

Fig. 1. Diurnal activity rhythm: showing, for hourly periods, the percentage of crocodiles counted ashore, partly in the water, and in the water. Mean shade and water temperatures are shown above.

all of which were shot in the water at night. Mr. H. Holloway, who has hundreds of night-long hunts to his credit, tells me that in his experience perhaps one in thirty crocodiles may be seen lying out on grass or papyrus at night, though the tendency to come ashore is more noticeable in rough weather (see p. 233).

The general movement from water to land begins in the hour before sunrise: thereafter the egress is rapid and by about 0730 hrs. (sun time) three-quarters of the population will have hauled out. There are two main basking periods—in

TABLE 1

Number of crocodiles counted lying ashore, partly in the water, and in the water, by hourly periods.

Time	*Land*		*Part*		*Water*	
	No.	*Percentage*	*No.*	*Percentage*	*No.*	*Percentage*
2400–0100	0	0·0	0	0·0	6	100·0
0100–0200	0	0·0	0	0·0	7	100·0
0200–0300	0	0·0	0	0·0	3	100·0
0300–0400	0	0·0	0	0·0	3	100·0
0400–0500	—	—	—	—	—	—
0500–0600	6	23·1	3	11·5	17	65·4
0600–0700	129	50·4	50	19·5	77	30·1
0700–0800	631	63·7	116	11·7	244	24·6
0800–0900	750	63·8	139	11·8	286	24·3
0900–1000	649	60·4	170	15·8	256	23·8
1000–1100	405	46·2	167	19·0	305	34·8
1100–1200	349	41·5	213	25·4	278	33·1
1200–1300	438	43·1	307	30·2	272	26·7
1300–1400	558	53·5	215	20·6	270	25·9
1400–1500	792	61·1	259	20·0	245	18·9
1500–1600	597	66·3	94	10·4	210	23·3
1600–1700	519	64·6	64	8·0	220	27·4
1700–1800	29	70·7	2	4·9	10	24·4
1800–1900	3	30·0	1	10·0	6	60·0
1900–2000	2	7·7	0	0·0	24	92·3
2000–2100	2	4·7	1	2·3	40	93·0
2100–2200	0	0·0	2	4·2	46	95·8
2200–2300	0	0·0	2	7·4	25	92·6
2300–2400	0	0·0	0	0·0	13	100·0

the morning between 0700 and 0930 hrs., and in the afternoon between 1430 and 1730 hrs. In the heat of the day when the sun is high and shadows are short, there is a secondary movement back to the water, and by midday only about 40 per cent. of individuals are seen ashore. After the second basking period there is a rapid return to the water: this movement begins about half an hour before sunset, and as darkness falls the grounds are once again deserted.

Observation posts and crocodile counts

To obtain more precise information on activity during the daylight hours, in relation to environmental factors, observation posts were established at two selected sites where crocodiles were both plentiful and relatively free from disturbance. Their location is shown in a sketch map (Fig. 2) largely based upon air photographs supplied by the Directorate of Overseas Surveys.

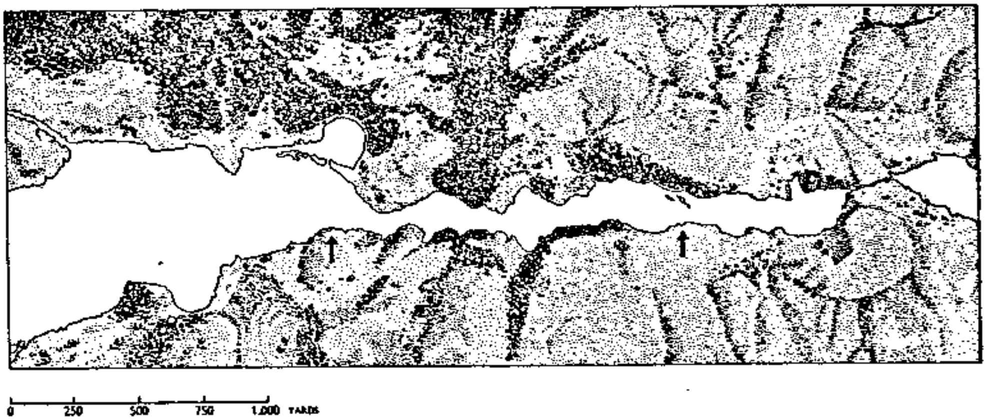

Fig. 2. Sketch map of the Victorial Nile below Murchison Falls. The arrows indicate the position of observations posts : left, Fajao O.P.; right, Murchison Falls O.P.

Murchison Falls O.P.

This observation post was situated on the steep south bank of the Nile, overlooking two rock islets about 850 yards below Murchison Falls (Plate 1, fig. 2). The elevated vantage point afforded a clear view not only of crocodiles ashore and awash round the islets and on a sector of the tree-shaded bank opposite, but also, owing to the narrowness of the river (about 120 yards) and clarity of the water, those which were keeping station against the current or lying submerged in shallows. The reptiles were entirely free from human interference, since the place was inaccessible by launch.

Fajao O.P.

The second post was on a hill top east of Fajao jetty, overlooking the Nile where it broadens from the hill-girt gorge into an estuary some 350 yards wide. This station commanded, at rather long range, a broad view of the north bank—embracing several isolated basking places, a large sand-spit, a lagoon, and an important sunning and breeding ground below the escarpment. The site offered a great concentration of crocodiles—the largest number counted *ashore* at one time being 158.

Crocodile counts

At Murchison O.P. counts of crocodiles lying (i) ashore, (ii) partly in and partly out of the water, and (iii) afloat or submerged, were recorded for each 15-minute observation period from 0700 to 1700 hrs. on the 8th, 10th and 12th July, 1956, and 4th Jan. 1957. The general state of the weather and the air temperature (shade) were also recorded for each observation period (see Table 2, and Fig. 3, a to d).

TABLE 2

Data for four ten-hour observation periods at Murchison O.P.; showing the number of crocodiles counted : *L*—lying ashore ; *P*—with part of the body in the water ; and *W*—in the water.

Time	*8.7.56*				*10.7.56*				*12.7.56*				*4.1.57*			
	Temp.	*L.*	*P.*	*W.*	*Temp.*	*L.*	*P.*	*W.*	*Temp.*	*L.*	*P.*	*W.*	*Temp.*	*L.*	*P.*	*W.*
0705	21·0	12	0	14	22·0	32	4	12	20·0	10	1	25	23·0	5	4	3
0720	—	5	2	14	23·0	31	5	9	21·0	10	4	23	22·5	7	5	5
0735	20·0	5	2	19	24·0	34	6	13	22·0	10	5	19	23·5	6	5	4
0750	—	5	3	22	24·0	31	4	11	22·5	9	2	20	24·0	6	4	7
0805	20·5	6	3	20	25·0	33	2	15	24·0	9	4	11	26·0	6	3	7
0820	—	7	3	25	25·5	27	4	12	25·0	9	6	4	25·5	5	3	6
0835	21·0	8	2	19	26·0	31	5	10	26·5	9	5	12	25·0	5	3	7
0850	—	9	6	23	26·0	30	7	14	27·5	10	8	11	26·0	4	3	11
0905	21·0	9	5	26	27·0	31	5	11	29·0	11	5	22	25·5	2	4	10
0920	—	8	9	18	27·0	32	6	12	29·5	9	2	7	27·5	2	5	10
0935	21·5	8	7	24	29·0	29	5	10	29·0	3	0	14	27·0	0	2	10
0950	—	8	5	18	29·5	28	4	9	28·0	0	0	14	28·0	0	0	9
1005	21·5	8	2	32	30·0	23	4	12	29·5	0	0	13	27·5	0	1	8
1020	—	8	2	30	31·5	25	6	18	30·5	1	0	14	28·5	0	1	8
1035	23·0	9	8	13	32·0	24	8	10	31·0	0	0	10	27·5	0	0	11
1050	—	10	6	17	33·0	21	4	15	31·0	0	0	12	30·5	0	1	9
1105	24·0	9	11	4	33·5	22	6	13	32·0	0	1	14	29·0	0	0	10
1120	—	10	7	12	35·0	16	9	17	33·0	0	0	11	26·5	1	3	7
1135	25·5	11	3	16	29·5	15	6	14	33·0	0	0	9	27·0	2	3	9
1150	—	10	2	13	30·0	15	8	15	34·0	3	3	7	28·0	2	5	5
1205	26·0	11	2	10	31·0	16	5	15	34·5	5	4	12	28·5	2	4	8
1220	—	11	3	15	35·5	15	4	16	35·0	11	5	8	29·0	2	5	9
1235	27·5	10	3	16	32·0	14	6	15	35·0	19	9	4	29·5	2	5	8
1250	—	10	3	9	31·0	12	2	15	36·0	19	9	5	29·0	1	6	8
1305	27·0	9	3	12	31·0	12	3	17	31·5	20	3	14	28·0	2	4	8
1320	—	9	2	11	31·0	14	4	21	30·0	19	5	14	23·5	2	2	10
1335	27·0	14	3	8	30·5	15	2	17	30·0	23	5	8	23·0	2	4	12
1350	—	17	5	8	30·0	14	2	20	28·5	24	4	13	23·5	2	2	10
1405	27·0	14	3	11	29·5	11	3	20	30·0	28	7	10	26·5	4	5	6
1420	—	14	2	9	31·5	13	3	13	27·0	33	7	4	27·0	5	6	2
1435	24·0	16	2	33	33·0	15	4	12	27·0	37	6	10	27·5	4	7	2
1450	—	15	2	21	32·0	17	5	10	31·0	34	5	9	28·0	2	6	6
1505	24·0	13	2	16	34·0	18	3	14	32·5	35	8	3	29·0	3	4	8
1520	—	13	2	12	32·0	18	4	15	29·0	38	8	3	29·0	3	4	5
1535	25·0	12	3	5	31·0	18	2	16	29·0	37	7	2	28·0	3	1	9
1550	—	13	2	11	30·0	18	2	11	29·5	39	7	3	27·0	3	1	8
1605	25·0	12	2	12	27·0	15	2	13	28·0	40	7	3	26·5	2	1	10
1620	—	14	0	12	28·0	15	2	17	29·5	38	7	4	27·0	2	0	14
1635	24·5	11	1	13	27·0	14	2	19	29·5	39	8	3	26·5	2	0	13
1650	—	13	1	9	26·5	13	2	15	30·0	38	7	4	26·5	2	0	11

At Fajao O.P. similar observations were made over dawn and dusk, and midday periods, on the 14th and 15th July, respectively ; from 0600 to 1445 hrs. on the 16th July, 1956, and from 0700 to 1700 hrs. on the 5th January, 1957. Owing to distance and difficulties of terrain, counts of crocodiles in the water, where recorded, include only those seen swimming at the surface. It is not claimed that records of crocodiles seen ashore from this post include all that were present ;

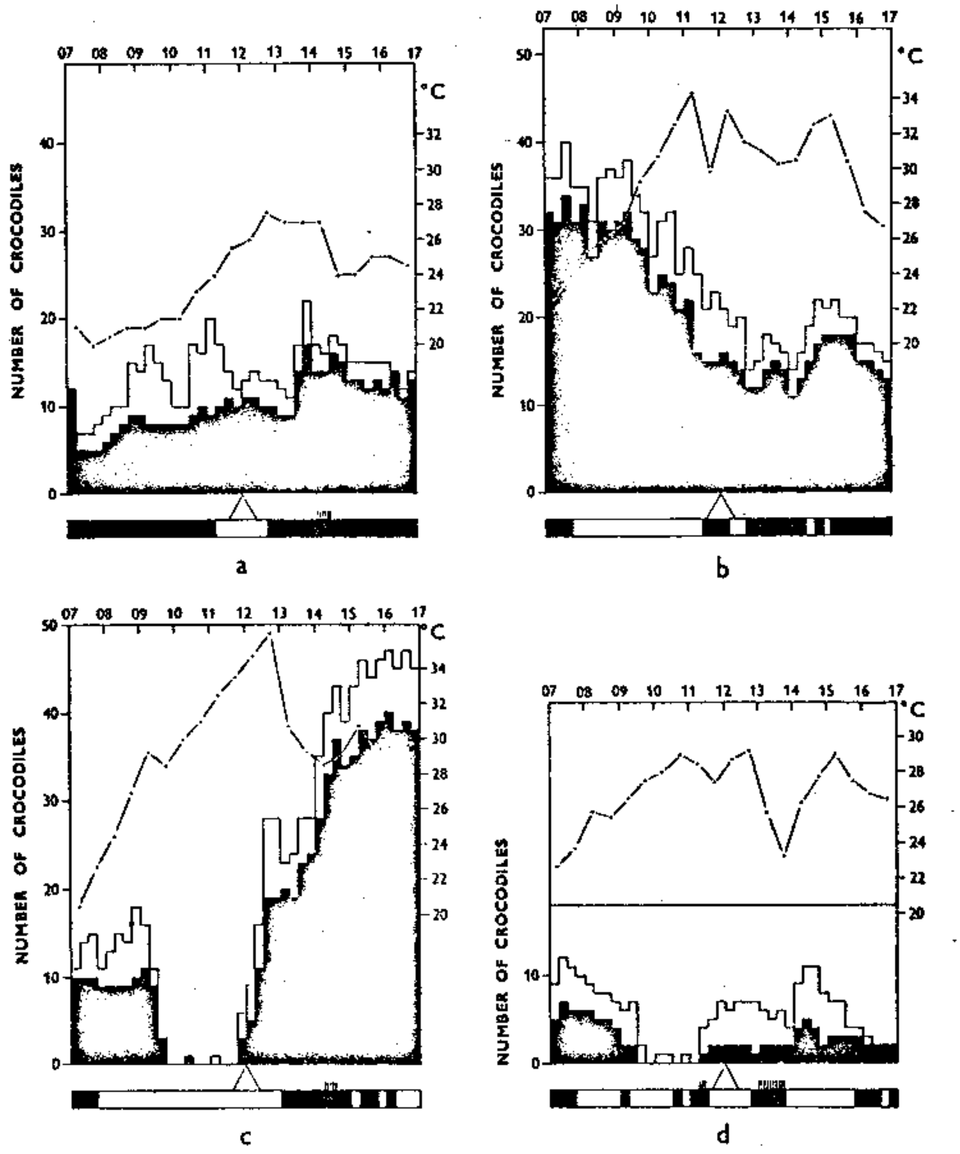

Fig. 3. Murchison O.P. (a) 8.7.56 ; (b) 10.7.56 ; (c) 12.7.56 ; (d) 4.1.57. Number of crocodiles counted per quarter-hour periods : black histogram—crocodiles lying ashore ; white histogram—crocodiles lying partly in and partly out of the water ; above—the greatest number of crocodiles counted in the water during any observation period. The lower strip indicates insolation ; white—clear sky ; black—overcast ; grid—rain. Shade temperatures are shown in the graph.

but errors of omission would be spread over all observation periods and so would not materially affect the observed pattern of activity (see Table 3 and Fig. 4, a to c).

These observations and the light they throw upon behavioural thermal control are discussed in the following section.

TABLE 3

Data for observation periods at Fajao O.P.; showing the number of crocodiles counted : *L*—lying ashore ; *P*—with part of the body in the water ; and *W*—in the water.

14.7.56		
Time	*Temp.*	*L.*
0550	17·5	9
0605	19·0	27
0620	18·0	50
0635	18·5	56
0650	19·0	58
0705	20·0	69
0720	20·5	70
0735	22·0	78
0750	24·0	94
0805	24·0	89
0820	25·5	103
0835	27·0	105
—	—	—
1620	27·5	158
1635	27·0	141
1650	26·5	149
1705	26·0	149
1720	25·5	143
1735	25·0	116
1750	25·0	115
1805	25·0	94
1820	24·5	84

15.7.56		
1135	29·0	38
1150	29·5	30
1205	30·0	26
1220	28·5	29
1235	30·5	33
1250	30·0	36

16.7.56			
Time	*Temp.*	*L.*	*P.*
0605	18·0	33	17
0635	18·5	62	20
0705	20·0	75	20
0735	23·0	96	16
0805	24·0	100	20
0835	24·0	107	19
0905	25·0	114	25
0935	26·5	121	26
1005	27·0	77	24
1035	27·5	51	34
1105	29·5	55	38
1135	28·0	65	43
1205	29·0	77	52
1235	30·0	83	55
1305	27·0	112	55
1335	27·0	133	58
1405	27·0	132	68
1435	28·5	131	66

5.1.57				
Time	*Temp.*	*L.*	*P.*	*W.*
0705	22·5	48	6	4
0720	22·0	58	2	1
0735	21·5	51	4	3
0750	22·0	48	6	2
0805	23·0	48	5	1
0820	24·0	42	7	3
0835	25·0	42	5	7
0850	25·5	38	5	4
0905	25·0	40	9	5
0920	26·0	39	9	9
0935	26·0	34	7	9
0950	28·0	33	9	2
1005	28·0	28	10	6
1020	28·0	20	7	9
1035	29·0	12	9	11
1050	30·0	12	12	16
1105	29·5	10	10	8
1120	30·0	9	8	10
1135	30·5	8	6	13
1150	30·5	6	6	11
1205	31·5	8	7	11
1220	30·0	8	6	15
1235	33·0	6	5	13
1250	33·5	9	6	24
1305	33·0	3	14	13
1320	32·0	15	8	16
1335	31·0	18	8	16
1350	30·0	19	7	18
1405	32·5	30	7	16
1420	33·0	40	7	18
1435	30·5	45	6	9
1450	31·0	43	6	9
1505	31·5	44	8	7
1520	31·5	44	8	12
1535	31·0	43	5	17
1550	30·5	53	5	14
1605	29·0	55	5	13
1620	29·0	55	4	11
1635	29·0	55	4	10
1650	28·0	54	4	11

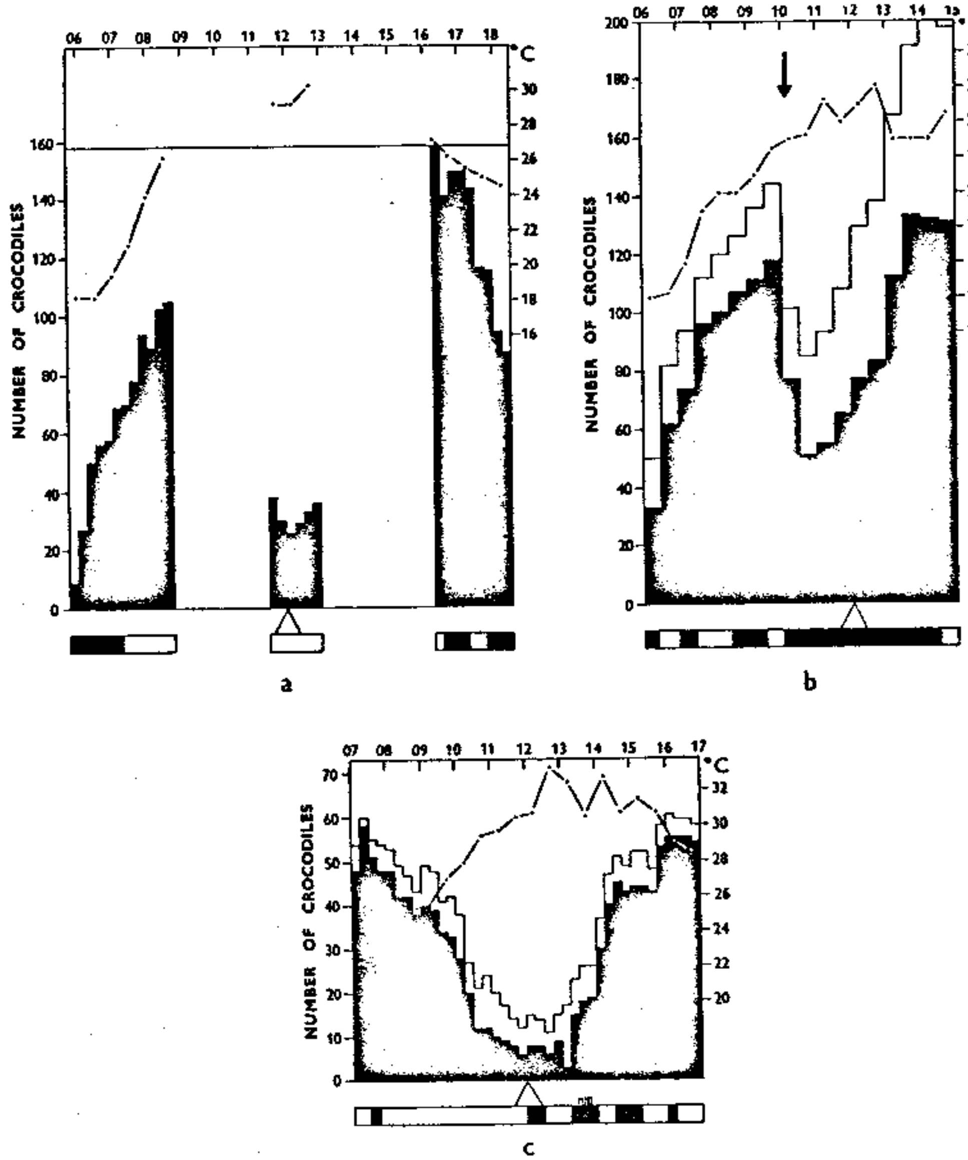

Fig. 4. Fajao O.P. (a) morning and evening, 14.7.56; midday, 15.7.56; (b) 16.7.56; (c) 5.1.57. Data are recorded as in Fig. 3. The arrow in (b) indicates disturbance caused by the arrival of a launch.

Thermoregulation

Many physiological experiments have been carried out with large reptiles—such as those by Isserlin (1902), Benedict (1932), Herter (1940), Colbert, Cowles & Bogert (1946) and Kirk & Hogben (1946)—to investigate the influence of thermal and other environmental factors upon body temperature. But the laboratory cannot reproduce the varied conditions obtaining in the natural habitat ; and as Bogert remarks, the ways of controlling temperature in these tests are available to the experimenter but not to the animals used. In nature the reverse is true : a wild crocodile is free to choose conditions which meets its immediate and varying thermal requirements.

The present observations demonstrate the important part played by habitat selection and behavioural adaptation in the free-living animals.

Body temperature of crocodiles

Cloacal temperatures of crocodiles recorded immediately after they had been shot are given in Table 4. Although the sample is too small to indicate reliably the thermal range, yet the records—taken as they are from animals shot under widely different conditions, and by day and night—point to a remarkable degree of thermal control.

Table 4

Date	*Locality*	*Serial No.*	*Sex*	*Length in m.*	*Place*	*Time*	*Temperature*			
							cloaca	*air, shade*	*substratum*	*water*
6. 8.56	Magungu, Victoria Nile	109	♂	3·69	mud-bank in sun	1000	29·0	26·0	44·0	—
17. 8.56	Kinweshewa lagoon, Bangweulu	110	♀	2·48	water	2030	23·0	—	—	20·0
2. 1.57	Magungu, Victoria Nile	223	♂	4·22	mud-bank in shade	1000	26·5	27·0	—	27·0
5. 8.57	Musukwe lagoon, Lunsemfwa Valley	258	♀	2·15	water	2000	24·8	19·3	—	22·8
31. 8.57	Iyeshya, Kafue Flats	395	♀	2·82	water	2000	24·8	—	—	21·8
31. 8.57	Iyeshya, Kafue Flats	396	♂	2·86	water	2300	26·3	15·0	—	21·5
19. 5.58	Luangwa River	At.1	♀	2·32	bank	0845	25·0	19·8	—	25·8

The series shows a mean temperature of 25·6° C. and a range of 6 degrees, with fluctuations from the mean of +3·4 and −2·6 degrees. The mean temperature of specimens shot on land is 26·8° C. and that of specimens shot in the water is 24·7° C.

Behavioural control

The environment

The crocodile's environment includes many thermal factors which vary in time and space. Mean water and air temperatures recorded at Murchison are as follows :

time . .	24	03	06	09	12	15	18	21	24	hrs.
water . .	23·5	23·5	24·0	24·5	25·0	25·0	24·5	24·0	23·5	C.
air, shade .	19·0	19·0	18·7	24·8	29·3	29·0	23·4	21·5	19·0	C.

The water readings were taken at a depth of one foot off the end of Fajao jetty: air temperatures are the means of recordings taken during July and January. It will be seen that the thermal levels of air and water are transposed twice every twenty-four hours.

Heat exchange between the body and substratum will be influenced by the latter's conductivity index, and by moisture, texture and contained shadow, which will differ for surfaces of bare rock, sand and earth, grass or lush vegetation. Effects of insolation will vary with the weather and time of day, and with orientation of the reptile in relation to the sun. Rate of evaporation from the body when wet after rain or recent emergence on land, and from the mucosa when the jaws are agape, will be affected by wind-force and relative humidity.

Superimposed upon these variables are the movements, rhythmic or sporadic, of the crocodiles themselves, between land and water, sun and shade. These movements are certainly to be interpreted in terms of thermal requirements.

Diurnal movements

Early morning basking evidently plays an important role in the restoration of heat lost during the night (Plate 2, fig. 1). In field studies of agamid lizards, Cowles (in Curry-Lindahl, 1956–7) has shown that solar radiation is far more important than air temperature as a source of heat. And it is to be noted that the early morning exodus of crocodiles to land begins long before the air temperature has risen to that of the water they have left.

The time of the early morning haul-out varies at the same place from day to day, apparently in relation to prevalent weather. For example, on a cool day a favourite sand-bank near Fajao was still vacant at 0545 hrs., and was tenanted by only one crocodile at 0630 hrs.: on that morning the shade temperature did not reach 20° C. until 0730 hrs. At the same spot on the following morning, when the shade temperature was 20° C. at 0600 hrs., six crocodiles were already ashore and three half-out at 0545 hrs.

Despite lack of proof, it seems evident that crocodiles bask until the body temperature has been raised to a point near the upper limit of the normal activity range. Thereafter, they crawl into shade, lie at the water's edge, or enter the water and so dissipate heat. Thus, on a cloudy day with relatively low temperatures (8th July—see Fig. 3 a) there was no typical return to the water around midday, such as was seen when the rocks had been long exposed to insolation (10th July—see Fig. 3 b).

The combined effect of prolonged insolation and high temperature is strikingly seen in the movements recorded on 12th July (see Fig. 3 c), when the shade temperature rose to 36° C. The ground temperature on the rocks is not known, but 58° C. was recorded at bulb-depth in the sun at the O.P. For about two hours the islets were entirely deserted.

Observations on orientation of basking crocodiles in relation to the direction of the sun—such as have been recorded for *Phrynosoma modestum* (Wesse, 1917)—are not available. But there can be no doubt that the reptile's habit of lying for long periods on a bank with part of the body submerged provides an effective means of adjusting the area of the body exposed to the sun (Plate 1, fig. 2, and Plate 9, fig. 2).

In the late afternoon the trends seen in the early morning are reversed, and by returning to the water before sunset the reptiles escape the low air temperatures and conserve their heat during the night in the warmer medium.

Size and thermoregulation

Size is an important factor in an animal's thermal relations with its environment. The larger the animal, the lower is its surface-to-bulk ratio and the greater its capacity for heat storage. In studies of temperature tolerance in a graded series of thirteen alligators, Colbert, Cowles & Bogert (1946) have demonstrated that during exposure to the sun, the rate of heat absorption is inversely proportional to the animal's bulk. The same relationship applies to the rate of heat loss.

Experiments by Kirk & Hogben (1946) have shown that when young alligators about a metre long and weighing 4 kg. were exposed to a sudden drop in temperature of 20° C., ten hours elapsed before the body temperature fell approximately to that of the chamber. The much greater bulk of an adult crocodile will greatly retard this cooling process—thus enabling it to maintain its thermal level within the normal activity range at night. Heat loss at night will also be countered by the heat produced in muscular exertion—for example, when the animal is actively swimming in search of prey.

When the crocodile is subjected to high temperatures in the day time, changes in the body temperature will again follow only sluggishly. The stabilising effect of bulk may be illustrated by an example. At the Murchison O.P. on 8th July a large male was observed to remain motionless, lying with its tail in the water and its body on the rocks, for a period of over nine hours (from 0705 to 1620 hrs.). Such sedentary behaviour is in striking contrast to the restless activity of tropical agamids in which voluntary exposure to the sun does not exceed twenty minutes at a time (Curry-Lindahl, 1956–7).

Mouth gaping

When they are lying ashore or partly submerged by day, crocodiles are commonly seen with the jaws held widely agape (Plate 2, fig. 2). The effect of this habit upon body temperature has not been directly demonstrated in *C. niloticus*. But from indirect evidence there can be no doubt that exposure of the moist mucosa does provide, through evaporation, an important accessory cooling mechanism.

(a) Behaviour analogous to mouth gaping in the crocodile is known among birds. For example, in hot weather and when exposed to insolation on the nest, gannets (*Sula bassana*), shags (*Phalacrocorax aristotelis*) and cormorants (*P. carbo*) commonly open the bill and rapidly vibrate the gular pouch. Similar behaviour is seen in the African *P. lucidus* and *africanus*. That gaping and fluttering of the throat is an efficient behavioural adaptation for the dissipation of heat has been clearly demonstrated by Cowles & Dawson (1951) in their studies of the Texas nighthawk (*Chordeiles acutipennis*).

(b) It is known that if a crocodile is restrained in direct sunlight with its jaws roped together, its temperature rises beyond the normal activity range and death ensues. Shelford (1916) states that this was in fact the normal method he used to kill specimens of *C. porosus* that were brought to the museum.

(c) Colbert, Cowles & Bogert (1946) have demonstrated experimentally that alligators are able to maintain the body temperature for a long time, even when this approaches the critical maximum (about 38° C.); that the method of control is by loss of water through evaporation; and that this loss—which may during twenty-four hours amount to as much as 20 per cent. of the body weight—is regained by absorption when the alligator is replaced in water.

(d) Further evidence is afforded by field studies of *C. niloticus* in Uganda. During routine observations records were kept to show, for crocodiles lying ashore, (i) the time of day, (ii) insolation, i.e. exposed, or shaded by cloud or cast shadow, and (iii) posture, i.e. jaws gaping or closed. Table 5 contains an analysis of these data arranged in hourly periods.

TABLE 5

Mouth-gaping in relation to time of day and to insolation: showing, for hourly periods, the number of crocodiles seen ashore with the mouth closed, and open.

Time	*In sun*			*In shade*			*Total*
	Closed	*Open*	*% Open*	*Closed*	*Open*	*% Open*	*% Open*
0500–0600	—	—	—	6	?	0·0?	0·0
0600–0700	9	4	30·8	11	3	21·4	25·9
0700–0800	129	85	39·7	170	65	27·7	33·4
0800–0900	223	212	48·7	49	10	16·9	44·9
0900–1000	124	243	66·2	37	7	15·9	60·8
1000–1100	60	145	70·6	44	20	31·3	61·3
1100–1200	57	86	60·1	39	39	50·0	56·6
1200–1300	81	111	57·8	45	40	47·1	54·5
1300–1400	11	28	71·8	145	116	44·4	48·0
1400–1500	66	98	59·8	166	160	49·1	52·7
1500–1600	121	132	52·2	158	99	38·5	45·3
1600–1700	200	56	21·9	110	52	32·1	25·8
1700–1800	1	0	0·0	9	0	0·0	0·0

It will be seen from Fig. 5: (a) that the proportion with jaws agape tends to increase progressively during the morning when the external temperature is rising and to decline again with falling temperatures in the afternoon; and (b) that the proportion of mouth gapers is generally higher, at any time of day, for crocodiles exposed to the sun than for those lying in shade.

During the heat of the day crocodiles frequently lie half out on shore, with part of the body or with the tail submerged (Plate 9, fig. 2), and with the jaws gaping. The inference is that these animals are losing heat by evaporation from the mucosa and simultaneously making good the loss of body-fluids by absorption through the submerged surfaces.

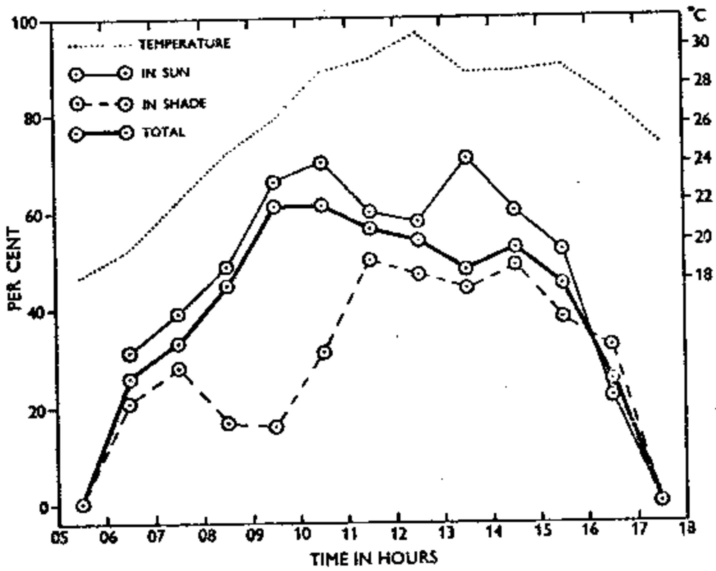

Fig. 5. Diurnal variation in mouth-gaping. The number of mouth-gaping individuals is expressed as a percentage of all crocodiles seen lying ashore; thin line—individuals exposed to the sun; broken line—those in shade; thick line—total. Mean shade temperatures are shown above.

Taken together, the foregoing observations indicate that by habitat selection and behavioural adaptation crocodiles are able to exercise a remarkable degree of control over the thermal level of the body. Indeed, they afford an extreme example of the approach, made by an ectotherm, towards endothermal life.

Terrestrial locomotion

Although about half a crocodile's life is spent ashore, during most of this time the animal lies sprawling, lazy and inert. From long observation in the field one gains the impression that crocodiles, and especially older animals, are most reluctant to carry their weight on land, and that terrestrial locomotion is a labour to be undertaken only in emergencies or in relation to the requirements of thermo-regulation. The mastery of terrestrial travel in no way compares with the grace and ease of movement in the water, which is the crocodile's real environment—both as a feeding ground and place of refuge.

When moving on land the crocodile has three distinct gaits. These may be described as the high walk, the belly run, and the gallop.

The high walk

This is the normal gait, and is the method of progression always seen when a crocodile is hauling its weight out onto the rocks or up a river bank. The high walk is also used in unhurried overland travel, for example, when a crocodile is going to its nest, or returning from the basking grounds to the water.

At such times the animal goes, not like a lizard with the legs splayed out sideways, but like a leopard, the legs swinging beneath the body and so carrying the belly high off the ground. The sacrum is held higher than the shoulder, the head is somewhat declined, and the back arched, only the lower surface of the tail-tip trailing (Plate 1, fig. 1, and Plate 3, fig. 1).

In this type of plantigrade locomotion, the legs move in diagonal pairs—the left fore and right hind legs coming forward together, to be followed by the right fore and left hind legs. At each stride two legs are on the ground and two in movement; and at the end of each stride the hind foot is placed close behind the fore foot of the same side, before the latter has been lifted to continue the sequence. The locomotory pattern, though not the swinging pace, is similar to that seen in the loping trot of a large cat.

When an adult crocodile is travelling up-hill, across country, or over broken terrain, such a means of locomotion is clearly related to the animal's great bulk, which could not be forced along the ground if the limbs were splayed sideways with the chin, belly and tail dragging. During the high walk the longer and stronger hind limbs, which have their origin not far behind the centre of gravity, take most of the weight, while the slender and shorter fore limbs act as props to support the head and shoulders. In going up-hill the animal's weight appears to be sustained almost entirely by the hind limbs as they haul the body upward and onward, the fore legs merely acting as mobile struts.

The belly run

When disturbed ashore a crocodile's immediate reaction is to make for the water at speed. The gait employed will then depend upon circumstances. If level ground has to be traversed crocodiles will make for cover, the run in this case being merely an acceleration of the high walk. But the way to the water generally lies down-hill. Then, and especially when hard pressed to make their escape, crocodiles adopt the belly run or scuttle.

In this gait the animal reverts to the crawling posture, and slides or toboggans over the ground, its polished ventral shields acting like the undercarriage of a sleigh, and the motive power being provided partly by gravity and partly by the action of the legs which are spread laterally like oars to propel the body forward (Plate 3, fig. 2). The belly run is much faster than the high walk, and is used not only on grassy or sandy slopes, but on precipitous rock descents. At Kigi I have seen crocodiles racing in this way from a height of forty or fifty feet, to hit the water with tremendous impact.

The gallop

The third gait is one that has very rarely been observed, and has not previously been recorded. In the gallop, the fore legs and hind legs work together in serial pairs. The body is carried forward by the backward thrust of both hind limbs while the fore limbs are extended to take the impact. The hind limbs are then brought forward beneath the belly during the backward thrust of the fore limbs. The leg action is rapid, the crocodile bounding along like a squirrel, with a pitching motion of the body, and at an estimated speed of about 7 or 8 miles per hour.

During months of observation I witnessed the gallop only four times—near Fajao, Paraa and Magungu on the Nile, and at Butiaba, Lake Albert. On two of these occasions I was accompanied, respectively, by Capt. J. R. F. Mills and Major R. E. P. Wyndham. The habit is so remarkable—and indeed improbable—that I am glad to have confirmation of this locomotory pattern from independent observers. Mr John Savidge (12.2.57) has sent me an account of the gallop which he witnessed at Buligi ; and Major B. G. Kinloch tells me he has also seen this unusual gait. The circumstances were generally similar in every instance. Crocodiles seen galloping have all been small specimens measuring between about one and two metres in length ; and on each occasion the animals had been suddenly surprised in sleep when some distance from the water, and had broken into this strange bounding gait on waking to find themselves discovered at close range.

Travel and Aestivation

During the rains crocodiles often follow the flood waters as they spread over the plains. This was observed, for example, at Lake Nyamiti, Ndumu Game Reserve, Zululand, where in early November, 1956, many crocodiles were seen moving into the newly-inundated areas—either to follow fish or to find warmer water. These movements sometimes take the animals far from permanent water ; and they get into pools where they are later marooned as the floods recede. Eventually, as the pool dries up, they attempt to regain the valley and are sometimes found moving overland far from water.

In Northern Rhodesia Major W. E. Poles (1956) came upon a seven-foot crocodile in the middle of an open plain about a mile and a half from the nearest lagoon. More remarkable is the instance reported by Trollope (6.7.54) to Player, from the Chobe River, where he met a crocodile travelling across country fifteen miles from the nearest water. Other records are given by Baker (in Anderson, 1898) and Cansdale (1955).

It is known that under such circumstances crocodiles can withstand drought by prolonged aestivation. In a tributary of the Dyoor River, Schweinfurth (1874) found crocodiles living in pools and puddles of the dry river bed where, as he says, " buried in the miry clay, they find a sufficiently commodious home."

In the Southern Province of Tanganyika, aestivation appears to be a regular habit. Mr G. H. Swynnerton told me that at Rukwa during the dry season the reptiles occupy roomy chambers which are reached by tunnels dug into the river banks. Evidence that they remain a long time in these retreats is provided by the growth of ambatch shoots in the entrances. This habit is also confirmed by Mr B. D. Nicholson, who tells me that on the Songwe River, south Rukwa, as many as fifteen crocodiles have been found occupying one cavern. In their torpid state, such crocodiles can be clubbed, one at a time, and put up no fight. Nicholson also states that when the Mbwemkuru waters dry, crocodiles work their way into the wet mud and as this cakes and cracks above them they get further down into the damp zone, till they may be found buried, and lying straight extended, five feet below the surface. Thus they remain for the five months' dry period.

Aquatic behaviour

The Nile Crocodile has perfect mastery of aquatic locomotion. However, perhaps on account of respiratory difficulties, the reptiles are reluctant to move into open water far from land, and they are rarely seen far from shore in Lakes Albert and Victoria. Even so, the species is not even restricted to the fresh water habitat. Player tells me he has, on several occasions, encountered crocodiles at sea off St. Lucia, Zululand ; and that formerly a great number of crocodiles used to lie at the mouth of the estuary, where a fight between a crocodile and a shark was once witnessed. W. M. Austen informed Player that during the 1917 floods a very large crocodile was seen swimming north about seven miles out to sea off St. Lucia—the occurrence being entered in the log of S.S. *Kathinwar* by the master, Captain Harper.

Swimming

When in its normal fresh water habitat, the crocodile rarely exerts itself. In lagoons and other still waters the animals spend much of the time floating idly at the surface. In rivers they generally keep station against the current with leisurely tail strokes. Where the water is clear, as for example off the rock islets below Murchison, they can often be seen lying motionless on the bottom in three to six feet of water during the heat of the day.

Active swimming is effected entirely by lateral undulations of the powerful tail (Plate 4, fig. 1). The limbs take no part in propulsion, being closely applied to the flanks. A few observations on swimming crocodiles are given in Table 6. Most of these records refer to specimens that were cruising slowly to maintain their position against the current. In general, the sweep of the tail is slow, and for any given swimming speed, slower in large than in small specimens. But when wounded, or when about to capture prey, a crocodile can dart forward with a tremendous spurt of activity and indeed may sometimes leap right out of the water like a great fish.

Respiration

In the unruffled waters which they normally frequent, crocodiles float low, with little more than the nasal disc, eyes and occiput above the surface. Immediately

TABLE 6

Date	*Locality*	*Period of observation in seconds*	*No. of tail cycles*	*Cycles per minute*	*Activity*
9.7.56	Fajao	61	30	29·5	Keeping station in shore.
14.7.56	Fajao	82	39	28·5	Leisurely swimming in slack water.
15.7.56	Fajao	87	30	20·7	Station keeping in slack water.
15.7.56	Fajao	62	30	29·0	Rapid swimming (in part).
15.7.56	Fajao	87	50	34·5	Heading up river for bank against fast current.
18.7.56	Fajao	45	23	30·7	Cruising speed.
30.12.56	Magungu	60	16	16·0	Keeping station against slack current off grounds.
6.1.57	Murchison	50	25	30·0	Cruising speed.
6.1.57	Murchison	63	25	23·8	Slow cruising speed.

before a dive the nares are closed, and the animal sinks—presumably by contracting the thorax and abdomen and so increasing the specific gravity.

In calm weather a submerged crocodile needs only to break surface with the nasal disc in order to breathe. Broken water interferes with the normal procedure, and in rough weather the snout has to be raised well above the surface and at a steep angle during inspiration. The animal then slips back, like a foundering ship, and disappears. For this reason, crocodiles tends to avoid rough water. According to Pitman (1931) they are not found in surf such as prevails along the shores of Lake Rudolf. And I am informed by Holloway that in windy weather crocodiles will even come ashore at night : this is quite contrary to their habitual routine.

Submergence

Since the reptiles can momentarily appear at the surface, in cover and unnoticed, it is extremely difficult to obtain reliable field data regarding submersion periods, and little is known of an adult's diving endurance. Holloway told me that in 1955 when hunting at night in a tributary of the Chambezi River he came upon an eight-foot crocodile which dived at the approach of his boat and lay on the bottom in about four feet of clear water. He waited above the reptile for an hour, during which it did not move. Player made a similar observation at Ndumu, where he watched a crocodile lie submerged for an hour.

Observations on captive crocodiles have proved that even small specimens can remain submerged for surprisingly long periods.

Submersion tests

Submersion tests were carried out at Jinja with four small crocodiles—each being held below the surface by a loose-fitting, weighted harness. The animals' reactions are summarized in Fig. 6. Numbers 1 and 3, both newly-hatched specimens, recovered after being submerged for thirty minutes. Numbers 2 and 4 failed to recover : but the latter (length 792 mm.) was still moving fifty-seven minutes after submersion, and would almost certainly have survived an hour's dive.

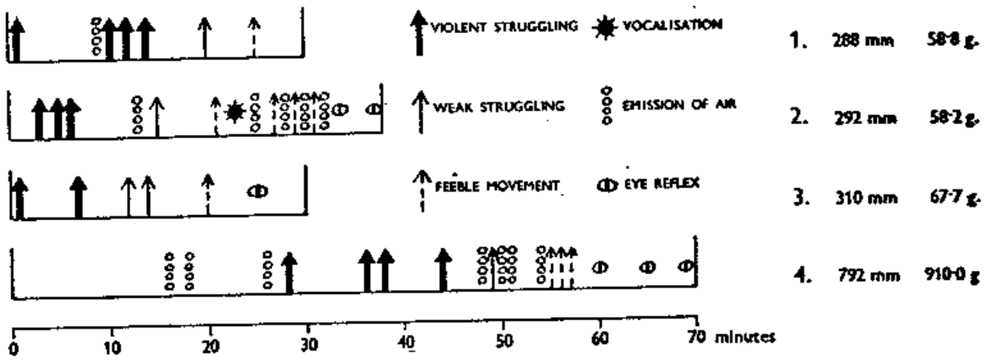

Fig. 6. Summary of activity of four crocodiles during submersion tests.

Diving times

In a second series of observations, a recently-hatched specimen, Jinja, 1952 (Number 1) and three larger specimens captured in Bangweulu Swamp, 1956 (Numbers 2, 3 and 4), were released in a pond—their diving and surfacing times being recorded over three- or four-hour periods. The results are summarized in Table 7 ; and the sequence of respiratory rhythm is shown in Fig. 7.

TABLE 7

Serial No.	*Length in mm.*	*Period of observation*	*Total time surfaced*		*Total time submerged*		*No. of submersions*	*Mean submergence time*		*Max. submergence time*	
		hours	*min.*	*sec.*	*min.*	*secs.*		*min.*	*secs.*	*min.*	*secs.*
1	290	3	94	0	86	0	12	7	10	16	0
2	661	4	48	20	191	40	17	10	27	25	30
3	982	4	2	24	237	36	13	18	17	35	15
4	992	4	3	12	236	48	15	15	47	44	0

The larger specimens from Bangweulu were very wary under observation and only surfaced momentarily for air before sinking again to the bottom. Some of the diving periods may therefore represent near maxima for specimens of the sizes given. In Fig. 8, the two longest diving times recorded for each of the four specimens are plotted against crocodile length. It will be seen that the maximum submergence times tend to vary in relation to size ; and that the largest specimen (measuring nearly one metre) was at one time submerged for forty-four minutes. If the trend here shown is maintained into the higher length-groups, then the maxima for adults would be far in excess of the one-hour periods that have been recorded in the field.

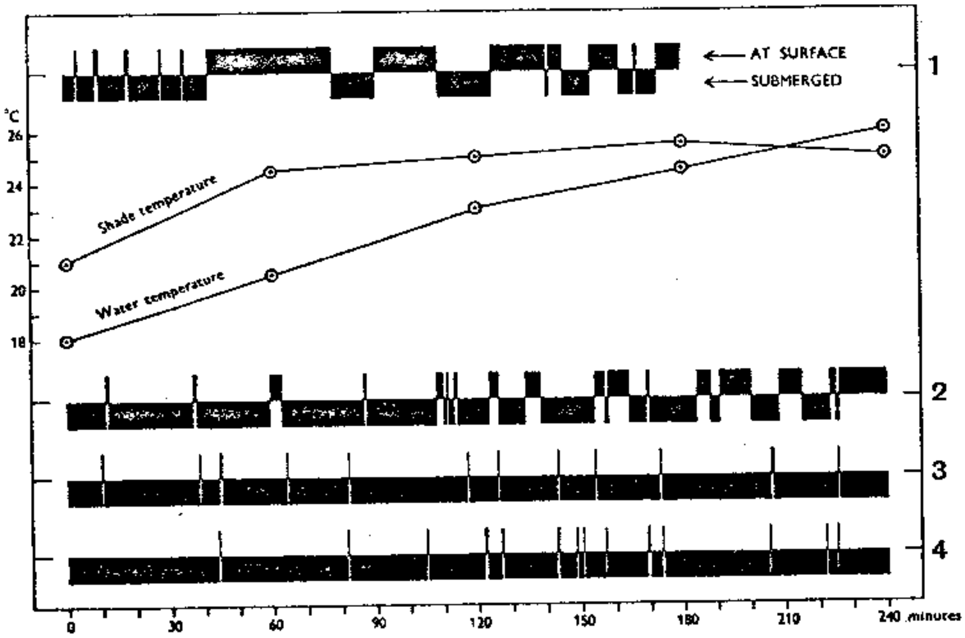

Fig. 7. Diagramatic representation of the respiratory activity of four crocodiles, measuring : 1–290 mm. (Jinja) ; 2–661 mm., 3–982 mm. and 4–992 mm. (Samfya). The indicated shade and water temperatures refer to the observations at Samfya, L. Bangweulu.

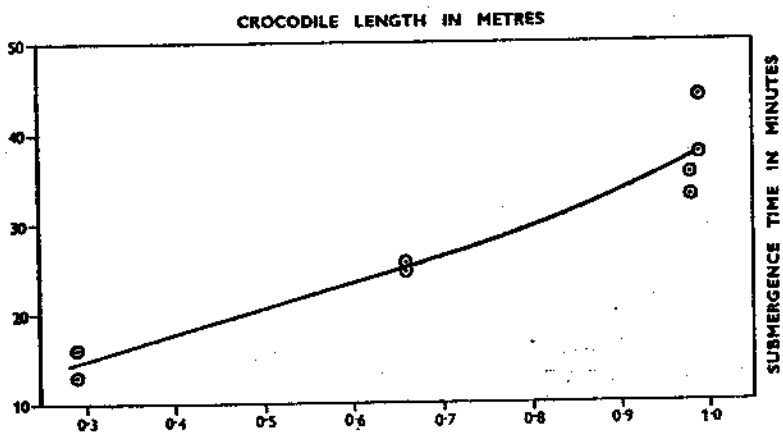

Fig. 8. Graph showing the relation of maximum submergence periods to crocodile length.

Stomach stones

The presence of stones in the stomach of crocodiles has often been reported, and commented upon; but hitherto the mode of occurrence of the stones themselves—as an essential basis for an enquiry into their possible function—has not been systematically studied.

Occurrence and weight

Material

The following summary is based upon data for occurrence of stones (presence or absence) in 681 crocodiles, examined in Uganda and Northern Rhodesia. Most of these were examined by the writer; but additional records received from Mr F. Wilson (23), Mr H. Holloway (45) and Mr H. H. Voigt (66) are here included. The material was examined in the following localities: Lake Victoria (84); Victoria Nile (27); Lake Kioga (4); Lake Albert (15); Semliki R. (2); Bangweulu Swamp (84); Mweru Wa Ntipa (41); Kalungwishi R. (12); Luangwa Valley (96); Kafue Flats (89); Upper Zambesi (227).

Further data relating to crocodile weight and weight of stones carried are available for 507 crocodiles from the same localities.

Occurrence of stomach stones

Data relating to occurrence of stones, in relation to crocodile length, are as follows:

Length in metres	0·3+	0·5+	1·0+	1·5+	2·0+	2·5+	3·0+	3·5+	4·0+	4·5+
No. examined	10	122	116	96	97	105	82	31	15	7
No. containing stones	0	61	78	79	87	105	82	31	15	7
Per cent.	0	50	67	82	90	100	100	100	100	100

Apart from very rare exceptions, it is true to say that crocodiles never carry stones during the first year of life, and that they have always acquired them before reaching maturity. Within these limits, the period of initial intake differs widely according to locality. For example, stones were present in the stomachs of *all* eighteen crocodiles in the 0·75 to 1·0 metre group from the Luangwa Valley; whereas from Bangweulu Swamp none were found in twelve crocodiles below 1·5 metres in length, and only four out of eleven in the 1·5 to 2·0 metre group contained stones.

The fact that the Luangwa Valley is stony, and Bangweulu Swamp stoneless, suggests that availability of mineral matter is the explanation of such differences. This explanation may be tested by an analysis of the data in relation to three main types of habitat: (a) rivers and lakes with stone-strewn shallows and shores (Lakes Albert and Victoria, Victoria Nile, Kalungwishi, Lunsemfwa and Luangwa Rivers); (b) meandering rivers, flowing through alluvial plains, with a bottom of sand or mud (Lower Semliki, Kafue Flats and Upper Zambesi); and (c) virtually stoneless swamps with a bottom of ooze and detritus (Kioga, Bangweulu and Mweru Wa Ntipa).

The occurrence of stones, expressed as a percentage of crocodiles of different length-groups examined from these three classes of habitat, is shown graphically in Fig. 9. Thus analysed, three patterns are seen—both as regards (i) the growth-stage at which stones are first ingested by individuals; and (ii) the length-group above which the whole population becomes stone-bearing.

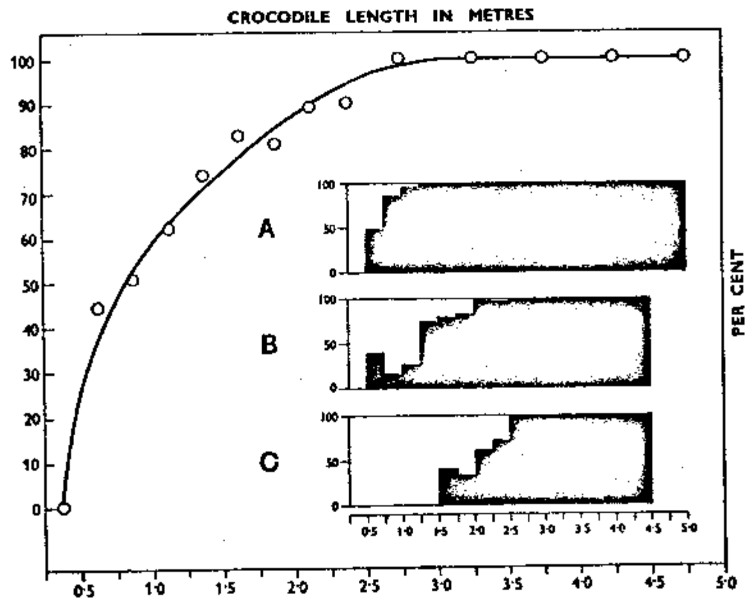

Fig. 9. Occurrence of stomach stones, expressed as a percentage of crocodiles examined in each length group. Inset—percentage occurrence of stones in stomachs of crocodiles taken in different habitats: A—stony; B—meandering river; C—swamp.

In stony habitats intake is early and rapid, being complete for the population at the 1·26 metre size. In alluvial flats, though a few crocodiles acquire stones early in life, at about 1·25 metre length only one in four contains stones, and the process of initial intake extends into the 1·75 to 2·0 metre group. In the swamp crocodiles, intake does not begin below 1·63 metres, and occurrence only reaches finality in the 2·25 to 2·50 metre group.

Weight of stomach stones

Data relating to weight of stones carried by crocodiles of different sizes are summarized in Table 8.

The results will be briefly discussed here under two heads: (i) the absolute weight of stones per stomach; and (ii) the weight of stones in relation to crocodile weight.

(i) *Absolute weight.*—Data for the combined collections show that the mean weight of contained stones increases progressively with age, from zero in the smallest length group to 3356 g. in the largest. (The greatest absolute weight is that recorded for No. 30, a male of 4·71 metres from Magungu, which contained 4766 g. of stones.)

TABLE 8

Stone weight in relation to crocodile length, showing maximum, mean and minimum values, and the weight of stones expressed as a percentage of the body weight.

Length group (metres)	*Number of stomachs examined*	*Mean body weight (kg.)*	*Stone weight (gm.)*			
			Max.	*Mean*	*Min.*	*Percent.*
0·3–0·5	10	0·146	—	0·0	—	0·0
0·5–1·0	101	1·524	16	2·044	0	0·134
1·0–1·5	102	4·518	125	11·70	0	0·259
1·5–2·0	76	16·54	480	88·87	0	0·537
2·0–2·5	73	40·90	980	312·5	0	0·764
2·5–3·0	69	79·39	2160	700·3	7	0·882
3·0–3·5	52	131·9	4540	1321·2	30	1·002
3·5–4·0	16	206·5	5100	1906·2	620	0·923
4·0–4·5	5	298·7	3600	2940·4	1450	0·984
4·5–5·0	3	325·5	4766	3356·0	2179	1·031

Specimens taken in different localities show a generally similar pattern of increase, which tends to be gradual in the lower, and to rise steeply in the higher length-groups (Fig. 10).

(ii) *Relative weight*.—When plotted against crocodile length, the mean relative weight of stones (expressed as a percentage of the mean body weight) is represented

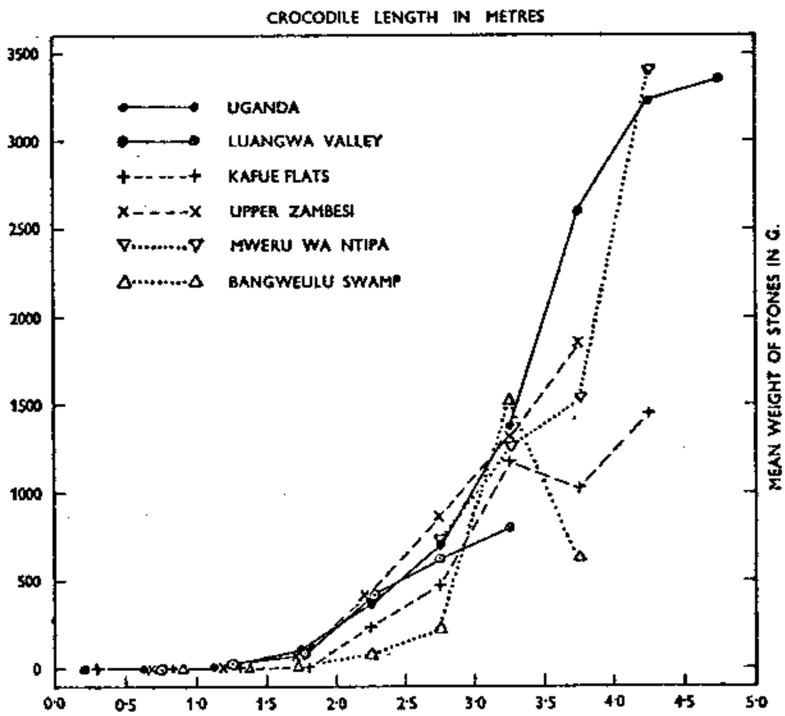

Fig. 10. Mean weight of stomach stones in relation to crocodile length, for six localities.

by a sigmoid curve which flattens out at a value of approximately one per cent. This may be regarded as the "standard load" for adult crocodiles.

Table 9 gives an analysis of the data for females and males separately; and in Fig. 11 the values for mean stone weight are plotted as a percentage of the

TABLE 9

Data for stone weight in relation to sex.

Length group	*Males*				*Females*			
	Size of sample	*Mean crocodile weight*	*Mean stone weight*	*Percent. stone body*	*Size of sample*	*Mean crocodile weight*	*Mean stone weight*	*Percent. stone body*
metres		*kg.*	*gm.*			*kg.*	*gm.*	
0·3–0·5	2	0·22	0·0	0·0	—	—	—	—
0·5–1·0	45	1·60	1·65	0·103	47	1·52	2·51	0·165
1·0–1·5	49	4·57	12·94	0·283	52	4·41	10·30	0·234
1·5–2·0	35	17·20	105·7	0·615	40	16·16	75·93	0·470
2·0–2·5	34	40·87	270·7	0·662	39	40·92	348·9	0·853
2·5–3·0	32	74·99	619·9	0·827	37	82·94	769·8	0·928
3·0–3·5	18	131·2	1189·9	0·907	34	132·3	1390·7	1·051
3·5–4·0	16	206·5	1906·2	0·923	—	—	—	—
4·0–4·5	5	298·7	2940·4	0·984	—	—	—	—
4·5–5·0	3	325·5	3356·0	1·031	—	—	—	—

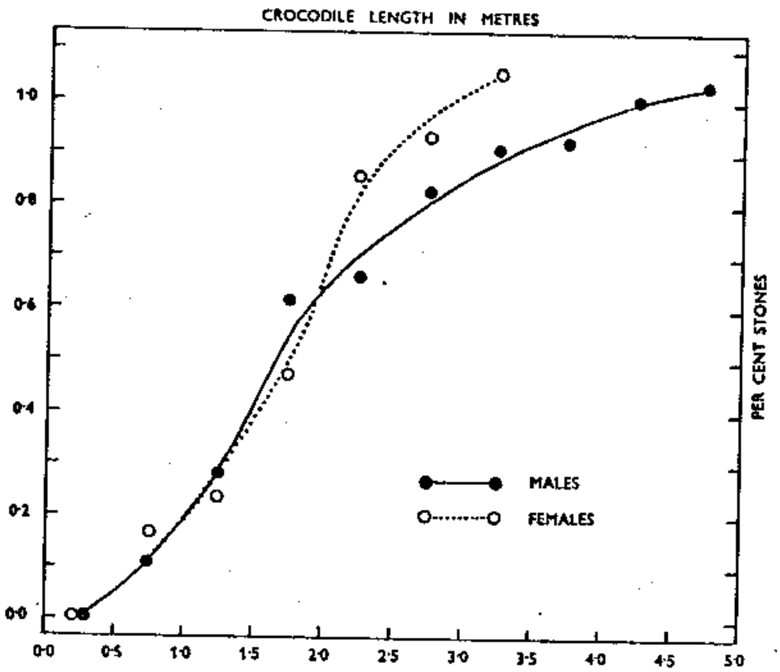

Fig. 11. Mean weight of stomach stones, expressed as a percentage of the mean body weight, in relation to crocodile length and sex.

body weight. The curves for the two sexes show the same characteristics—though they become horizontally displaced in the higher length-groups owing to sexual disparity in adult size (see p. 252). On attaining sexual maturity the length of females is about 2·4 to 2·8 metres, that of males about 2·9 to 3·3 metres. The values indicated by the smoothed graphs under these length-groups are close, being 0·88 to 0·97 for females, and 0·83 to 0·89 for males. Thereafter, the curves for large crocodiles of both sexes tend to level off at the standard load of about one per cent.

Further analysis of the data, in terms of the three types of habitat previously referred to (p. 236) is shown graphically in Fig. 12. Different availability of stones in stony, meandering and swamp waters seems to be the factor responsible for the marked differences seen under the lower length groups. The curves for crocodiles in stony and alluvial habitats are the first to converge with growth, and for the

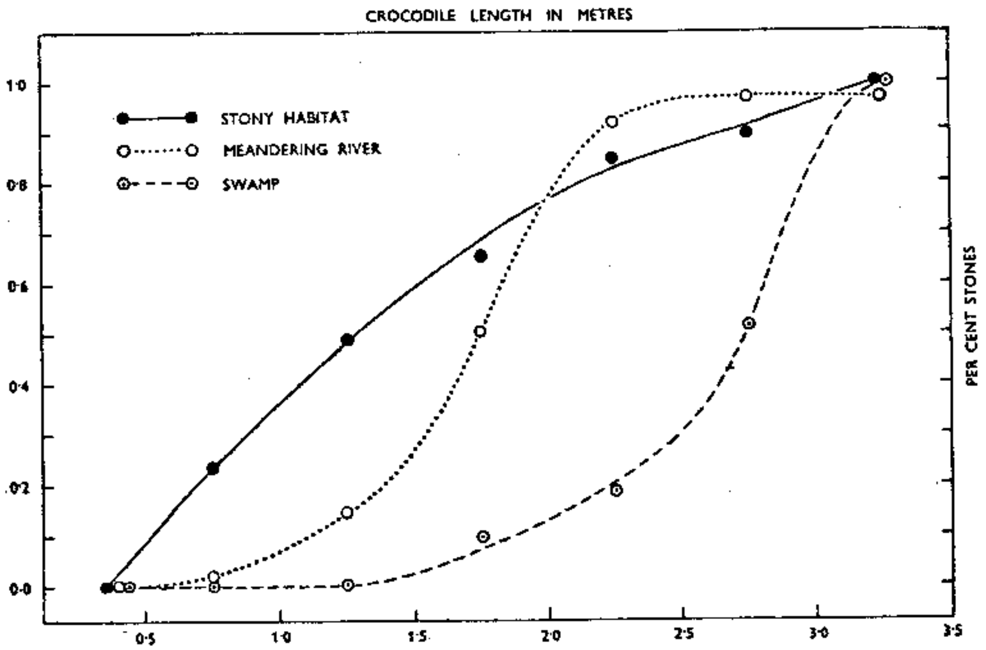

Fig. 12. Mean weight of stomach stones, expressed as a percentage of the mean body weight, in relation to crocodile length and habitat.

length-group above 1·5 metres they run approximately together. Swamp crocodiles lag behind in their intake: those in the 2·5 to 3·5 metre group still carry only about half the relative weight found in crocodiles of comparable size from other habitats. Yet the remarkable fact emerges that the relative weight of stones carried by mature crocodiles living in a virtually stoneless terrain eventually increases to conform with the general pattern, until in the 3·0 to 3·5 metre group (the largest for which adequate swamp records are available) the graphs converge.

The relevant figures for this length-group are as follows :

Habitat where shot	Stony habitat	Meandering river	Swamp
Size of sample	14	27	11
Mean body weight, kg.	137·9	132·4	123·2
Mean stone weight, gm.	1377·0	1281·0	1350·0
Percent, stones/body	0·999	0·968	1·096

The significance of the standard load of stones, found in adults of both sexes, and from every type of terrain, is discussed below.

Acquisition of stones

The circumstances under which crocodiles acquire pebbles are not certainly known. There appear to be three possible explanations : (a) that stones are accidentally ingested ; (b) that they are adventitiously derived from the stomachs of prey ; or (c) that they are deliberately swallowed. All the evidence now available points to the third explanation as the only satisfactory one.

(a) The distribution of stones throughout the populations, and the quantity found in individuals, render the first hypothesis unlikely. (i) Many juveniles have already acquired pebbles when they are still feeding in weedy shallows. (ii) Adults living in almost stone-free swamps contain approximately the same mean weight of stomach stones as others, of comparable size, living in stony habitats. (iii) Very old crocodiles do not carry a disproportionately large cargo of stones.

(b) Secondary derivation from the bodies of prey cannot be supported by evidence. (i) Young crocodiles commonly carry stones at a period when they are still feeding on prey (invertebrates and amphibia) which could not contribute stones. (ii) The victims of older crocodiles could scarcely supply the demand. For example, of 300 Pelecaniformes of five species examined by the writer in Uganda, only one contained one small pebble. Mr P. H. Greenwood tells me (22.12.57) that he has found *no* stones in any *Bagrus*, *Clarias*, *Synodontis*, *Protopterus*, *Barbus*, *Tilapia* or *Haplochromis*. The only other source under this head would be via cannibalism, which obviously cannot account for the stone-carrying habit.

(c) The third supposition, that stones are voluntarily ingested, finds indirect support from what has been said above, and also from the following considerations. Crocodiles living in virtually stone-free waters must of necessity make extensive journeys to collect their mineral load. For example, specimens from Bweramule, on the Semliki, were shot miles from any known source of supply. The same applies to specimens shot on certain stretches of the Kafue Flats and Upper Zambesi. More remarkable is the fact that adults collected in Bangweulu Swamp carried their quota, though stones could not have been acquired anywhere in the neighbourhood. Several crocodiles shot near swamp villages in Bangweulu had also collected (in lieu of stones) pieces of broken glass and pottery—these could only have been deliberately swallowed. Again, Player tells me (8.2.56) that crocodiles examined by him in St. Lucia Estuary contained water-worn pebbles that must have been gathered from the sea shore—in some cases this would have involved a journey of many miles.

Function of stones

It seems certain from the above evidence that stones are deliberately swallowed ; and, from their regular occurrence in stomachs of adult crocodiles, it is reasonable to suppose that they serve some physical or physiological function.

Various suggestions have been put forward : (1) that stones aid digestion, by the trituration of food ; (2) that they serve to relieve the pangs of hunger during periods of enforced starvation ; or (3) that they serve a hydrostatic function. These may be considered in order.

Digestive function

Hasselquist (1766) states : " The crocodile swallows stones to assist digestion, after the manner of seed-eating birds, which commit to the stomach the work of mastication, as well as concoction, being destitute of the instruments adapted to that purpose." Although this explanation has been reiterated by most authors who refer to the subject and has become the one commonly accepted, it is unsupported by evidence, and the following facts tell against it.

(a) The analogy with graminivorous birds is false, because the crocodile has no gizzard.

(b) In early life, before stomach stones have been acquired, crocodiles feed largely upon prey with hard chitinous or calcareous exoskeletons ; whereas adults, carrying stones, take more fleshy foods that require less trituration.

(c) Brittle structures such as the thin horny opercula of gastropods would be the first to be affected by gastric trituration ; yet these are commonly found unbroken in stomachs containing stones, long after the calcareous shells and fleshy parts of the snails have been digested. Nematodes remain alive and unaffected.

(d) Most carnivorous animals which swallow their prey whole, without mastication, such as predaceous fishes, and pelicans and many other fish-eating birds, digest their food without the aid of stones. In cormorants and darters the gastric juices are quite adequate to deal with armoured and spine-bearing fish such as *Clarias*, *Bagrus*, *Auchenoglanis* and *Synodontis*—often the very species which crocodiles are themselves taking.

(e) Examination of stomach contents of crocodiles reveals entire bones in all stages of digestion ; and there is no evidence that stones aid the process.

Filling function

In certain Pinnepedia, the second explanation seems to be the most satisfactory one. Thus Laws (1956) concluded from his study of their mode of occurrence in the Elephant Seal, that stomach stones serve "to relieve 'hunger pangs,' by providing the stomach muscles with bulk, upon which they may contract," when the animals are fasting ashore.

But no such explanation could be valid for crocodiles, which, as in Uganda, inhabit permanent waters with a plentiful food supply, and which feed throughout the year. Nor is there any evidence that females contain more stones during the incubation period when they may be fasting, than at other times.

Hydrostatic function

The suggestion that stones serve as ballast in the crocodile which "requires the finest adjustment and poise in the water" was apparently first made by Brander (1925). Now that adequate data are available, his suggestion—then unsupported by evidence—warrants further consideration.

(a) The relation, already referred to, between body weight and the weight of stomach stones carried by adult crocodiles is itself suggestive of an explanation in terms of specific gravity of the swimming or submerged animal. If a crocodile carries a cargo amounting to one per cent. of its body weight, how will this affect its weight in the water? The information in Table 10 provides a partial answer to this question.

TABLE 10

Weight of the body on land, compared with weight when submerged.

Serial No.	*Locality*	*Sex*	*Length*	*Body weight kg.*		*Submerged weight as percentage of body weight*	*Specific gravity*
				on land	*submerged*		
400	Kafue	♂	1·005	2·45	0·190	7·76	1·084
399	Kafue	♀	1·060	2·97	0·210	7·12	1·077
380	Kafue	♂	1·210	4·80	0·340	7·08	1·076
388	Kafue	♂	1·230	4·95	0·375	7·58	1·082
379	Kafue	♀	1·290	6·30	0·490	7·78	1·084
573	Zambesi	♂	1·310	5·80	0·420	7·24	1·078
398	Kafue	♂	1·370	7·80	0·600	7·69	1·083
574	Zambesi	♂	1·860	19·50	1·400	7·18	1·077
At. 1	Luangwa	♀	2·320	44·00	3·200	7·27	1·078

The submerged weight, when expressed as a percentage of the weight on land, ranges in the nine specimens examined from 7·07 to 7·78 (mean 7·41); and the specific gravity from 1·076 to 1·084 (mean 1·080).

Assuming that the weight relationships are similar for large specimens (the series examined shows no apparent change in the ratio with growth) a standard (one per cent.) load of stones will account for about one-eighth of the crocodile's weight when submerged, and will raise the specific gravity from 1·08 to about 1·09. This loading effect will of course be proportionately greater for individuals that have ingested more than the normal quota of stones: examples are given in Table 11.

TABLE 11

Serial No.	Locality	Sex	Crocodile		Stomach stones	
			Length in metres	*Weight in kg.*	*Weight in gm.*	*Percent. weight*
441	Mongu, Zambesi	♀	2·310	45·0	850	1·89
214	Ollandi, Kalungwishi	♀	3·160	143·0	2700	1·89
446	Mongu, Zambesi	♀	1·560	11·5	225	1·96
416	Mongu, Zambesi	♂	3·040	106·5	2100	1·97
509	Mongu, Zambesi	♂	2·990	109·5	2160	1·97
210	Ollandi, Kalungwishi	♂	3·840	239·0	5100	2·13
519	Mongu, Zambesi	♂	1·890	22·3	480	2·15
34	Fajao, Nile	♀	3·480	162·5	3675	2·26
345	Lochinvar, Kafue	♀	3·160	119·0	2700	2·27
460	Mongu, Zambesi	♀	2·250	42·5	970	2·28
313	Ndevu, Luangwa	♂	2·940	83·8	2050	2·45
136	Mutwamina, Bangweulu	♂	3·375	164·0	4540	2·77

For example, a 2·5 per cent cargo of stones will account for about one-quarter of the crocodile's submerged weight, and will raise the specific gravity to about 1·11.

(b) The biological value of ballast is likely to be two-fold. (1) It will enable the crocodile to lie submerged on the bottom (as commonly observed below Murchison Falls) in places where the strong current would tend to dislodge an animal of lower specific gravity. (ii) Crocodiles have need of extra effective weight when holding a large prey under water until it is drowned. When a large animal, such as a buffalo or waterbuck, has been captured, there follows a prolonged struggle during which the victim may several times regain the surface (as was seen below Paraa in 1956). Stomach ballast cannot fail to favour the predator in these circumstances.

(c) There is also evidence that stomach stones subserve further hydrostatic functions—acting (i) as an anterior counterpoise, and (ii) as a ventral stabilizing force. In this connexion, it is important to appreciate the position which the stones occupy in the body of the swimming animal. Firstly, the stomach lies anterior to the centre of gravity which is near the posterior end of the body. Secondly, X-ray photographs (Plate 5, figs. 1 and 2) of living crocodiles show that the stones lie low in the stomach and adjacent to the ventral body-wall. In this position they will lower the centre of gravity and act in a manner analogous to cargo in a ship's hold, making for stability in the swimming animal. This downward stabilizing force will be enhanced by the upward and lifting component from the more dorsal lungs.

The need for such a mechanism is demonstrated by the instability of stoneless young when placed in deep water. In nature, young crocodiles shun open water, even when feeding at night. Experiments have shown that they tend to be both tail-heavy and top-heavy. They cannot lie level at the surface like their stone-carrying elders, and movements of the limbs are often necessary to counteract rolling. This is in marked contrast to the easy poise seen in the floating adult (Plate 4, fig. 1).

Growth and age

Growth rate

Information hitherto available on the rate of growth under natural conditions is largely conjectural, and the assessments are highly conflicting. For example, Pitman (1931) estimated that in early life growth does not exceed one inch per annum. According to Brehm (1914) the rate is at first four inches per annum and in later life slower. In contrast, Siggins (1931) states that growth during the first few years is very fast and that at six years of age the crocodile will be as many feet in length.

Long-term field measurements of marked crocodiles of known age—comparable to those given by McIlhenny (1934) for the American alligator (see p. 255) are clearly needed ; and it was with great interest that I learned of a specimen that had been measured, over a period of twenty-two years, by Mr E. Davison, Chief Game Warden, Southern Rhodesia. Davison (25.2.58) has most kindly sent me details, and permission to publish his observations.

The specimen was hatched on the Shangani R. in December 1935 and has been under observation in natural conditions. For the first nineteen months it was kept in a large pond, where it fed on grasshoppers, crickets, moths and other insects. It was seen to catch a bird when eighteen months old. In July 1937 it was transferred to a natural pan and in 1939 to a larger pan, containing *Clarias*. This and another pan to which it wanders in the wet season, are used by a large variety of game—from baby warthogs to elephant. The crocodile is known to have killed a wild cat and a full-grown warthog, and it has frequently been seen to catch fish and birds, including doves, duck, pelicans and plovers : during the rains toads are also taken.

Measurements, in inches, recorded by Davison are as follows :

Dec. 1935 ..	.. c. 11	Aug. 1937 ..	.. 26·5	Dec. 1945 ..	.. 88
June 1936 ..	.. 12	Dec. 1937 ..	.. 30	Dec. 1946 ..	.. 90
Aug. 1936 ..	.. 16	Oct. 1938 ..	.. 44	Dec. 1949 ..	.. 93
Nov. 1936 ..	.. 22	Dec. 1941 ..	.. 72	Nov. 1957 ..	.. 104
Mar. 1937 ..	.. 26·5	Dec. 1942 ..	.. 84		

Growth of this crocodile is plated in Fig. 13.

Flower (1933) gives details for four specimens of *C. niloticus* in the Giza Zoological Gardens, Cairo, where the animals were kept under fairly natural conditions of climate and environment. Bigalke (1929) records the length of a specimen from Pretoria, known to be twenty-two years old. Dr L. Harrison Matthews (20.3.57) has sent me further measurements of two specimens of known age now living in the Reptile House, Regent's Park. The relevant data for these and some other crocodiles are listed (p. 246), in order of age, and plotted for comparison with Davison's measurements in Fig. 13.

Cambridge	6 weeks	0·312 m. (12·3 ins.)	—
Cambridge	1 year	0·530 m. (20·8 ins.)	0·39 kg.
London	1 year, 7 months	0·594 m. (23·5 ins.)	0·45 kg.
Cairo	1 year, 8 months	0·705 m. (28 ins.)	1·8 kg.
Cambridge	2 years, 10 months	0·993 m. (39 ins.)	3·3 kg.
Cairo	4 years	1·657 m. (65 ins.)	18·0 kg.
London	4 years, 4 months	1·850 m. (73 ins.)	—
Cairo	4 years, 6 months	1·840 m. (72 ins.)	30·0 kg.
Cairo	8 years	2·340 m. (92 ins.)	72·5 kg.
London	12 years, 9 months	2·400 m. (94 ins.)	—
Pretoria	22 years	2·850 m. (112 ins.)	—

It will be seen that the growth rates for the free living and captive specimens are generally similar up to the age of twenty-two years, when the recorded lengths are 104 and 112 inches respectively. In Davison's crocodile growth is rapid during the first seven years, the mean annual increment being 10·4 inches (or 265 mm.). Thereafter the growth-rate is slower and remarkably steady over a period of fifteen years, during which the animal gained only a further 20 inches in length, with a mean increase of 1·4 inches (or 36 mm.) per annum. The corresponding mean annual increments shown in captive specimens are : for the first seven years, about 11 inches (or 280 mm.) ; for the next fifteen years, about 1·5 inches (or 40 mm.).

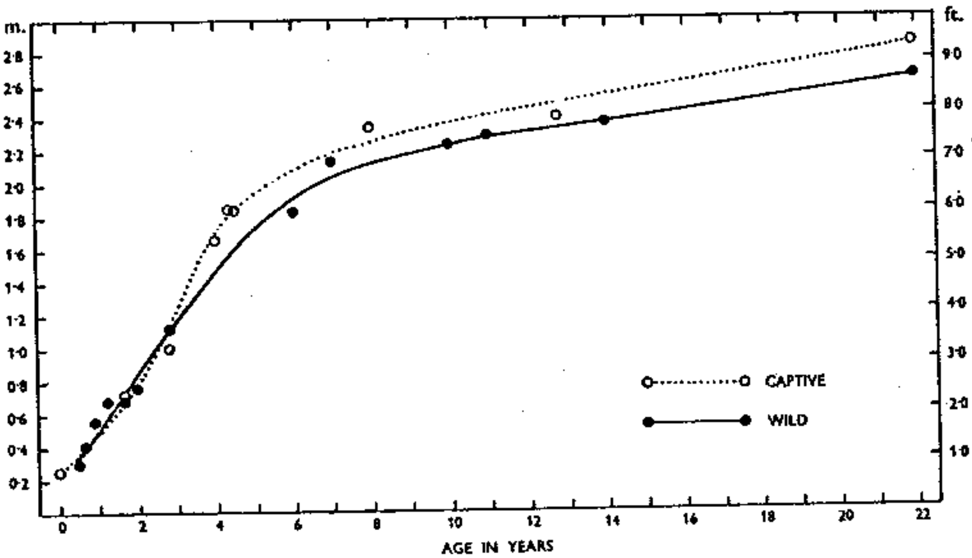

Fig. 13. Growth rate of *C. niloticus*, based upon observations of specimens in captivity and upon a free-living specimen (Davison's data).

The length of crocodiles examined from the Luangwa, Lunsemfwa, Kafue and Zambesi rivers, plotted against dates of capture, is shown in the scatter diagram, Fig. 14 : (males, black ; females, white ; sex unrecorded (records by Voigt), black and white circles). Although these measurements come from an area where there is a well-marked breeding season, the length frequency distribution defies interpretation in terms of growth and age beyond the third year of life, since evidently the variation in length within respective year groups is large in comparison with the mean yearly increments. The superimposed year groups (shown in dotted lines) are based on Davison's data.

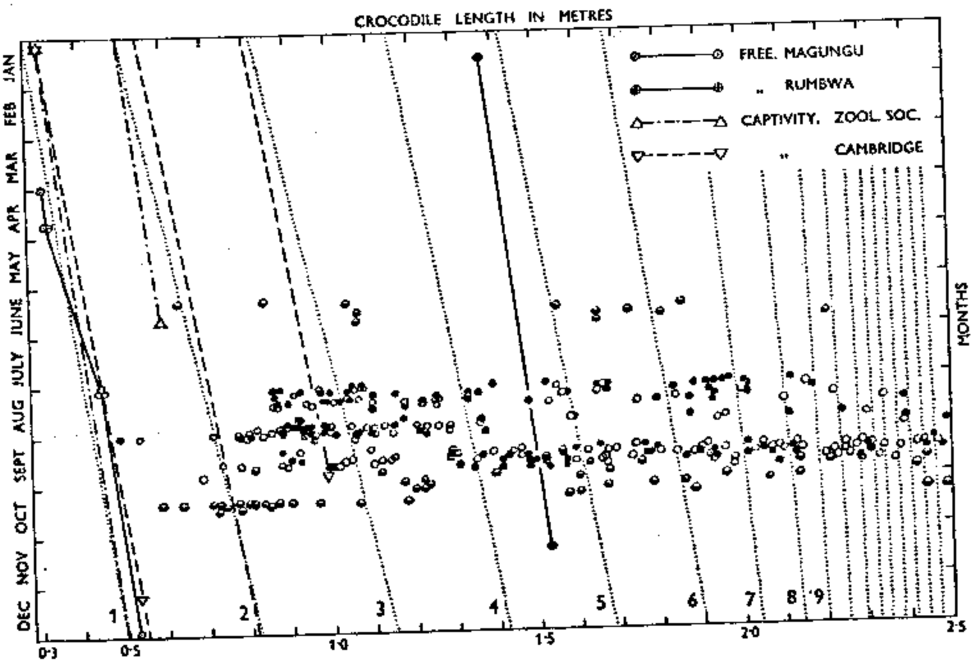

Fig. 14. Growth rate of *C. niloticus*. The scatter diagram shows the total length and date of capture of crocodiles examined from Luangwa Valley, Kafue Flats, and Upper Zambesi ; males—black ; females—white ; sex unknown—black and white circles. The dotted lines, indicating year groups, are based on Davison's data. The continuous and broken lines show growth rates based on measurements in the field and in captivity respectively.

Also plotted in this figure are various growth data for young specimens measured in captivity and in the wild state. (a) The former are based on a series of newly-hatched young captured on Buvu Island and reared in Cambridge and the Society's Gardens. (b) Comparative data of growth during the first year of life in the wild state are provided by specimens caught in the meres near Magungu, Victoria Nile (see Table 12).

Table 12

No.	*Authority*	*Date*	*Age*	*Length in mm.*	*Weight in gm.*
S.2	J.S.	31.3.57	newly-hatched	315	—
S.3	J.S.	23.4.57	3 weeks	320	—
S.4	J.S.	24.4.57	3 weeks	325	—
106	H.B.C.	1.8.56	4 months	450	140
107	H.B.C.	3.8.56	4 months	455	*c.* 150
108	H.B.C.	3.8.56	4 months	447	*c.* 150
222	H.B.C.	29.12.56	9 months	530	250

For the records made in March and April 1957, I am indebted to Mr John Savidge. The hatching date of all specimens listed is taken to be about the end of March.

Two further records, of larger crocodiles of unknown age, relate to specimens shot in the remote islet of Rumbwa, Sese, as follows : No. 2, 16.1.52, length 1.375m., weight 7·0 kg.; No. 101, 10.11.52, length 1.525 m., weight 10·75 kg. The increase in length of 150 mm. (about 6 ins.), over a period of 10 months, shown by these measurements agrees well with the known growth-rate of crocodiles of comparable size, and it is probably that the two specimens were hatched in the same season and perhaps from the same clutch.

It will be seen on reference to Fig. 14 that the growth rates recorded for these various specimens conform closely to the gradients derived from Davison's measurements.

Size attained

It is not easy to assess the validity of records of very large crocodiles that have been reported from various parts of Africa. Visual estimates of length, like those of Brue (25 ft.) and Barbot (30 ft.) cited by Cuvier (1831) are always unreliable ; and the only valid information is that provided by measurements, with steel-tape or otherwise, of the distance between pegs set at the snout and tail-tip.

The question of the maximum length attained by *C. niloticus* is never likely to be satisfactorily settled. Some herpetologists have undoubtedly erred in understatement. Thus Ditmars (1922) accepts 16 feet as the maximum. In their recent works, Pope (1957) and Schmidt & Inger (1957) repeat this figure—which is far below measurements reliably reported.

Against the scepticism with which older records are to be regarded, must be set the fact that crocodiles require a long time, perhaps at least 100 years, to attain spectacular size : under modern conditions, veterans have little chance of survival, and have already vanished from most African waters.

Nor are the verified measurements of specimens in museums a reliable criterion. On the rare occasions when exceptionally large individuals have been killed, it is almost inevitable that they should be lost to science as specimens. But the absence of such material cannot be accepted as sufficient reason for rejecting evidence from the field.

The following records provide some indication of the maximum length attained by *C. niloticus* in Central and South Africa.

Central Africa.—Exceptionally large crocodiles do not appear to have been encountered recently in the Rhodesias. L. E. Vaughan (Senior Game Ranger) reports that the largest actually measured by him in Northern Rhodesia was 16 feet 7 inches. He states that he has measured several over 16 feet in length ; but that the average large crocodile in the Kafue appears to be in the 13 to 15 feet range. A photograph of a 16-foot crocodile shot in the Kafue by Clyde Sussens was published in the *N.R. Journal* (1955) : its weight was stated to be between

1,500 and 1,600 lbs. In former years, Hubbard (1927) shot a specimen in the Kafue which, measured by steel-tape, was "just a fraction larger than seventeen feet five inches."

From Nyasaland, Loveridge (1953) reports a specimen shot by C. C. Yiannakis, near Chipoko, that was said to measure 18 feet 10 inches.

East Africa.—A number of very large specimens have been reliably reported from Uganda, where the species appears to reach its greatest size in the Lower Semliki and the Murchison reach of the Victoria Nile. At Fajao, Murchison Falls, Hobley (1921) shot a crocodile in 1900 of which he writes: "The only authentic measurement . . . that I can vouch for was one of my own, it was 18 feet from tip of snout to tip of tail, measured between perpendiculars." Two males, killed and measured on the Semliki by a Game Ranger in 1950, were 16 feet 10 inches and 18 feet 2 inches in length (Kinloch, 1951). In 1952, the Marketing Corporation which employed hunters on the Lower Semliki received a skin which measured 19 feet 6 inches. Mr E. V. Hippel, an experienced professional hunter, tells me (29.10.54) that during a penetrating safari in the Lower Semliki in June, 1954, he shot his largest crocodile—a female which measured 18 feet 4 inches. If the sex has been correctly reported, it must stand as a record; this crocodile exceeds by over three feet the maximum length reported by Pitman for a female in Lake Victoria, and is in fact slightly larger than Pitman's largest male—an 18-foot specimen shot in 1942.

Mr Douglas Jones informed me that crocodiles of exceptional size were formerly found in the Juba River: one which he measured at Bardera was just over 21 feet. The largest recorded by Mr Bousfield (Swynnerton, unpub. report) from Lake Rukwa was 17 feet 4½ inches. In Lake Victoria the biggest crocodiles have been reported from the Emin Pasha Gulf area. In 1905 the Duke of Mecklenberg killed one near Mwanza which was said to measure 6·5 metres, or nearly 21 feet 6 inches (Hubbard, 1927). Mr J. D. Kelsall (L.V. Fisheries Service) has sent me (25.10.53) the following information supplied by a professional hunter named Erich Nowotny. He states that the only really big crocodile he could personally vouch for was one he shot about a mile west of Nungwe, Emin Pasha Gulf, in 1949, which measured exactly 21 feet, and at a rough estimate weighed about a ton. When hunting one night near Senga Point at the N.E. entrance to Nungwe Bay, in 1948, Nowotny drew alongside a crocodile that was apparently asleep on the water: he states that this specimen was "appreciably longer than the 20-foot canoe" and he estimated its length at not less than 22 feet. Nowotny also told Kelsall that in 1950 an Indian, trapping crocodiles in the Butundwi Bay area, offered him twenty-seven skins for sale: only two were under 18 feet in length—allowing for the fact that these were measurements of skins, he estimated that the crocodiles in this batch must have averaged about 19 feet in length. In the late forties, according to the same hunter, crocodiles of 20 to 22 feet were quite commonly taken in the Gulf by natives using hooks.

In some waters, the Nile Crocodile never attains a large size. For example, the largest of over 1,000 shot by Nowotny in Malagarasi Swamp was only 12 feet in length. Hippel tells me that the largest he obtained in Lake Kioga measured only 12 feet 6 inches ; and 90 per cent. of 500 collected by him in 1944 were from 7 to 10 feet long (Pitman, 1948). Again, according to Hobley (1919), crocodiles in Lake Baringo rarely exceed 9 feet. More remarkable, in this connexion, are the so-called " pigmy crocodiles " of the Aswa River in Northern Uganda (Pitman, 1931, 1934 ; Salmon, 1933), measuring between 5 and 6 feet.

Thus it is evident that the maximum size attained differs widely according to locality. Where conditions for maximum growth are favourable, there seems to be reliable evidence that the species may reach a length of at least 20 feet ; while some records of even larger crocodiles appear to be valid.

Longevity

The potential length of life in the Nile Crocodile is not known. Some light is thrown upon the subject by authentic life-records of animals kept in captivity. But as criteria such records are far from satisfactory. It is often impossible to verify the dates when specimens, reputed to have lived to a great age, were first received into captivity. And it is probable that crocodiles live longer in the wild state than in the restricted and artificial conditions that obtain in a reptile house : as Flower (1937) has remarked—" in general . . . reptiles do not *live* in captivity, but pine away."

Yet from records which Flower (1925, 1937) accepted as absolutely authentic, it is clear that crocodilians are long lived. The ages, in years, attained by the oldest-known individuals of various species, as given by Flower, are as follows :

Gavialis gangeticus (Indian Gharial)	London	24
Tomistoma schlegelii (Malay Gharial)	New York	23
Osteolaemus tetraspis (Broad-fronted Crocodile)	Frankfurt	24
Crocodilus niloticus (Nile Crocodile)	Berlin	25
Crocodilus cataphractus (Long-nosed Crocodile)	Amsterdam	20
Crocodilus palustris (Mugger)	Trivandrum	31
Crocodilus porosus (Estuarine Crocodile)	? Frankfurt	21
Crocodilus siamensis (Siamese Crocodile)	London	16
Crocodilus intermedius (Orinoco Crocodile)	Amsterdam	23
Alligator sinensis (Chinese Alligator)	Berlin	50
Alligator mississippiensis (American Alligator)	Dresden	56
Caiman niger (Black Cayman)	Munster	28, ?30

Dr H. G. Vevers tells me (1.12.59) that a Gharial which died in the Reptile House in 1941 had lived in the Gardens for 28 years 9 months. Fullest information is available for the American alligator. In his summary Flower writes : " We know of twenty individual Mississippi alligators that show an average life of thirty-three years and two-and-a-half months. No fewer than eleven out of these twenty individuals being still alive at the time when these notes were made, proves that the average duration of life will be longer still. Five of these twenty reached an age of forty or more years. . . . The oldest known . . . is the still living veteran of Dresden of 56 years."

Such evidence from zoological gardens, taken together with what is known (a) of the growth-curve in free-living and captive specimens of *C. niloticus*, and

(b) of the length attained by this species in nature, undoubtedly points to a very long potential life-span. If growth after 22 years continues at the rate indicated by Davison's field measurements, at about 1·4 inches per annum, then a crocodile measuring 15 feet in length would be about 76 years old, and one measuring 18 feet would be over 100 years old. But if, as is most likely, the growth curve flattens out in late life, then the largest known specimens must have survived well into their second century.

Size and sex ratio

The sexes of 651 crocodiles of known length have been recorded during the present investigation, and the data available throw some light upon the changing constitution of the population as it ages. The relevant data are given, under 0·25 metre length groups, in Table 13.

Table 13

Number and percentage of the sexes, by length groups.

Crocodile length in metres	*Size of sample*	*Number*		*Per cent.*	
		males	*females*	*males*	*females*
0·25—0·50	3	3	0	—	—
0·50—0·75	9	5	4	55·6	44·4
0·75—1·00	93	47	46	50·5	49·5
1·00—1·25	74	36	38	48·6	51·4
1·25—1·50	47	24	23	51·1	48·9
1·50—1·75	46	20	26	43·5	56·5
1·75—2·00	41	24	17	58·5	41·5
2·00—2·25	46	20	26	43·5	56·5
2·25—2·50	52	24	28	46·2	53·8
2·50—2·75	51	22	29	43·1	56·9
2·75—3·00	59	22	37	37·3	62·7
3·00—3·25	59	17	42	28·8	72·1
3·25—3·50	29	18	11	62·1	37·9
3·50—3·75	19	19	0	100·0	0·0
3·75—4·00	11	11	0	100·0	0·0
4·00—4·25	4	4	0	100·0	0·0
4·25—4·50	5	5	0	100·0	0·0
4·50—4·75	3	3	0	100·0	0·0

For the series as a whole, sexes are almost equal in number, there being 324 males and 327 females. This equality is also seen among crocodiles of the smaller length groups. Thus, 226 specimens measuring less than 1·50 metres occur in the proportion of 115 males and 111 females; and 185 specimens measuring between 1·5 and 2·5 metres, in the proportion of eighty-eight males and ninety-seven females. For the 411 specimens below 2·5 metres, the ratio is 49·4 and 50·6 respectively.

Above this length, the proportions of the sexes diverge and in successive length groups show the following trends. At first there is a fall in the percentage of males, until in the 3·0 to 3·25 metre group, containing fifty-nine specimens, only seventeen (or 28·8 per cent.) are males. Thereafter the trend is steeply reversed. Of seventy-one specimens above 3·25 metres, only eleven (or 15·5 per cent.) are females, and all these fall within the 3·25 to 3·5 metre group. These changing ratios are shown graphically in Fig. 15. They are explained by the fact that the males (whether by faster growth or by longer-continued growth, see p. 255) attain a greater length than the females. The disparity in adult size is expressed graphically in Fig. 16, which shows the length frequency distributions for each sex.

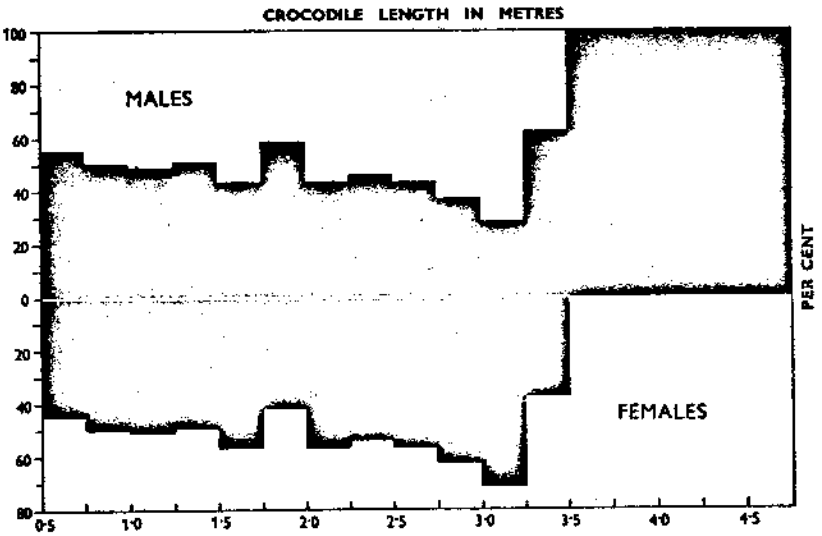

Fig. 15. Histogram showing sex ratio in relation to crocodile length.

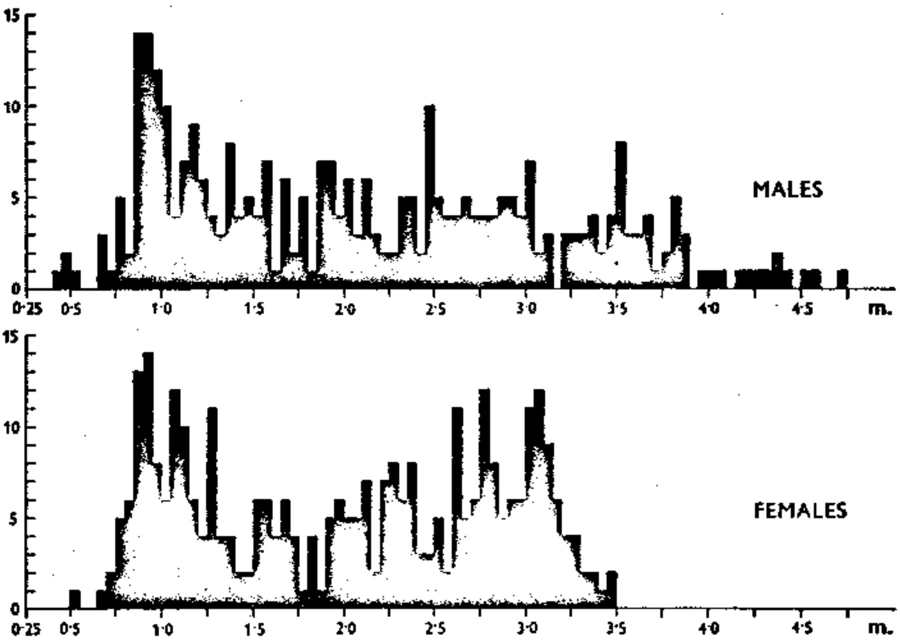

Fig. 16. Length frequency distribution, by sexes, of 651 crocodiles (324 males, 327 females) examined in Uganda and Northern Rhodesia (1952, 1956 and 1957).

with ova ranging from about 2 mm. in diameter upwards ; (b) those with oviduct eggs, unshelled or shelled ; and (c) spent females, in which the ovaries, undergoing resorption, are flaccid, granular and discoloured, and the oviducts still much distended and with prominent vasularization.

Data are available for all females from Bangweulu Swamp, Mweru Wa Ntipa and the Kalungwishi River in the Northern Province, and from Luangwa, Kafue and Zambesi Rivers. In the three northern localities the smallest measurements for breeding females are 2·38, 2·51 and 3·02 metres respectively ; and from the southern localities 2·59, 2·70 and 2·82 metres respectively. The weight of such animals is between about 60 and 120 kg. But these are minimum sizes : about half the females are breeding at about 3 metres length and 120 kg. weight.

Pitman's measurements of nesting crocodiles provide further valuable information on the size-range of breeding females, and, in the present context, on the length at which sexual maturity is reached. In view of the crocodile's decline in recent years, it is virtually certain that such extensive observations will never be repeated, and I am most grateful for him for permission to place on record the following analysis of measurements recorded in his unpublished notes.

Fig. 17 shows the length frequency distribution of 855 females shot on the breeding grounds and known to have nests, during the years 1940 to 1949. The largest numbers of breeding females occur in the length ranges between 9 feet

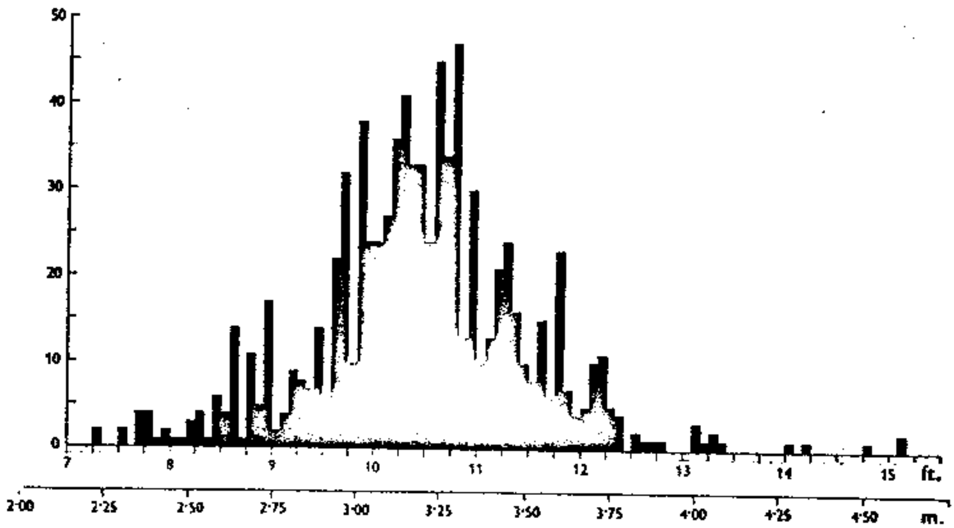

Fig. 17. Histogram showing the length frequency distribution of 855 breeding females shot at the nest in northern Lake Victoria. (Pitman's unpublished notes.)

6 inches and 11 feet 6 inches ; and the mean length is 10 feet 5 inches. Specimens within the size range between 8 feet 6 inches and 12 feet 6 inches comprise 807 (or 94.4 per cent.) of the total.

Very few females (less than 2 per cent.) were nesting before they had attained a length of 8 feet (2·44 m.). The smallest among this large sample are as follows :

four, 7 feet 8 inches ; two, 7 feet 6 inches ; and two, 7 feet 3 inches ; all from the Sese Islands. Pitman (19.1.56) further confirms that over a period of some fifteen years, during which he and his Fish Guards measured between 1,500 and 2,000 females, 7 feet 2 inches (or 2·19 m.) was the smallest size recorded on the breeding grounds.

The sexes compared

Comparative data for breeding crocodiles, of both sexes, from Northern Rhodesia, are given in Tables 15 and 16. Fig. 18 shows the percentage of males and females that were in breeding condition, by length groups. Length and weight of breeding

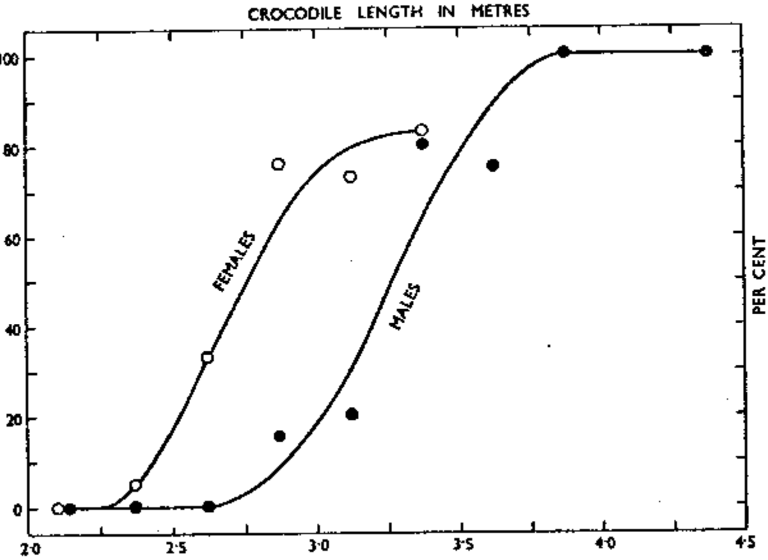

Fig. 18. Smoothed curves, showing the percentage of males and females breeding, in relation to crocodile length.

specimens of both sexes, from the southern localities, are plotted in Fig. 19. It will be seen that for crocodiles of comparable length, the females are considerably heavier than the males, but that the females become sexually mature at a considerably shorter length than the males.

If the rate of growth is the same for both sexes, the females must mature at an earlier age than the males. On the other hand, if the sexes attain maturity at about the same age, growth in the male must be more rapid. From what is known of growth in the American alligator the disparity is almost certainly due to differential growth rate.

Working in the Wild Life Refuge on Avery Island, Louisiana, McIlhenny (1934) toe-marked thirty-eight alligators in 1921 and kept them under observation for

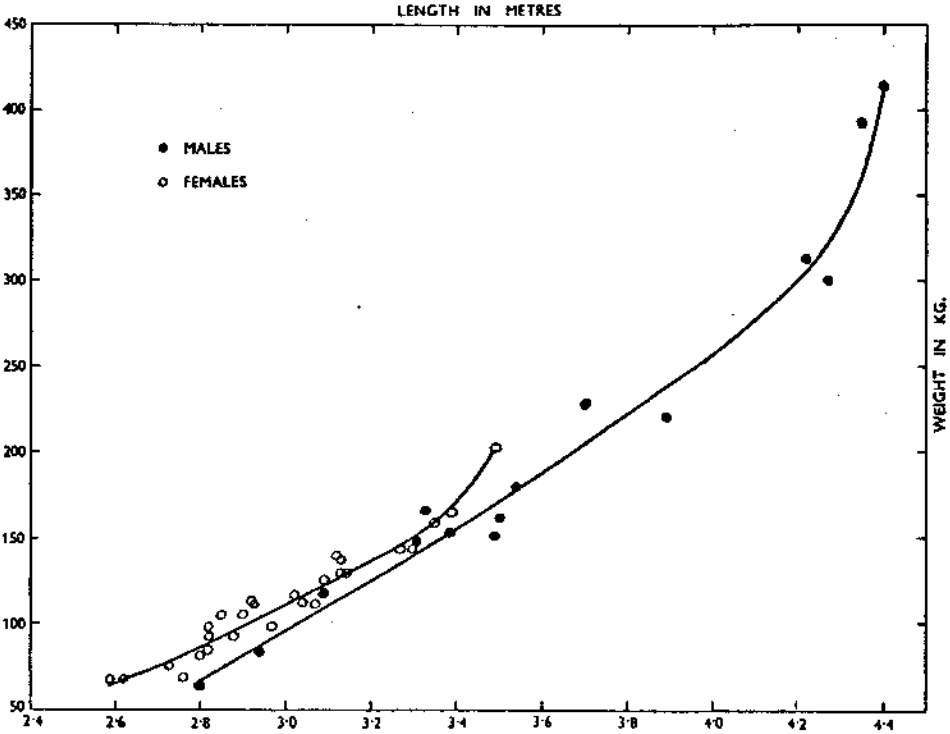

Fig. 19. The relation of length to weight in breeding crocodiles, of both sexes, from Luangwa Valley, Kafue Flats and Upper Zambesi (to which one record from Magungu is added).

eleven years. His protracted observations are of great interest, for they give the only available accurate picture of growth, in the wild state, of specimens whose ages are known. His records reveal a growth differential between the sexes; and indicate the size and age at which the female attains sexual maturity.

TABLE 15

Number and percentage of crocodiles in breeding condition, by length groups. Males—records from Luangwa, Kafue and Upper Zambesi; females—in addition, records from Bangweulu and Mweru.

Length group metres	*Males*			*Females*		
	No. not breeding	*No. breeding*	*Per cent. breeding*	*No. not breeding*	*No. breeding*	*Per cent. breeding*
2·00–2·25	12	0	0·0	18	0	0·0
2·25–2·50	10	0	0·0	20	1	4·8
2·50–2·75	12	0	0·0	12	6	33·3
2·75–3·00	11	2	15·4	6	19	76·0
3·00–3·25	4	1	20·0	7	19	73·1
3·25–3·50	1	4	80·0	1	5	83·3
3·50–3·75	1	3	75·0	—	—	—
3·75–4·00	0	1	100·0	—	—	—
4·00–4·25	—	—	—	—	—	—
4·25–4·50	0	3	100·0	—	—	—

TABLE 16

Length and weight of male and female crocodiles in breeding condition.

Locality	*Size of Sample*	*Length, in m.*			*Weight, in kg.*		
		Max.	*Mean*	*Min.*	*Max.*	*Mean*	*Min.*
Males							
Luangwa Valley	2	2·940	2·870	2·800	83·7	73·3	63·0
Kafue Flats	6	4·400	3·932	3·330	414·5	280·0	166·5
Upper Zambesi	6	3·890	3·445	3·090	221·7	159·0	118·0
Females					?	—	52·2
Bangweulu Swamp	5	3·140	2·840	2·380	143·0	103·4	65·8
Mweru & Kalungwishi	17	3·180	2·951	2·510	75·2	70·0	67·5
Luangwa Valley	4	2·760	2·675	2·590	165·0	126·3	81·5
Kafue Flats	10	3·390	3·075	2·700	201·7	117·0	84·0
Upper Zambesi	14	3·490	3·014	2·820			

Data given by McIlhenny are plotted as a graph in Fig. 20. (a) It will be seen that growth is most rapid in early life. Animals of both sexes show an average increase of about a foot per annum up to the fifth year. This rate of increase is continued by the males until about the seventh year, but after the fifth year the females grow more slowly. The rate becomes progressively slower in both sexes with increasing age. (b) Measurements of specimens killed and sexed between 1927 and 1932 clearly show the disparity in size (amounting to about 1 foot 9 inches in the tenth year) between males and females of corresponding ages.

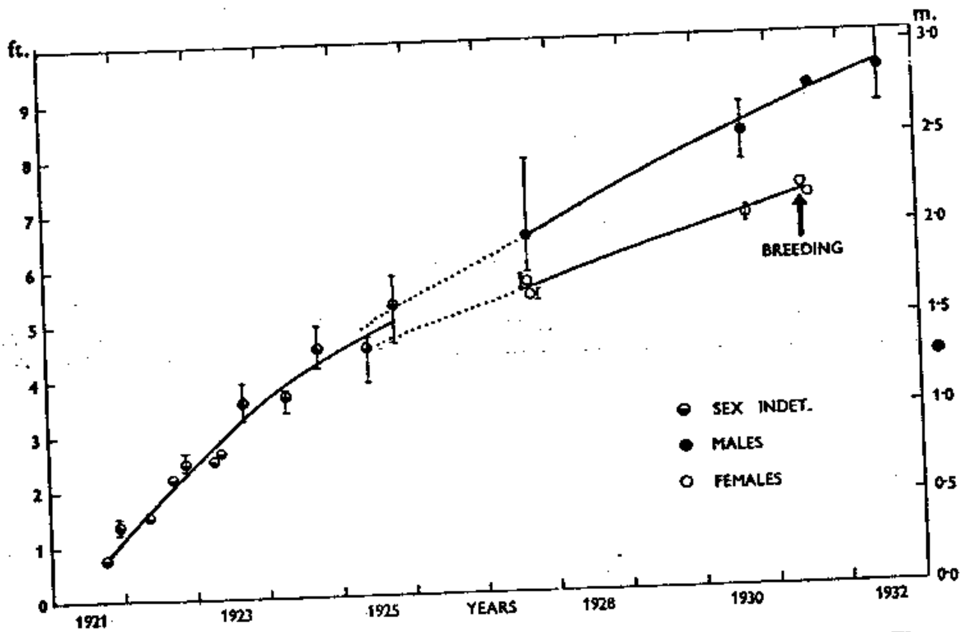

Fig. 20. Growth rate and breeding maturity in *Alligator mississippiensis* (based upon McIlhenny's observations from Avery Island, Louisiana).

this growth differential is not known, but reference to the graphs suggests that divergence may begin as early as in the fourth year of life. (c) The first of the marked females to breed began to nest at the age of nine years ten months, when 7 feet 3 inches in length and 116½ lbs. in weight.

Finally, as regards the age at which sexual maturity is attained: growth in *C. niloticus* is slower than in *A. mississippiensis;* but the recorded minimum length for a breeding female is the same for both species. Thus the female crocodile certainly does not reach maturity before ten years. Assuming that Davison's data represent the growth curve for a female, the age at minimum breeding length—the mean minimum for five localities (Table 16) is 2·60 metres (or 8 feet 6 inches)—would be about nineteen years. But only about half are breeding (see Fig. 18) at the length of 2·75 metres. If Davison's growth curve is that of a male, the time required for a female to attain maturity would be proportionally longer. The age of the average breeding stock will of course be much greater. Apart from mere academic interest, these conclusions have an important bearing upon the problem of crocodile conservation (see p. 327).

The breeding season

The breeding season, here defined as the season between laying and hatching of the eggs, was determined (a) by examination of the gonads in the female; and (b) from the condition of embryos in nest-eggs. By either method it was often possible to determine, within a day or two, the date when eggs were about to be, or had been laid, i.e. as indicated by the presence of fully-shelled eggs in the oviducts or of newly-laid eggs in the nest. In other cases, the laying date could be estimated, more or less accurately, from the developmental stage of embryos.

Dates and localities

Tables 17 and 18 contain the relevant data, including estimated laying dates, for twenty-seven clutches in Uganda and twenty-five clutches in Northern Rhodesia and Barotseland. In all localities other than Lake Victoria there is a single, and apparently fairly well-defined breeding season. In the Upper Victoria Nile and Lake Kioga eggs were laid during the last three weeks of December; in Lake Albert and the Victoria Nile below Murchison, in late December and the first week of January; in Bangweulu Swamp, during the last week of August and the first half of September; and in Mweru Wa Ntipa, the Kalungwishi, Kafue, Luangwa and Upper Zambesi Rivers, during the first three weeks of September. In northern Lake Victoria the situation is anomalous, in that fresh eggs may be found during two periods of the year—in August and early September, and again in December and January.

TABLE 17

Breeding dates : Uganda.

Locality	*Clutch Ser. No.*	*Date found*	*Condition*	*Estimated laying date*
L. Victoria : Nasu Point ..	Ug. 1	11. 1.52	c. 5 days	6. 1.52
Victoria Nile : Namasagale	Ug. a	13. 1.52	c. two weeks	30.12.52
" Namasagale	Ug. b	13. 1.52	c. four weeks	16.12.52
" Namasagale	Ug. c	13. 1.52	c. five weeks	9.12.52
Lake Victoria : Simu ..	Ug. 2	26. 2.52	c. five weeks	22. 1.52
" Simu ..	Ug. 3	26. 2.52	near hatching	11.12.51
" Mu ..	Ug. 4	28. 2.52	c. ten weeks	20.12.51
L. Kioga : Kigi	Ug. 5	4. 3.52	c. ten weeks	24.12.51
" Kigi	Ug. 6	4. 3.52	c. ten weeks	24.12.51
" Kigi	Ug. 7	4. 3.52	hatched 5–10.3.52	10.12.51
L. Victoria : Dagusi ..	Ug. 8	14. 8.52	c. 5 days	9. 8.52
" Buvuma ..	Ug. 9	16. 8.52	new laid	15. 8.52
" Buvuma ..	Ug. 10	30. 8.52	c. 4 days	26. 8.52
" Bulago ..	Ug. 11	2. 9.52	new laid	1. 9.52
" Bulago ..	Ug. 12	2. 9.52	c. 3 days	30. 8.52
" Bulago ..	Ug. 13	2. 9.52	new laid	1. 9.52
" Masovwe ..	Ug. 14	5. 9.52	c. two weeks	22. 8.52
" Mbazi ..	Ug. 15	5. 9.52	new laid	4. 9.52
" Buvu ..	Ug. 16	8. 9.52	c. ten weeks	30. 8.52
" Buvu ..	Ug. 17	8. 9.52	hatched 10–22.11.52	24. 8.52
Albert Nile : Buligi.. ..	Ug. 18	23.12.56	new laid	22.12.56
Victoria Nile : Fajao ..	Ug. 19	2. 1.57	new laid	2. 1.57
" Fajao ..	Ug. 20	5. 1.57	new laid	4. 1.57
" Fajao ..	Ug. 21	5. 1.57	c. 36 hours	3. 1.57
" Fajao ..	Ug. 22	5. 1.57	c. 10 days	26.12.56
" Fajao ..	Ug. 23	5. 1.57	c. 36 hours	3. 1.57
" Fajao ..	Ug. 24	7. 1.57	new laid	6. 1.57

While it is not suggested that the breeding season is confined within the narrow limits shown by the above observations, the dates are supported by information given me from the same localities by other observers. Thus, in Uganda, Wajalubi found crocodiles laying in the Semliki valley in December and hatching in March. Miss R. H. Lowe found crocodiles hatching at the end of March at Buhuka, Lake Albert, and in Lake Victoria Pitman (1936) reports laying in early August and hatching in late October and early November.

The following additional information is available from Northern Rhodesia. In the Luapula River and Bangweulu Swamp Holloway found newly-hatched young between 6th and 26th November during several seasons prior to 1952. According to the village headman at Kansenga (Bangweulu) crocodiles hatch in November in Lake Chali. Ansell (1.10.58) records a clutch new-laid on 11th September from the Luombwa River ; and (in litt. 8.12.59) a clutch ready to hatch in mid-November in the Kabompo District. From the Kafue, Poles (1956) found shelled oviduct eggs on 6th September. A clutch taken at Kafue Hook hatched on 8–17th December (Taylor, 1957). The late P. I. R. Maclaren (30.1.56) again confirmed that hatching takes place during the early rains in Northern Rhodesia.

TABLE 18

Breeding dates : Northern Rhodesia

Locality	*Clutch Ser. No.*	*Date found*	*Condition*	*Estimated laying date*
Bangweulu : L. Chali ..	NR. 1	21. 8.56	shelled oviduct eggs	24. 8.56
,, L. Bumba ..	NR. 2	30. 8.56	unshelled oviduct eggs	15. 9.56
,, L. Bumba ..	NR. 3	30. 8.56	shelled oviduct eggs	2. 9.56
,, Chambesi R. ..	NR. 4	1. 9.56	shelled oviduct eggs	4. 9.56
,, L. Bumba ..	NR. 5	2. 9.56	shelled oviduct eggs	5. 9.56
,, L. Bumba ..	NR. 6	2. 9.45	shelled oviduct eggs	5. 9.56
Mweru Wa Ntipa : Katema ..	NR. 7	13. 9.56	c. one week	6. 9.56
,, ,, Katema ..	NR. 8	13. 9.56	new laid	12. 9.56
,, ,, Kampinda	NR. 9	14. 9.56	unshelled and shelled oviduct eggs	22. 9.56
,, ,, Kampinda	NR. 10	15. 9.56	shelled oviduct eggs	18. 9.56
,, ,, Kampinda	NR. 11	15. 9.56	shelled oviduct eggs	18. 9.56
Kalungwishi R. : Ollandi ..	NR. 12	18. 9.56	shelled oviduct eggs	21. 9.56
,, Ollandi ..	NR. 13	18. 9.56	shelled oviduct eggs	21. 9.56
,, Ollandi ..	NR. 14	18. 9.56	shelled oviduct eggs	21. 9.56
Kafue Flats : Chimwajila ..	NR. 15	22. 8.57	unshelled and shelled oviduct eggs	28. 8.57
,, ,, Iyeshya ..	NR. 16	30. 8.57	shelled oviduct eggs	1. 9.57
Kafue R. : Kafue Hook ..	NR. 17	7. 9.57	new laid	7. 9.57
Luangwa R. :	NR. 18	25. 9.57	new laid	24. 9.57
Upper Zambesi : Mongu ..	NR. 19	10. 9.57	shelled oviduct eggs	13. 9.57
,, ,, Mongu ..	NR. 20	12. 9.57	shelled oviduct eggs	15. 9.57
,, ,, Mongu ..	NR. 21	13. 9.57	shelled oviduct eggs	16. 9.57
,, ,, Mongu ..	NR. 22	16. 9.57	shelled oviduct eggs	19. 9.57
,, ,, Mongu ..	NR. 23	16. 9.57	shelled oviduct eggs	19. 9.57
,, ,, Mongu ..	NR. 24	18. 9.57	shelled oviduct eggs	21. 9.57
,, ,, Mongu ..	NR. 25	18. 9.57	shelled oviduct eggs	21. 9.57

Environmental factors

In all localities the breeding season is found to coincide with changes in one environmental factor, namely, the water level. Figs. 21–25 and 27 show (a) the breeding season ; and (b) the annual fluctuations in water levels—for six localities and over a period of several years—plotted from data supplied by the Water Development Department, Entebbe (Stations at Jinja and Fajao), and by the Water Development and Irrigation Department, Hydrological Section, Northern Rhodesia (Stations at Samfya, Mofwe, Namwala and Lukulu).

It will be seen that in all localities (other than northern Lake Victoria) the eggs are laid during the dry season at a time when the water level has already been falling for several weeks ; that some part of the incubation period coincides with the phase of lowest water ; and that hatching occurs after the onset of rains when the lakes and rivers are again rising into flood.

TABLE 18

Breeding dates : Northern Rhodesia

Locality	*Clutch Ser. No.*	*Date found*	*Condition*	*Estimated laying date*
Bangweulu : L. Chali ..	NR. 1	21. 8.56	shelled oviduct eggs	24. 8.56
" L. Bumba ..	NR. 2	30. 8.56	unshelled oviduct eggs	15. 9.56
" L. Bumba ..	NR. 3	30. 8.56	shelled oviduct eggs	2. 9.56
" Chambesi R. ..	NR. 4	1. 9.56	shelled oviduct eggs	4. 9.56
" L. Bumba ..	NR. 5	2. 9.56	shelled oviduct eggs	5. 9.56
" L. Bumba ..	NR. 6	2. 9.45	shelled oviduct eggs	5. 9.56
Mweru Wa Ntipa : Katema ..	NR. 7	13. 9.56	c. one week	6. 9.56
" " Katema ..	NR. 8	13. 9.56	new laid	12. 9.56
" " Kampinda	NR. 9	14. 9.56	unshelled and shelled oviduct eggs	22. 9.56
" " Kampinda	NR. 10	15. 9.56	shelled oviduct eggs	18. 9.56
" " Kampinda	NR. 11	15. 9.56	shelled oviduct eggs	18. 9.56
Kalungwishi R. : Ollandi ..	NR. 12	18. 9.56	shelled oviduct eggs	21. 9.56
" Ollandi ..	NR. 13	18. 9.56	shelled oviduct eggs	21. 9.56
" Ollandi ..	NR. 14	18. 9.56	shelled oviduct eggs	21. 9.56
Kafue Flats : Chimwajila ..	NR. 15	22. 8.57	unshelled and shelled oviduct eggs	28. 8.57
" " Iyeshya ..	NR. 16	30. 8.57	shelled oviduct eggs	1. 9.57
Kafue R. : Kafue Hook ..	NR. 17	7. 9.57	new laid	7. 9.57
Luangwa R. :	NR. 18	25. 9.57	new laid	24. 9.57
Upper Zambesi : Mongu ..	NR. 19	10. 9.57	shelled oviduct eggs	13. 9.57
" " Mongu ..	NR. 20	12. 9.57	shelled oviduct eggs	15. 9.57
" " Mongu ..	NR. 21	13. 9.57	shelled oviduct eggs	16. 9.57
" " Mongu ..	NR. 22	16. 9.57	shelled oviduct eggs	19. 9.57
" " Mongu ..	NR. 23	16. 9.57	shelled oviduct eggs	19. 9.57
" " Mongu ..	NR. 24	18. 9.57	shelled oviduct eggs	21. 9.57
" " Mongu ..	NR. 25	18. 9.57	shelled oviduct eggs	21. 9.57

Environmental factors

In all localities the breeding season is found to coincide with changes in one environmental factor, namely, the water level. Figs. 21–25 and 27 show (a) the breeding season ; and (b) the annual fluctuations in water levels—for six localities and over a period of several years—plotted from data supplied by the Water Development Department, Entebbe (Stations at Jinja and Fajao), and by the Water Development and Irrigation Department, Hydrological Section, Northern Rhodesia (Stations at Samfya, Mofwe, Namwala and Lukulu).

It will be seen that in all localities (other than northern Lake Victoria) the eggs are laid during the dry season at a time when the water level has already been falling for several weeks ; that some part of the incubation period coincides with the phase of lowest water ; and that hatching occurs after the onset of rains when the lakes and rivers are again rising into flood.

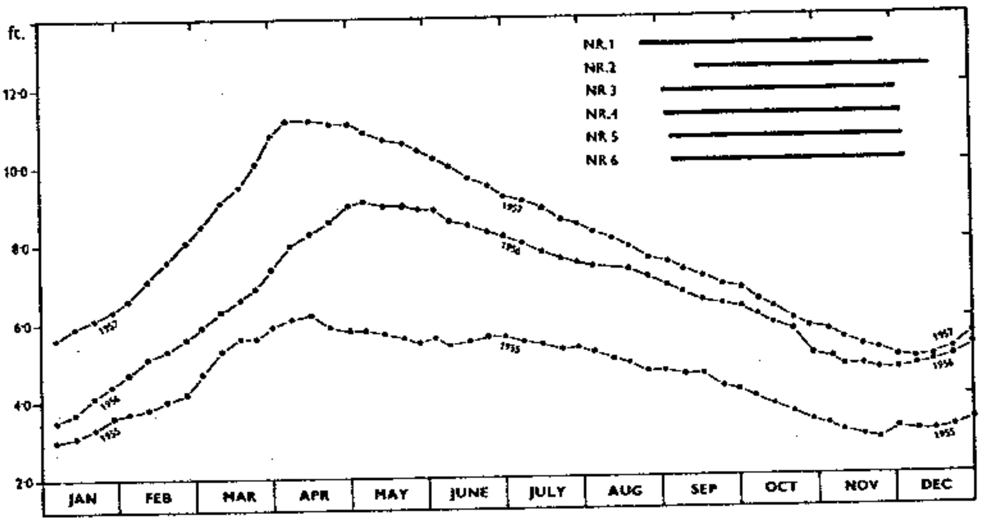

Fig. 21. Breeding records for *C. niloticus* from Bangweulu Swamp. Water levels are those recorded at Samfya for the years 1955–57.

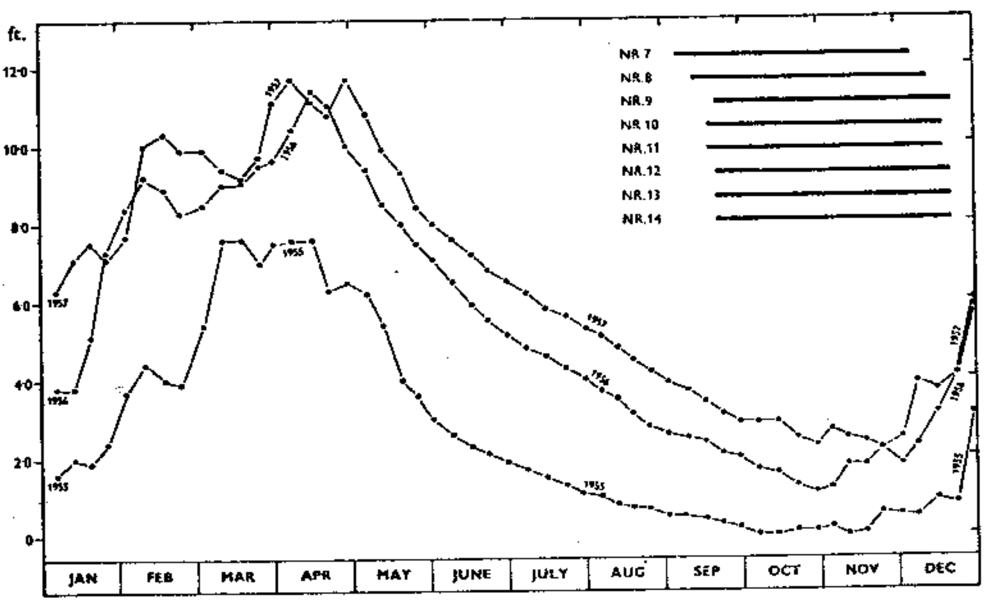

Fig. 22. Breeding records for *C. niloticus* from Mweru Wa Ntipa and Kalungwishi River. Water levels are those recorded at Mofwe for the years 1955–57.

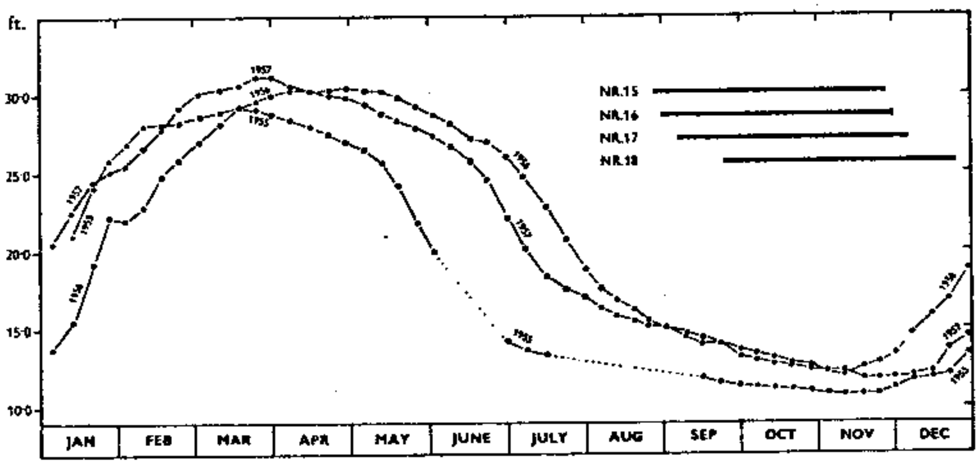

Fig. 23. Breeding records for *C. niloticus* from Kafue Flats and Luangwa River. Water levels are those recorded at Namwala for the years 1955–57.

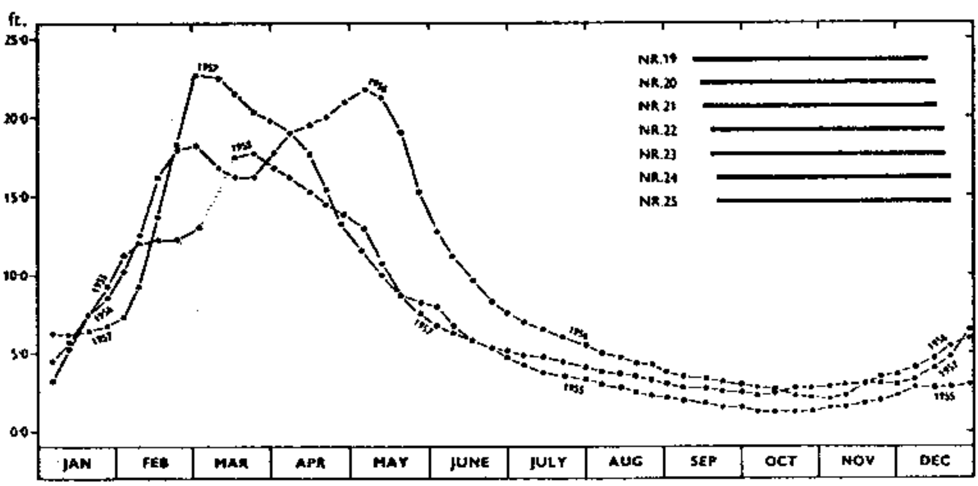

Fig. 24. Breeding records for *C. niloticus* from Upper Zambesi, Barotseland. Water levels are those recorded at Lukulu for the years 1955–57.

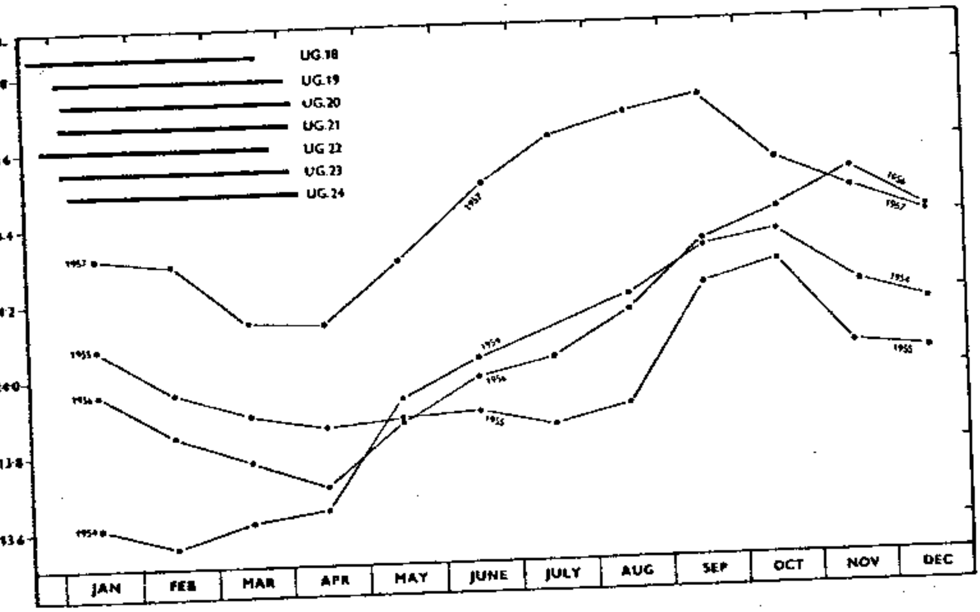

Fig. 25. Breeding records for *C. niloticus* from Victoria Nile below Murchison Falls. Water levels are those recorded at Fajao for the years 1954–57.

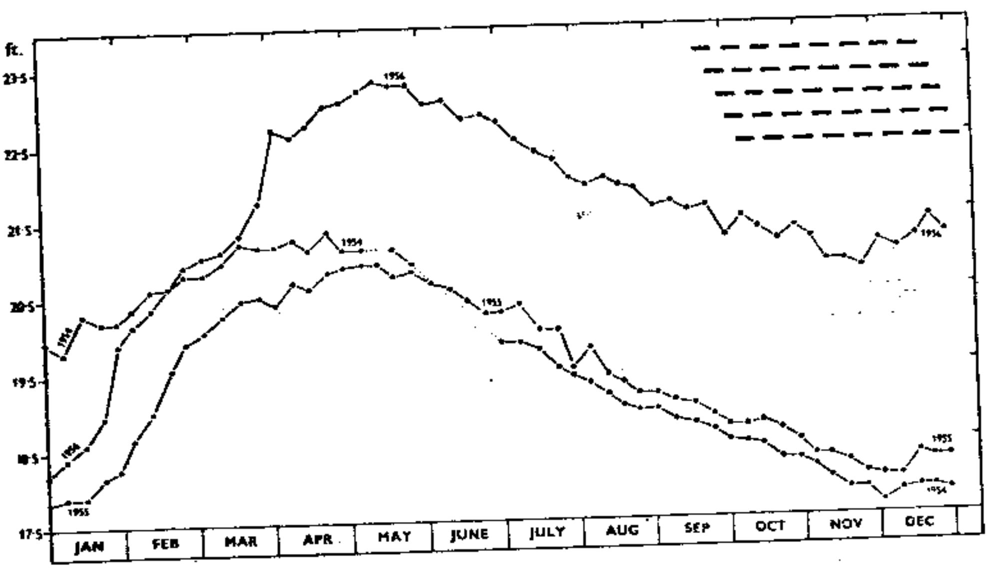

Fig. 26. Breeding season of *C. niloticus* in Lake Nyasa. Water levels are those recorded at Fort Johnston for the years 1954–56.

The correlation between breeding and climatic cycles also obtains in certain localities which lie outside the scope of the present survey. Thus Mitchell (5.6.57) reports from Lake Nyasa: "Nests containing new laid eggs can be found from about the 20th September into the first week of October. I have examined many nests near Karonga in the Northern Province, Domira Bay in the Central Province, and Fort Johnson in the Southern Province, and the breeding season holds over the whole lake." Mitchell has supplied me with data for water levels in Lake Nyasa (Station, Fort Johnson). The cycles in this lake are shown graphically in Fig. 26.

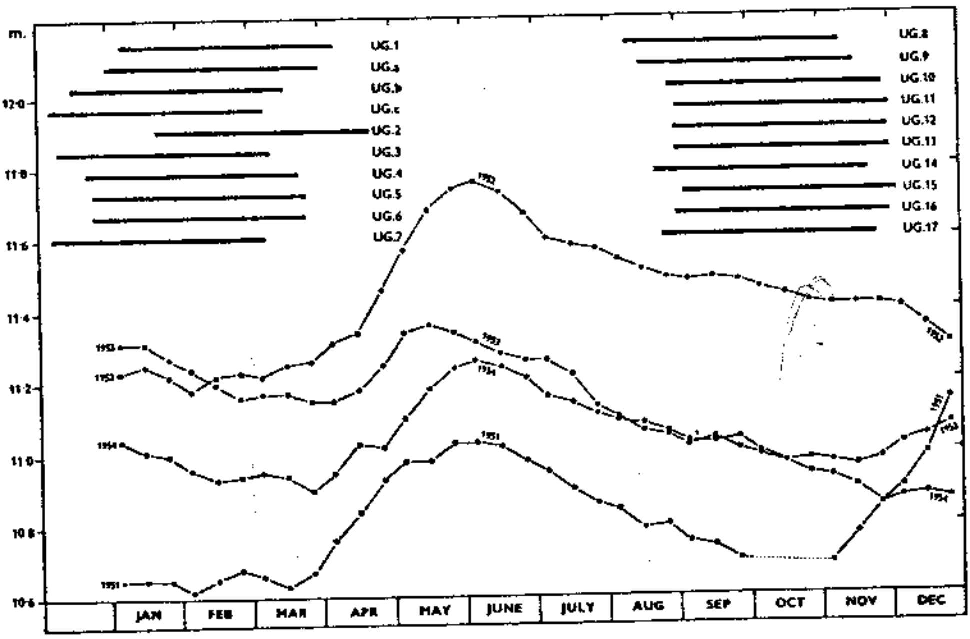

Fig. 27. Breeding records for *C. niloticus* from Lakes Victoria and Kioga. Water levels are those recorded at Jinja for the years 1951–54.

The situation in northern Lake Victoria is complicated by the ill-defined wet and dry seasons—which occur twice annually. Mean monthly rainfall data for Entebbe, over a period of 55 years, are as follows (Annual Report, 1951, East Africa Met. Dept.):

Jan. 2·69 ins.	Apr. 10·26 ins.	July 2·98 ins.	Oct. 2·76 ins.
Feb. 3·46 ,,	May 9·38 ,,	Aug. 3·02 ,,	Nov. 5·08 ,,
Mar. 6·31 ,,	June 4·71 ,,	Sept. 2·93 ,,	Dec. 4·53 ,,

The relation of the breeding season in northern Lake Victoria to monthly rainfall is shown diagramatically in Fig. 28. The lake water reaches its lowest level in February-March, but there is a second low water period in October-November. The two incubation periods are here again synchronised with the time of low water, and the laying periods with falling, and the hatching time with rising levels (see Fig. 27).

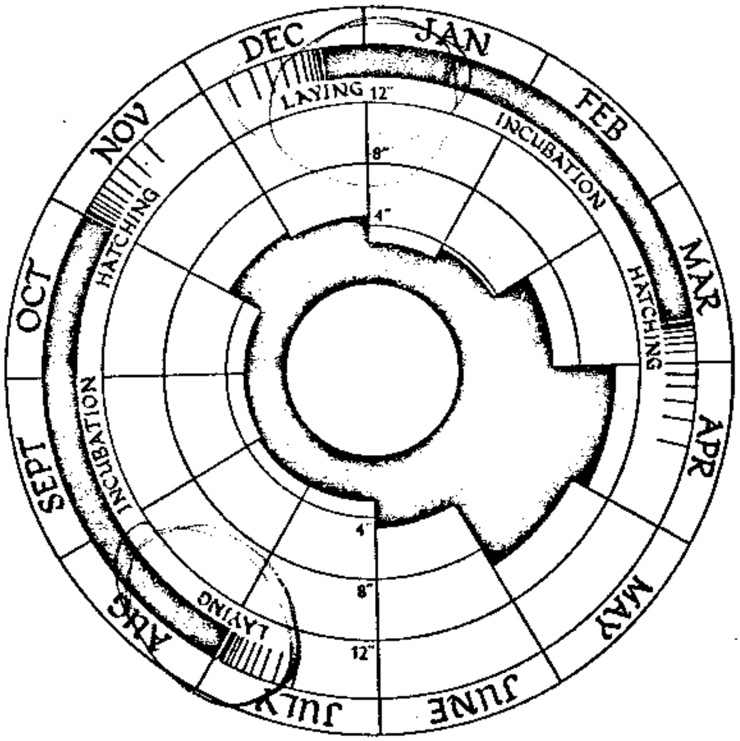

Fig. 28. Diagram showing the relation of breeding seasons of *C. niloticus* in northern Lake Victoria to seasonal changes in rainfall. Rainfall data are taken from East Africa Met. Dept. Annual Report 1951 and show monthly average for 55 years.

As is well known, in many other animals the reproductive cycle is in some way correlated with the seasonal rhythm of rainfall. In tropical regions especially, where dry and rainy seasons alternate, the breeding of birds and other animals is adapted to this environmental variant. In such cases, nesting normally occurs after the first heavy rains. For example, in Australian birds of many orders, reproduction is influenced or controlled by the breaking of the monsoon (Matthews, 1910–27 ; Marshall, 1954 ; Keast & Marshall, 1954). This connexion between precipitation and breeding is strikingly illustrated in Ceylon, where the north-east and south-west monsoons affect the island, and so affect the breeding season, at different times of the year (Baker, 1938).

In other species, rainfall affects the breeding season in an opposite, and indirect way. Such birds breed in the dry season and appear to respond to falling water levels and the consequent emergence of suitable nesting sites. For example, in Bear Island, Lack (1933) found that the breeding time of the Arctic Tern (*Sterna macrura*) was influenced by the condition of the nesting place, and that where low-lying grounds were flooded by late melting snow ovulation might be deferred for over three weeks. Similarly, the Australian Pelican (*Pelecanus conspicillatus*) is reported by MacGillivray (1923) to breed on islands that form as the floods subside—the laying dates coinciding with the progressive exposure of nest sites.

The Southern Carmine Bee-eater (*Merops nubicoides*) which nests in steep river banks left exposed in the dry season, is found breeding in late September in Nyasaland, in the first half of October in Portuguese East Africa, and in early November on the Zambesi (Chapin, 1939): in the Luangwa Game Reserve, Northern Rhodesia, we found these birds nesting in late September. These dates roughly coincide with the time of low water.

The Pied Kingfisher (*Ceryle rudis*) is another river-bank nester which makes its burrows as soon as the water level has fallen far enough for it to do so. It breeds in early May in Egypt (Meinertzhagen, 1930) and in August onwards in South Africa (Macworth-Praed & Grant, 1952-55). In India this kingfisher nests from November to March " after the rains have ceased sufficiently long for the rivers to fall and expose their banks and before they rise enough to flood the nest-holes " (Baker, 1932–35). The Indian Sand Martin (*Riparia riparia*) nests similarly and during the same months.

Another Indian kingfisher, *Halcyon smyrnensis*, breeds in February and March in rivers subject to spring floods, the young being fledged before the melting snows cause the first rush of water; but in the banks of canals, which are not subject to flooding, the laying season is two months later (Baker, *ibid.*).

In all these cases reproduction is in some way related to falling levels and to the emergence of suitable nesting places, as also in the case of the Nile Crocodile. Indeed, in *M. nubicoides* the parallel is close, both bird and reptile nesting at approximately the same time of year in the same river beds. Again, an alternative breeding season, such as obtains among crocodiles in Lake Victoria, has also been recorded among birds. An example is the Wood-swallow (*Artamus melanops*) of Western Australia, which nests in February and March, or in June and July, or at both times, according to the rainfall (Robinson, 1933)—though in this case nesting is related to precipitation, rather than drought.

It is not known how the seasonal variants achieve their effect in the crocodile, and no experimental work has been done on this problem. Nor is it possible to say what is the extrinsic regulating factor—whether drought, temperature, insolation, water level or the psychological effect of available breeding grounds. An environmental factor which may be considered of importance is falling water, but there is no proof that this variant *per se* stimulates ovulation.

On the other hand, the biological advantages resulting from the habit are evident. (1) Crocodile eggs are known to be sensitive to moisture (Voeltzkow, 1893); and they would in any case be destroyed if the nest was flooded. Yet they must be located near enough to permanent water to allow easy access to the young on hatching. The siting of the nest and the timing of the incubation period are both nicely adjusted to meet these requirements. (2) We have seen that the hatching time normally coincides with the breaking of the rains, and thus with rising floods. This timing affords optimum conditions for the newly-hatched young, because the inundation of the plains facilitates their dispersal and opens up new retreats and feeding grounds in the wide-spreading shallows; while the rains are followed by a rich harvest of insect food on which the early young subsist.

Breeding behaviour

Territory and combat

Little is precisely known regarding territorial behaviour in the breeding season. However the fact is well established that inter-male rivalry frequently finds expression in combat (see p. 307). Pitman (1931, 1941, 1942) states that crocodiles are notorious for fighting among themselves, and that where they are abundant they indulge in terrific contests, which often terminate fatally. Mr F. Wilson tells me that he has himself seen two large crocodiles, which he believed to be males, fighting in the water, in Kadam Bay.

What is not clear, however, are the circumstances under which these contests take place. Some of the inter-male fighting at breeding time may be for the possession of mates. According to Deraniyagala (1939) males of *C. porosus* are said to fight each other for the females ; Clarke (1891) refers to fierce battles among males of *A. mississippiensis* in the breeding season ; and Bartram (1791) gives a graphic description of a fight he witnessed.

On the other hand, fighting in defence of territory does occur, at any time of the year, the area so defended being a basking-ground or feeding-place. Below Murchison Falls, particular individuals were seen in possession of the same basking site on different occasions. And several instances are known of a large male taking possession of a favourite watering place, from which it will drive away all rivals (Stevenson-Hamilton, 1954 ; Pitman, 1931). For example, the famous "Lutembe" of Entebbe, which would come for food when called and always occupied a particular part of the water-front, for years drove away rivals and thus ensured the safety of his domain, until, in old age, he was no longer able to do so.

Vocalization

Crocodiles utter a variety of sounds, at different periods of the life-history and under different circumstances.

(1) There is the yapping or croaking call—"umph" or "aõ" of the unhatched, or newly-hatched young, which is the signal for maternal help, or, after birth, a distress signal.

(2) A sharp, coughing hiss is uttered as part of the threat display when a crocodile is cornered and unable to make its escape to the water. This was observed by me in the Luangwa Game Reserve, and similar behaviour has been reported by Player from Zululand.

(3) A low growl is sometimes heard when a female is surprised guarding her eggs (Charles Magala, pers. comm.). Hippel tells me that a crocodile caught in a trap will, when approached, growl like an angry bull.

(4) Wounded crocodiles sometimes utter a bellow of pain ; and Pitman's report (unpub. notes) of an eleven-foot female which he shot at Lwera, and which "died bellowing in the swamp," proves that loud vocal effects are not confined to the male sex.

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(5) During the breeding season, basking males often bark or cough, as I heard them do on many occasions at Magungu, the note being deep, loud, hollow and abrupt.

(6) The most powerful and remarkable demonstration of a crocodile's repertoire is the full roar. The animal, which has been lying on the mud with jaws agape, first elevates its head and opens its jaws yet wider in what appears to be a prodigious yawn (Plate 4, fig. 2). The roar is a growling rumble, very deep in pitch, rattling, vibrant and sonorous, like distant thunder or the roll of a big drum, which is protracted and may persist for six or seven seconds. Jobson (in Cuvier, 1831) gives an apt comment when he speaks of the sound as if coming from the bottom of a well.

In my experience, roaring is only heard in the breeding season. It is generally believed that the roar is an attribute of the male, but it is not certainly known whether the female responds vocally. Judging by the large size of animals seen roaring on the grounds at Magungu and Fajao, these were undoubtedly males. In this connexion, Schmidt (1919) states : " Though I have never had conclusive proof that females were not endowed with so strong a vocal organ, in several instances bullets snuffed out the lives of actual performers and they proved to be males."

While the biological function of the roar is not clearly understood, from the available evidence it appears to be a mating call directed towards members of the opposite sex, rather than a threat directed against rivals. In the first place, it is known that the call does attract crocodiles to the caller : indeed, in 1952 there was a native at Butiaba who collected crocodiles for sale by imitating the roar with vocal and drumming effects. Again, in reference to the reduction of crocodiles resulting from his campaign against females on the breeding grounds in Lake Victoria, Pitman (1948) has pointed out that unless the males attract the females, it is difficult to account for the continued replacements of casualties to the adult female stock. A case is also reported from the Belgian Congo by Schmidt (1919) of a large solitary male which announced its presence by bellowing, and was later joined by two other crocodiles. Hippel told me he believes the female also calls the male—the sound being a growling roar rising to a crescendo and quite distinct from the male's roar.

Copulation

Copulation of the Nile Crocodile has very rarely been witnessed in the field ; and nothing useful has been published on the subject. Sonnini (1800) was certainly mistaken in believing that during congress the female is turned upon her back ashore. Equally improbable is the report of Sinhalese crocodile hunters that, in *C. porosus*, " copulation is effected by both animals raising themselves in an embrace in shallow water, the forequarters in the air, the jaws usually interlocked " (Deraniyagala, 1939).

On January 1st, 1956, from the Magungu hide, I witnessed the preliminaries to pairing. At 2.54 p.m., while attending to one of the cameras, I heard splashing and commotion in the water but a few yards away, where two crocodiles were lying in the shallows. The smaller of the pair then thrust her head and forequarters high out of the water, the mouth widely agape and pointing heavenwards, and uttered a creaking or groaning sound. Immediately afterwards the male, who had been lying awash, reappeared at the surface, approached his mate from behind, and mounted her. Then both crocodiles moved off into deeper water and submerged together.

On several previous occasions at Fajao crocodiles near the opposite shore had been seen to rear high out of the water, and with the head pointed towards the sky, indulge in a prolonged yawning display, but at the time I had not appreciated the possible significance of this demonstration—as a pre-nuptial display by a breeding female. This interpretation is supported by observations (then unknown to me) of Dharmakumarsinji (1947), who witnessed a somewhat similar display in *C. palustris* on the Shetrunji River. As one crocodile (sex not noted) came close to its partner, he says : "I distinctly saw it with closed mouth raise its head and neck high out of the water, pointing its snout at an angle of about 70 degrees for a few seconds." Copulation followed the display, near the surface in deep water.

In Northern Rhodesia a member of the Game Department witnessed copulation in *C. niloticus*; and in response to enquiries Major W. E. Poles (5.2.57) has been kind enough to send the following particulars which, on account of the rarity of such observations, I quote in full. "A young ranger named Hough, who was drowned by a crocodile shortly afterwards, accompanied me on a long tour down the Luangwa in July and August, 1951. On the 2nd August he was watching crocodiles where the reptiles are very plentiful and witnessed the mating of two large ones. He described how one was basking in the shallows, with its head and shoulders out of the water, resting on a sand bank. Another crocodile appeared from deep water and swam alongside. The basking crocodile, which seemed to be the female, rolled over, exposing her belly and the male covered her with his shoulders. The female rolled over again and the male mounted her and copulation took place. . . . The mating took place in shallow water and lasted only a short time, after which both crocodiles returned to deep water and submerged. They made no vocal sound. At the time I was unaware of the importance of Hough's observation or I would have questioned him more closely and made detailed field notes".

Apart from the above observations, little is known. When questioned, Wajalubi assured me that in his experience copulation takes place in the water ; and he also stated that a female on land which is ready to mate, raises up the tail as she goes into the water. Wosseler (1915), who observed courtship of *C. niloticus* in Hamburg Zoological Gardens, reports a "gasping roar" during copulation. And Descourtilz (1809) also states that *C. americanus* roars during copulation.

NESTING ACTIVITY

The nest site

Choice of a nesting site is governed by three factors : (1) a sufficient depth of soil to provide a pit where the eggs can be deposited ; (2) nearby shade into which the guardian mother can retire during the heat of the day ; and (3) access to permanent water.

Soil

The eggs are usually found in the coarse sand of spits, riverside mud-flats, low-lying islets, lake-side beaches, or in the bed of a dried watercourse. But in rocky habitats, where deep earth is not available, crocodiles will lay in shallow gravel beds : this was the case both on Katema Island in Mweru Wa Ntipa, and on precipitous rocky islands near Bugondo, Lake Kioga. At Kigi Island in this lake the reptiles had to climb steep stone screes to reach the nesting ground at the summit, some fifty feet above the water. In 1956–7, along the Murchison reach of the Nile, several females were found nesting in isolation away from the main grounds, high up on precipitous, eroded banks (Plate 7, fig. 1).

Shade

A crocodile cannot lie exposed to the full glare of the sun for protracted periods : hence nearby shade or cover, from which the female can continue to watch over the eggs, is essential. In Uganda the sites—while differing greatly in other respects—were almost invariably on dunes overgrown with scrub, in lake-side thickets or near the fringing forest, beside isolated forest trees, or beneath an overhanging cliff. This need for shade is confirmed by the experience of Hippel (pers. comm.) and Pitman (unpub. notes). In Northern Rhodesia, however, Attwell told me that nests were sometimes dug in the open, and in September 1957 we found one nest far from any adequate cover, on top of an exposed sandhill of the Luangwa River.

Water

The nesting grounds are usually within easy reach of permanent water. But in dry water courses of the Murchison Nile some nests were found over a hundred yards from the main river. Savidge (27.4.57) also reports four nests from the Nansika tributary which were 200 yards from the river. A nest at Buvu Island was separated from the lake by a 200-yard belt of impenetrable fringing forest. And Charles Magala assured me he had known crocodiles to go about 400 yards from water to reach a suitable nesting place.

Colonial sites

Where crocodiles are entirely free from disturbance, and allowed to breed as they have doubtless done from time immemorial, they nest gregariously, the nests lying so close together that, after hatching time, the rims of the craters are almost contiguous. At Ntoroko peninsula (Fig. 29), between the Wasa and Muzezi Rivers, S. Lake Albert, two such communal sites still remained in 1952. Here in April I found many craters—the young having hatched—spaced apart, somewhat like Sandwich Terns' nests in territories, in places only three to four yards from centre to centre. In one colony, near the sandspit at the north end of the peninsula (Fig. 30), seventeen craters were found in an area 25 x 22 yards ; in the other (Fig. 31), in dunes a mile south, between the Muzezi and a lagoon, twenty-four craters were concentrated in an area 26 x 24 yards.

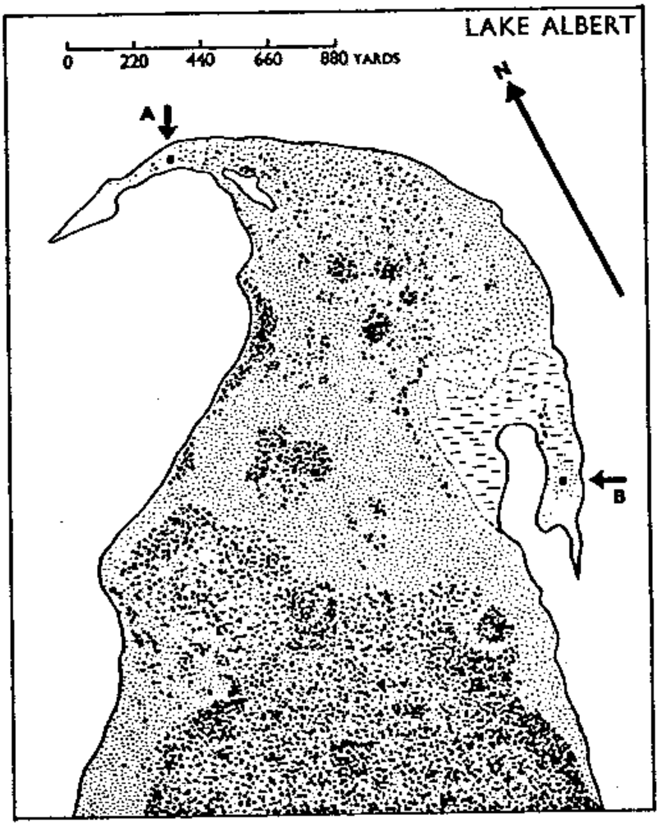

Fig. 29. Sketch map of peninsula between the Waza and Muzezi Rivers, at Ntoroko, Lake Albert. The arrows indicate the position of two colonial nesting grounds.

In the thirties, Pitman knew many such communal grounds in Lake Victoria. On the Buvu site (since deserted) he told me he had seen about thirty nests. Colonial nesting has also been reported from other parts of Africa. Thus Grabham (1909) found three nests, about a yard apart, in the bed of the Rahad River, a tributary of the Blue Nile ; and Adamson (1955) has published a photograph of a communal site on the uninhabited island in Lake Rudolf, which shows nine or ten craters dispersed at intervals of about two yards. In Nyasaland, Mitchell (1946) reports finding six nests in an area ten yards square, and nearby the crowded nests could not be counted as they were overlying each other.

This aspect of the nesting behaviour is of special interest, since the colonial habit is probably normal for the species. But it is incompatible with present-day disturbance. In most areas the breeding population has been depleted, the ancestral nurseries are deserted, and the crocodiles that survive are dispersed. Meanwhile, we remain almost ignorant of the ecology of breeding crocodiles in their former state of abundance. For example, it is not known whether, on the communal

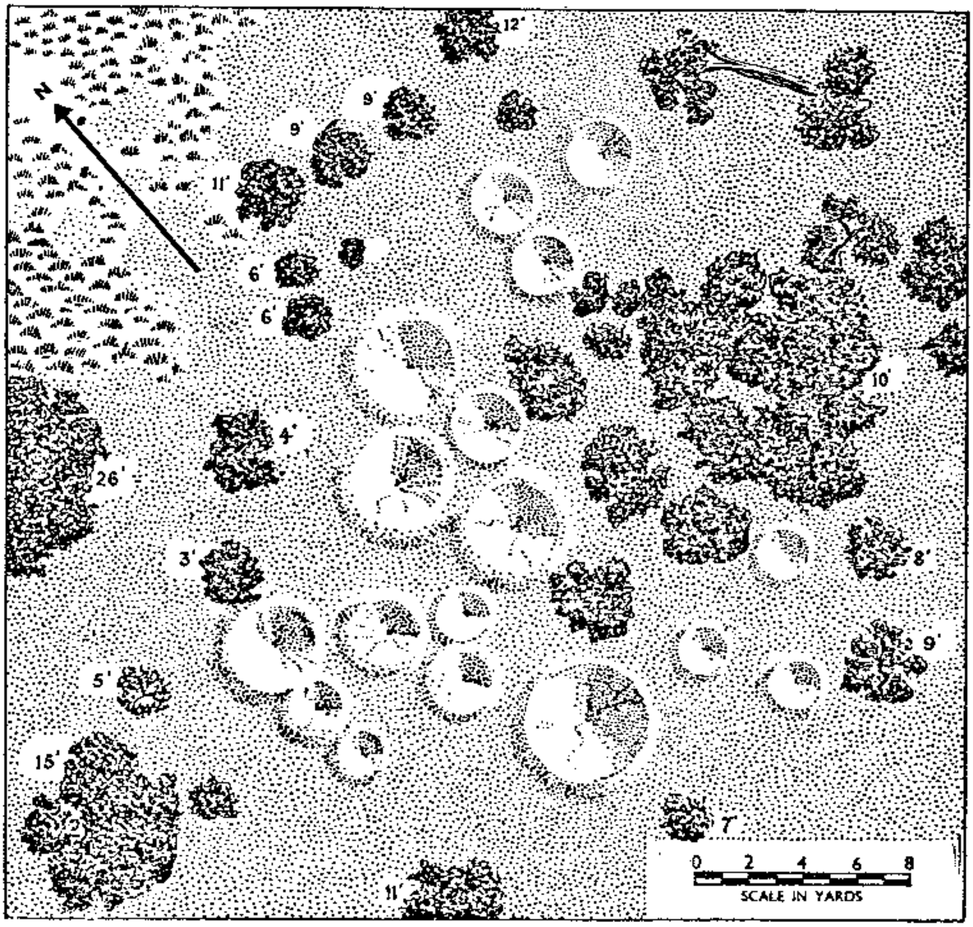

Fig. 30. Colonial nesting ground at A (See Fig. 29) : showing diameter and proximity of excavated nests and position and approximate height of shade trees and bushes.

grounds, a female occupied and defended the territory round her nest ; whether she covered her own clutch or lay on the grounds indiscriminately ; whether the site was guarded by all the females that had nests there, or by a few members of the group. Nor is anything certainly known of conditions at night—whether the grounds were occupied or deserted ; nor of the relations between breeding females to each other and to the young when the eggs were hatching. With the rapid changes now taking place all over Africa, such questions relating to the primeval breeding behaviour may well remain unanswered.

Fig. 31. Colonial nesting ground at B (See Fig. 29) ; other details as in Fig. 30.

Egg laying

Little is precisely known of the female's procedure at laying time. Observations of Voeltzkow (1899) suggest that the eggs are deposited at night, as are those of marine turtles, such as *Chelonia midas* (Hendrickson, 1958) and *Dermochelys coriacea* (Tweedie, 1953), or shortly before dawn. A game guard reported to Major G. E. Taylor that he had seen a crocodile digging its nest near the river at Kafue Hook " in the early morning," 5th September, 1957 : eggs were found in the nest two days later.

Where there is a sufficiency of sand, the female digs a hole about two feet deep, and lays the eggs in tiers. During the process sand falls, or is shovelled, among the eggs, so that though closely-packed they are yet separated, more or less, from one another, like the currants in a cake. The upper eggs are generally about one foot beneath the surface ; but in gravel they are sometimes scantily covered, and in such situations the eggs are tightly packed and the shells often dented.

After laying the female fills in the cavity with earth and leaves the surface flush, so that, save for tracks or the imprint of her belly shields, no sign of the nest remains visible.

Clutch size

Clutches over 80 are uncommon, and over 85 rare. Wilson & Felkin (1882) record a nest of 82 eggs from the Sudan ; L. E. Vaughan (29.3.56) reports 87 eggs from Northern Rhodesia ; and L. Trollope found a clutch of 92 eggs on the Chobe

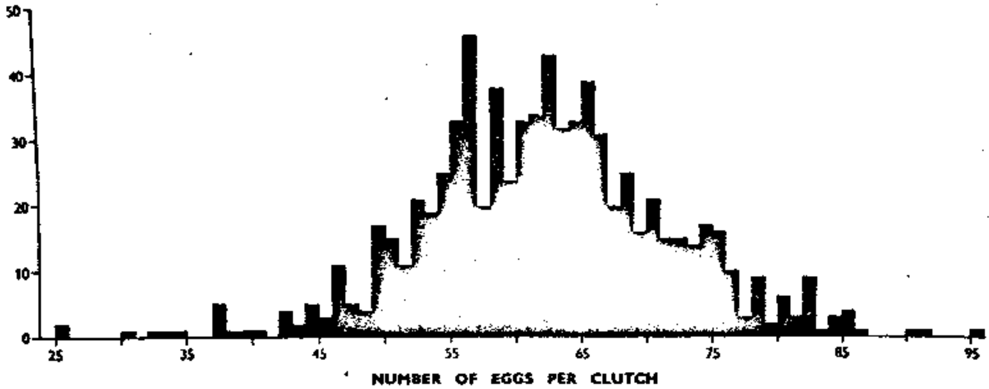

Fig. 32. Histogram showing clutch-size frequency distribution for 775 nests in northern Lake Victoria. (Pitman's unpublished notes.)

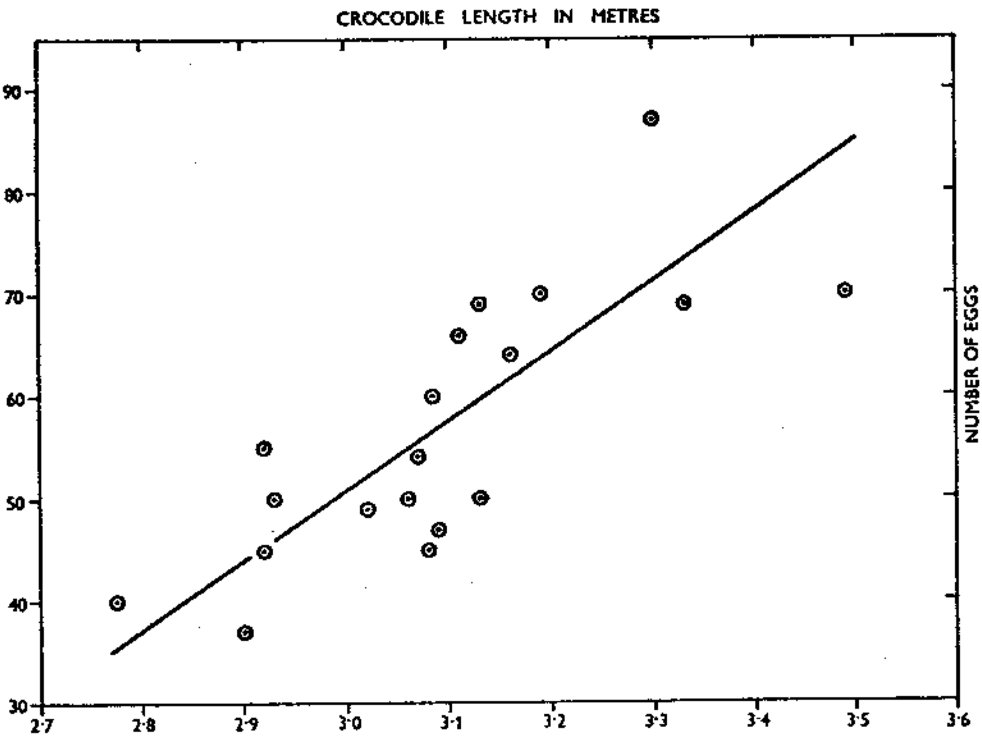

Fig. 33. Scatter diagram showing relation between clutch size and length of female.

River. Crocodile No. 321, shot on the Kafue, contained 87 shelled oviduct eggs. Yet larger clutches are recorded by Pitman, who found three nests in Lake Victoria containing 90, 91 and 95 eggs.

Pitman made a large series of observations on the size of clutches destroyed by him and he has most kindly allowed me to make use of the following data which I have taken from his unpublished annual records. Between the years 1940 and 1949 clutch counts for 775 nests show an extreme range from 25 to 95 eggs, with an average of 60·4 per nest (Fig. 32). My own records show an average of 54·9 eggs for seventeen clutches in Uganda, and of 56·2 for twenty-three clutches in Northern Rhodesia and Barotseland.

Though scanty, the present observations seem to show some correlation between the number of eggs laid (but not the size of the eggs) and the size of the parent—large crocodiles laying the larger clutches (Fig. 33).

Incubation period

The incubation period of *C. niloticus* is generally stated to be about ninety days (Pitman, 1936), as compared with seventeen or eighteen weeks for *C. palustris* (Schultze, 1914), and nine weeks for *A. mississippiensis* (McIlhenny, 1934).

In 1957, at several sites below Murchison Falls, laying commenced in the first week in January. At my suggestion, Mr John Savidge kindly continued observations when I had to leave. He reports (27.4.57) that by 31st March twelve nests on the Nansika tributary had been excavated by the parents, and four were still unhatched. On the same day at another nesting ground he found eleven excavated nest-craters and two females still "sitting". These observations fix the incubation period at between twelve and thirteen weeks.

Parental care

Nest guarding

Crocodiles found covering the eggs are always females. During the whole incubation period the mother remains in attendance—either lying over the nest with the lower throat or thorax above the eggs (Plate 7, fig. 1), or in nearby cover. Wajalubi told me (1952) that the females remain on the grounds by night as well as by day. This may well be the case, for it appears almost certain that brooding females fast. Hippel informed me (1952) that he had never found food in the stomachs of females taken at the nests. Pitman's experience was similar (1930). Stomachs of nesting females examined by me were likewise empty.

During this period—and, in my experience especially when nesting at some distance from the water—the females become torpid and are most reluctant to leave the grounds even when approached. For example, I came upon one female in a ravine below Murchison which refused to stir even when large stones were thrown on her back, and when finally driven off, instead of making for the river, she merely crawled a few yards away into dense bush. Pitman (unpub. notes), Hippel (pers. comm.) and Savidge (27.4.57) all refer to this strange "trance-like" condition of brooding crocodiles, which seems similar to the state of aestivation which has been recorded of crocodiles in other circumstances.

Release of the young

The young croak as hatching time approaches, and this is the signal for the mother to uncover and so liberate her offspring. As with many other aspects of the breeding biology, details of the process have rarely been observed. Mr L. J. Sim, a crocodile hunter in Tanganyika, informs me that on the 30th January, 1956, in Tanganyika, he saw a crocodile lying flat on its belly, wriggling and squirming. On reaching the spot he heard the young croaking from beneath a shallow depression that the female had made—the sand having been scooped out laterally. Next morning, broken shells were lying in the sand, and the young had gone. An African, named Stefan, told Sim that he had witnessed the same method of liberation, and he was most insistent that the feet were not used. This method is certainly consistent with the appearance of the broad and shallow nest craters that are found after the young have hatched : some of these basin-like excavations are over four yards in diameter.

Liberation by the female is necessary because, after three months' incubation and trampling, the earth above the eggs becomes compacted. At some nests opened by me the ground had to be chipped away with a knife and the eggs were set in a matrix as hard as mud-brick. Emergence through a foot or more of sun-baked and hard-packed soil would be impossible for the unaided young.

Care of the young

At hatching time, the female becomes bolder than usual, in defence of her offspring, and will even attack a man on land. Sonnini (1800) was told by an Egyptian who brought him some newly-hatched crocodiles that he had been attacked while collecting them. This observation may well be reliable, for similar instances have been reported of other species—*C. porosus* (Boake, 1870; Shelford, 1916) ; and *A. mississippiensis* (McIlhenny, 1934).

An interesting case of a crocodile (*C. palustris*) attacking enemies other than man is given by Dharmakumarsinji (1947), who watched a female for a whole day maintaining guard over its brood. "I saw this crocodile rush out of the water," he writes, "at least a dozen times, to drive away Black-necked Storks (*Xenorhynchus*), Herons (*Ardea*) and large Egrets (*Egretta*) when they ventured to alight near the young which were lying helpless at the water's edge."

There is also some evidence that the parental instinct lasts at least until the young crocodiles reach the safety of the water. In Nigeria, Lambron (1913) was told by natives that young crocodiles attach themselves to the dorsal fringe of the mother's tail and thus are conveyed to the water. Early authorities have also referred to maternal transport of the brood. According to Goldsmith (1805), when the young have been freed from the nest—"a part run unguided to the water ; another part ascend the back of the female, and are carried thither in greater safety." Stefan also told Sim (personal communication) that " when the young emerge, they mount the back of the mother, and as soon as it is dark, she transports them through shallow water to a patch of reeds. Here the young instinctively cling to the reeds."

While these stories may not be entirely reliable, there is good modern evidence of some after-care. In Lake Victoria, F. Wilson once saw a female crocodile with seventeen or eighteen recently-hatched young sunning on a bank. As he approached the parent went into the water, followed by her offspring. H. Holloway assured me that on several occasions he has seen crocodiles in the Kabompo River near Ndola accompanying new-hatched young in the water—like a duck with her brood. Several of these escorting crocodiles were shot, and as the stomachs never contained young crocodiles, they were certainly not cannibals caught in the act. More recently I am informed by J. Savidge (27.4.57) that on the Nansika grounds below Murchison he saw young crocodiles all around an adult in the water ; and visitors to the same place later recorded babies resting on a crocodile's back.

Early life

At birth the Nile Crocodile measures about 28 cms. The young have no immediate need of food, for a large quantity of yolk—about equal to that of a hen's egg—remains enclosed in the body, and provides a store of nutriment for several months. When eight weeks old, this yolk mass is still as large as a walnut ; and according to Pitman (1929) traces of it have been found after the age of six months.

The feeding habits of the young have been described elsewhere (see p. 293). The young are very agile from birth ; and, like their elders, when surprised ashore they make for the water and readily dive to avoid capture. At first they are strongly gregarious, each pack probably representing a family group : and as Pitman (1936) has pointed out : " They quickly disperse when frightened, but soon pack again, calling to each other loudly with a chirruping cry."

At this early period of life crocodiles are active climbers. Dr Hoare (in Pitman, 1929) saw them lying along overhanging branches of trees onto which they climb direct from the water. In Northern Rhodesia, L. E. Vaughan found them climbing up grasses and " hanging on like chameleons." N. H. Searle tells me that on the Lower Semliki he has seen them climbing in *Phragmites* to a height of six or eight feet, whence they drop off into the water at the approach of a canoe.

A few days after hatching the young lead a life of seclusion, shunning both the basking grounds and the open water, and seeking sanctuary from numerous enemies, including members of their own species, among the papyrus, in sudd, weedy shallows, backwaters, or in isolated pools—occasionally at some distance inland. A striking instance of this segregation of the young from their elders was seen at Magungu, where yearlings occupied a chain of shallow, weed-choked meres a mile back from the river. All those which I saw in the meres in 1956 were first-year juveniles (see p. 247) ; and J. R. F. Mills (1954) reported seeing small crocodiles " a foot or so in length " at the same place in 1953. By their second year they have vanished, and their disappearance illustrates a curious and little understood phenomenon. For with growth, there follows a period when juveniles mysteriously disappear from the scene in all habitats. One sees those that have recently hatched, and again crocodiles of five feet and upwards. But although the intervening sizes can be shot in the shallows at night, their diurnal whereabouts remains an enigma. Many experienced hunters and naturalists have commented upon the absence of individuals measuring from about two to four feet in length. Pitman (1935) refers to this anomaly as " a conspicuous feature of African inland waters ;" and elsewhere (1931) he writes : " One could almost believe that crocodiles of smaller size were non-existent and there was no intermediate stage." Hippel, with years of field experience as a professional hunter, told me he had never seen or taken young crocodiles between one-and-a-half and three-and-a-half feet. Magala's experience was similar. In areas, where under protection, crocodiles are still abundant, as below Murchison, in the Kafue and Luangwa Reserves, at Mweru Wa Ntipa, and Ndumu Reserve in Zululand, the apparent absence of small crocodiles seems the more remarkable. All that one can certainly say is that between the ages of about two and five years crocodiles go into retreat ; and since they can have few enemies other than larger individuals of their own kind, it is probable that this cryptic behaviour has been forced upon them by the habit of cannibalism.

PART III. ECOLOGICAL AND ECONOMIC STATUS

Food and feeding habits

A study of the food and feeding habits is a first essential in any attempt to assess the status of the crocodile in the ecology of inland waters. Such a study calls for the examination of stomach contents, which will provide not only a general picture of predator-prey relations, but will also afford a comparison between the habits of crocodiles of different sizes, and between those from different localities.

The present observations are based upon an analysis of stomach contents of 851 crocodiles from the following localities—the numbers here given refer to stomachs examined and (in brackets) those containing food : Uganda above Murchison Falls, 106 (95) ; Uganda below Murchison Falls, 34 (29) ; Bangweulu Swamp, 145 (110) ; Mweru Wa Ntipa and Kalungwishi River, 63 (49) ; Luangwa Valley, 98 (87) ; Kafue Flats, 101 (91) ; Upper Zambesi, 272 (212) ; Zululand, 32 (28). Most of this material was examined by me in 1952, 1956 and 1957. Also included are various records received from Mr F. Wilson and Mr P. H. Greenwood (L. Victoria), Mr H. Holloway (Bangweulu and Upper Zambesi), Mr Grobler (Bangweulu), and Mr H. H. Voigt (Zambesi). The records from Zululand were supplied by Mr I. H. Player.

Food in relation to growth

In a preliminary report on work done in Uganda in 1952 (Cott, 1954, a) attention was drawn to the fact that feeding behaviour and diet of the Nile Crocodile change markedly and progressively throughout life. From the present survey it is now clear that these changes are of such magnitude—and this in every locality for which we have adequate information—as to make body-length a key factor in the crocodile's feeding ecology.

The proportional occurrence of different categories of food taken by crocodiles, in relation to length, is given in Table 19; and Fig. 34 presents these data, serially, for each prey category. A glance at the histograms will show that for almost

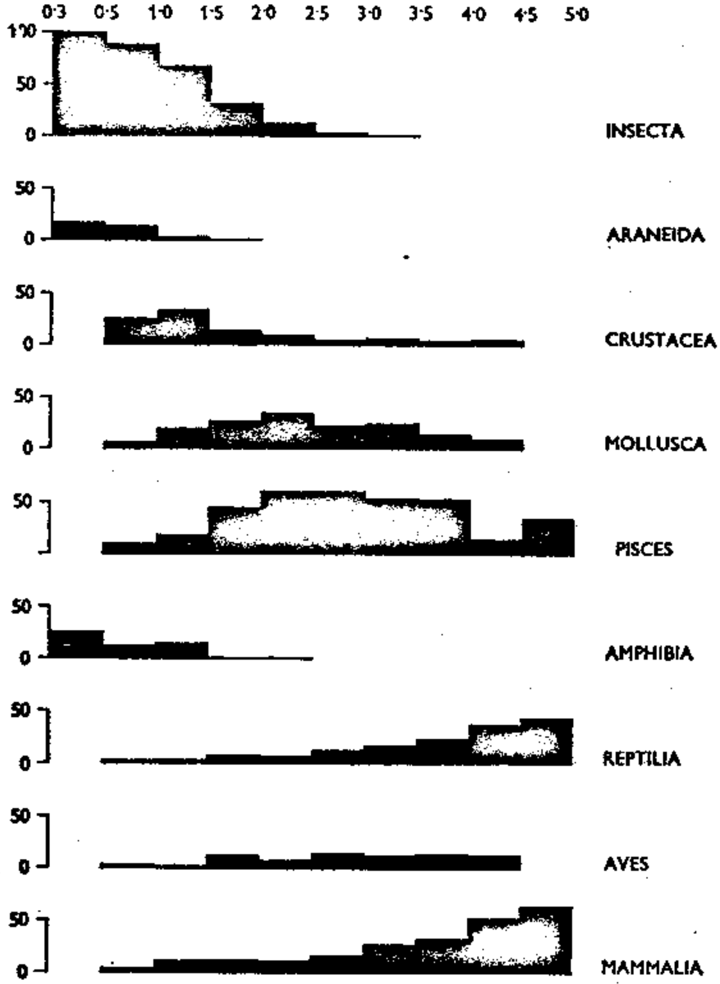

Fig. 34. Frequency of occurrence of different kinds of food, in relation to crocodile length. For each length group, occurrences are expressed as a percentage of stomachs containing food of any kind.

any type of prey (birds are an exception) the feeding pattern tends to change, often in a regular manner, throughout life. Three main patterns can be recognised; and these are in accordance with what is known of the crocodile's changing habitat requirements.

(i) In the first, are prey for which the curve begins at its maximum and falls away to zero: this is the general intake pattern for insects, spiders and anura.

TABLE 19

Food of the Nile Crocodile: expressed as the number of occurrences, and percentage occurrence, of different kinds of prey, and in relation to crocodile length.

Crocodile length-group in metres	*No. of crocodiles examined*	*No. of crocodiles with prey*	*Insecta*	*Araneida*	*Crustacea*	*Mollusca*	*Pisces*	*Amphibia*	*Reptilia*	*Aves*	*Mammalia*
0·3–0·5	12	11	11 100·0%	2 18·2%	0 —	0 —	0 —	3 27·3%	0 —	0 —	0 —
0·5–1·0	142	133	117 88·0%	19 14·3%	34 25·6%	10 7·5%	14 10·5%	17 12·8%	4 3·0%	5 3·8%	7 5·3%
1·0–1·5	141	121	82 67·8%	3 2·5%	40 33·1%	25 20·6%	23 19·0%	18 14·9%	4 3·3%	3 2·5%	15 12·4%
1·5–2·0	111	91	29 31·9%	1 1·1%	12 13·2%	25 27·5%	42 46·2%	1 1·1%	8 8·8%	11 12·1%	12 13·2%
2·0–2·5	117	89	12 13·5%	0 —	9 10·1%	31 34·8%	53 59·6%	1 1·1%	7 7·9%	7 7·9%	11 12·4%
2·5–3·0	129	94	3 3·2%	0 —	4 4·3%	23 24·5%	56 59·6%	0 —	12 12·8%	14 14·9	16 17·0%
3·0–3·5	113	88	1 1·1%	0 —	6 6·8%	23 26·1%	48 54·6%	0 —	16 18·2%	11 12·5%	24 27·3%
3·5–4·0	49	41	0 —	0 —	1 2·4%	6 14·6%	22 53·7%	0 —	10 24·4%	6 14·6%	13 31·7%
4·0–4·5	23	21	0 —	0 —	1 4·8%	2 9·5%	3 14·3%	0 —	8 38·1%	3 14·3%	11 52·4%
4·5–5·0	12	11	0 —	0 —	0 —	0 —	4 36·4%	0 —	5 45·5%	0 —	7 63·6%
5·0–5·5	1	1	0	0	0	0	0	0	0	0	1 100·0%

Such prey are captured by day and night, both in and above the water, by young crocodiles during the period when they lead a secluded life among waterside vegetation, papyrus debris, and weed-choked shallows.

(ii) In the second, are those for which the curve rises towards middle-life period, and falls away in old age : such is the frequency distribution for crabs, molluscs and fish—under-water prey which are captured mainly at night and often well out from the shore.

(iii) In the third, are those for which the curve begins low and rises steeply in old age : such a pattern is shown for reptiles and mammals—prey which may be captured by stealth and surprise when crocodiles are lying inshore or ashore during the daytime.

These various progressive changes in diet are illustrated in generalized form in Fig. 35.

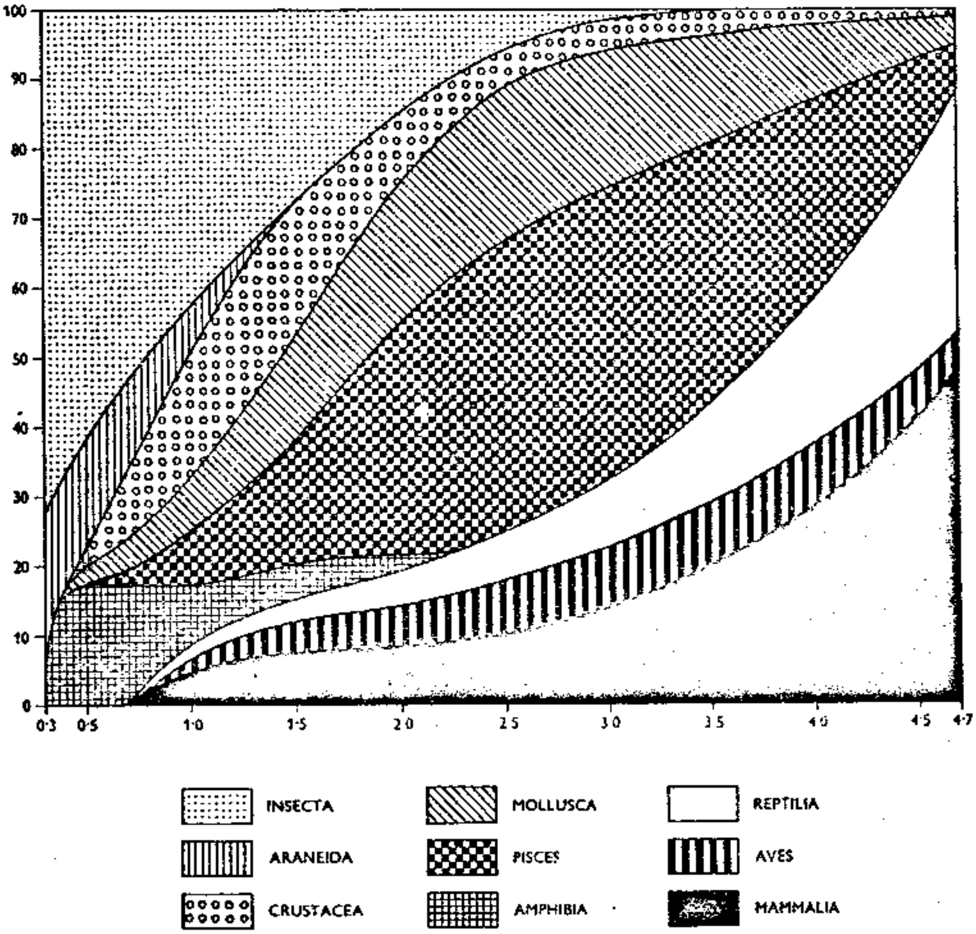

Fig. 35. Generalized diagram showing the progressive changes in feeding habits which accompany growth. The smoothed curves are based upon the number of occurrences, in crocodiles of each half-metre length group, of different foods, expressed as a percentage of the occurrences of all foods.

Quantity of food eaten

It is commonly stated, or assumed, that crocodiles are voracious feeders, daily consuming enormous quantities of fish and other prey. Such notions are quite unsupported by evidence. Indeed, stomach examinations have shown that a large meal is a rarity.

Four repletion categories are here recognized : (i) stomachs empty, except for stones ; (ii) those which contained fragmentary, but recognizable remains of prey—such as insect wings or elytra, gastropod opercula, fish scales, horny chelonian shields, feathers, hair, or claws ; (iii) those which were from a quarter to half full ; and (iv) those which were about three-quarters full and including a few fully-distended stomachs. These quantitative data are analysed, in relation to crocodile Length-Groups, in Table 20.

TABLE 20

Bulk of food in the stomachs of crocodiles of different length-groups.

Length in metres	*No. of records*	*Empty*	*Fragments only*	*¼–½ full*	*¾-full*
0–1	138	7 (5·1%)	46 (33·3%)	61 (44·2%)	24 (17·4%)
1–2	190	25 (13·2%)	84 (44·2%)	67 (35·3%)	14 (7·4%)
2–3	164	31 (18·9%)	68 (41·5%)	55 (33·6%)	10 (6·1%)
3–4	89	18 (20·2%)	22 (24·7%)	42 (47·2%)	7 (7·9%)
4–5	10	2 (20·0%)	3 (30·0%)	4 (40·0%)	1 (10·0%)

Of 591 stomachs (from all length groups) only fifty-six (9·5 per cent.) were near repletion ; eighty-three (14·1 per cent.) were empty ; and more than half of the total were either empty or contained indigestible fragments only. Data for the various length groups suggest that in relation to their capacity, young crocodiles feed more actively than their elders. Thus it is in Length Group I that we find the highest proportion of full stomachs (17·4 per cent.); while conversely the percentage with empty stomachs tends to increase with age—from 5·1 in Length Group I to 20·0 in Length Group V.

Analysis of the data, by localities, calls for brief comment. Among ninety-eight Luangwa stomachs, only four were nearly full. Of 369 stomachs examined from Luangwa (98), Kafue (92) and Upper Zambesi (179), 63·2, 56·6 and 60·9 per cent., respectively, were either empty or contained fragments only. Crocodiles from Mweru Wa Ntipa (51) show the lowest percentage of full stomachs (3·9) for any locality, and also the highest percentage (27·5) containing no trace of food.

Crocodiles are usually credited with extraordinary powers of digestion, and to this has been attributed the frequency of empty stomachs. This is contrary to evidence. For example, the stomach of a specimen killed in captivity at Jinja still contained partly digested remains of a small crocodile it had eaten a week previously (Cott, 1954 a). Thus the relative scarcity of food recovered appears to indicate infrequent feeding rather than rapid digestion.

More than half the specimens examined (i.e. categories i and ii) had probably not taken a large meal for at least a week, although they were shot in waters where fish and other prey abounded. In short, it seems clear that the Nile Crocodile leads an idle life, expending little energy in an environment ideal for a large poikilotherm, and troubles to take only the little food it needs. The field observations suggest that adults take, in bulk, not more than fifty full meals in a year.

These conclusions find support from what is known of the food requirements in captivity. For example, Dr H. G. Vevers tells me (25.5.54) that two crocodiles in the Society's Gardens, each measuring about 2·3 metres, consumed the following rations over an observation period of thirty-six days (16th February to 23rd March):

(a) *Food*	*Weight in g.*	(b) *Food*	*Weight in g.*
20 Whiting ..	4,120	17 Whiting ..	3,420
7 Rats	700	5 Rats	500
Meat	8,300	Meat	6,200
Total	13,120	Total	10,120

The average daily intake is thus shown to be only about 365 and 280 grams respectively. These crocodiles were not weighed: but specimens of the same length are known, from field measurements, to weigh about 45 kg. These two animals would therefore take, respectively, about 124 and 160 days to consume their own weight of food.

Such slight requirements appear the more striking when compared with the food eaten by waterfowl in nature. For example, stomach examinations of *Pelecanus onocrotalus* in Uganda have shown that a pelican takes at least 6 lbs. (or 2·8 kg.) of fish daily, and may carry prey amounting to one third of its body weight.

Prey of the Nile Crocodile

So far as possible, prey recovered from stomachs has been identified, and the results are tabulated below (Table 21) to afford a comparison between feeding habits in different waters.

Insecta

Insect prey are represented numerically as follows: Coleoptera, 577; Hemiptera, 208; Odonata, 74; Orthoptera, 57; Hymenoptera, 44; Diptera, 17; Dermaptera, 2; Lepidoptera, 1. The distribution by families, of prey belonging to the first five orders, is given below:—

Coleoptera	
Cicindelidae	29
Carabidae	87
Dytiscidae	54
Gyrinidae	2
Hydrophilidae ..	93
Tenebrionidae ..	8
Scarabaeidae	70
Cerambycidae ..	1
Curculionidae ..	1

Hemiptera	
Hydrometridae ..	37
Reduviidae	1
Belostomatidae ..	84
Naucoridae	72
Nepidae	9
Corixidae	1

Hymenoptera	
Apidae	2
Formicidae	41

Odonata	
Gomphidae	28
Corduliidae	1
Libellulidae	27
Agrionidae	1

Orthoptera	
Blattidae	1
Acridiidae	6
Tettigoniidae ..	11
Gryllidae	3
Gryllotalpidae ..	31

TABLE 21

Food of the Nile Crocodile: showing the number of stomachs in which each food was found, and (in italics) the total number of each food organism.

	Uganda (a)*	*Uganda* (b)*	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
INSECTA								
ORTHOPTERA								
Blattidae								
Indet.	—	1 *1*	—	—	—	—	—	—
Acridiidae								
Schistocerca gregaria Forskal	—	—	1 *1*	—	—	—	—	—
Ornithacris cyanea Stoll	—	—	—	—	—	—	1 *1*	—
Paracinema tricolor (Thunberg)	—	—	—	—	—	2 *2*	—	—
Trilophidia sp.	—	1 *1*	—	—	—	—	—	—
Indet.	—	—	—	—	—	1 *1*	—	—
Tettigoniidae								
Conocephalus conocephalus (Linn.)	1 *1*	—	—	—	—	—	—	—
? *Homorocoryphus nitidulus* (Scop.)	—	—	—	—	—	1 *1*	—	—
Pseudorhynchus sp.	—	—	—	—	—	—	3 *3*	—
Indet.	1 *1*	—	—	—	2 *2*	1 *1*	2 *2*	—
Gryllidae								
Brachytrypes membranaceus (Drury)	—	—	—	—	1 *1*	—	—	—
Paraloxoblemmus angulifrons Chop.	1 *1*	—	—	—	—	—	—	—
Indet.	—	—	—	—	—	—	1 *1*	—
Gryllotalpidae								
Gryllotalpa africana (Beauv.)	—	1 *1*	—	1 *1*	13 *26*	1 *1*	1 *1*	—
Indet	—	—	1 *1*	—	—	—	—	—
Orthoptera indet.	1 *1*	—	2 *2*	—	—	—	2 *2*	—
DERMAPTERA								
Labiduridae								
Labidura riparia Pall.	—	1 *1*	—	—	—	—	—	—
Forficulidae								
Forficula sp.	—	—	—	—	—	1 *1*	—	—
ISOPTERA								
Termitidae								
Macrotermes bellicosus (Smeathman)	2 *14*	—	—	—	—	—	—	—
ODONATA								
Gomphidae								
Phyllogomphus aethiops Selys	1 *1*	—	—	—	—	—	—	—
Ictinogomphus ferox Rambur	6 *8*	4 *10*	—	—	—	—	3 *4*	—
Phyllogomphus sp.	—	—	—	—	—	—	2 *4*	—
Indet.	—	—	—	—	—	—	1 *1*	—
Corduliidae								
Phyllomacromia picta Selys	1 *1*	—	—	—	—	—	—	—
Libellulidae								
Brachythemis leucosticta (Burm.)	3 *3*	4 *5*	—	—	—	—	—	—
Sympetrum navasi Lacroix	1 *2*	—	—	—	—	—	—	—
Trimethis annulata (Beauv.)	1 *1*	1 *1*	—	—	—	—	—	—
Trimethis sp.	1 *1*	—	—	—	—	—	—	—
Urothemis edwardsi Selys	3 *3*	—	—	—	—	—	—	—
Indet.	2 *11*	—	—	—	—	—	—	—

*(a) above Murchison ; (b) below Murchison.

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Agrionidae								
Ceriagrion sp.	—	—	1 *1*	—	—	—	—	—
Odonata indet.	4 *10*	1 *1*	2 *2*	—	1 *1*	1 *1*	2 *2*	—
HEMIPTERA								
Gerridae								
Limnogonus hypoleucus (Gerst)	2 *16*	—	—	—	—	1 *1*	—	—
Limnogonus sp.	—	—	1 *20*	—	—	—	—	—
Reduviidae								
? *Serthenea* sp.	—	—	—	—	1 *1*	—	—	—
Belostomatidae								
Hydrocyrius columbiae Spin.	9 *11*	1 *1*	2 *2*	—	—	3 *3*	1 *1*	—
Hydrocyrius sp.	—	—	1 *1*	—	—	—	—	—
Lethocerus niloticum Stal.	—	—	—	—	2 *2*	—	—	—
Lethocerus sp.	1 *1*	1 *1*	—	—	—	—	—	—
Limnogeton fieberi Mayr	8 *15*	—	—	—	—	—	—	—
Poissonia longifemorata Brown	—	—	4 *5*	—	—	—	—	—
Indet.	15 *22*	—	4 *6*	—	3 *3*	4 *4*	5 *5*	—
Naucoridae								
Laccocoris limigenus Stal.	—	—	—	—	1 *1*	—	—	—
Sphaerodema ampliatum Bergr.	—	—	—	—	1 *1*	4 *6*	—	—
Sphaerodema nepoides F.	10 *23*	2 *5*	—	—	1 *1*	2 *2*	—	—
Sphaerodema sp.	7 *20*	2 *3*	6 *6*	—	1 *1*	—	3 *3*	—
Nepidae								
Laccotrephes ater Linn.	—	—	—	—	2 *3*	1 *1*	—	—
Ranatra ? *nodiceps* Gerst.	1 *1*	—	—	—	—	2 *2*	—	—
Ranatra sp.	1 *1*	1 *1*	—	—	—	—	—	—
Corixidae								
Indet.	—	1 *1*	—	—	—	—	—	—
Hemiptera indet.	1 *1*	—	1 *3*	—	—	—	—	—
LEPIDOPTERA								
Noctuidae								
Larva indet.	1 *1*	—	—	—	—	—	—	—
COLEOPTERA								
Cicindelidae								
Cicindela dongalensis Klug.	—	—	—	—	8 *29*	—	—	—
Carabidae								
Scarites aestuans Klug	—	—	—	—	13 *34*	—	4 *10*	—
Scarites sp.	—	—	1 *1*	1 *1*	2 *3*	—	2 *4*	—
Eudema sp.	—	—	—	—	1 *1*	—	1 *1*	—
Chlaenius ? *circumscriptus* Dej.	—	—	—	—	1 *2*	—	—	—
Chlaenius sp.	—	—	—	—	2 *3*	—	—	—
Macrochlaenites lugens Chaud.	—	—	—	2 *6*	—	—	—	—
Cyclosomus equestris Boh.	—	1 *6*	—	—	—	—	—	—
Pheropsophus transvaalensis Pér.	—	—	—	—	2 *2*	—	—	—
Pheropsophus ? *kersteni* Gerst.	1 *1*	—	—	—	—	—	—	—
Pheropsophus sp.	2 *7*	—	—	—	—	—	1 *1*	—
Indet.	1 *2*	—	—	—	2 *2*	—	—	—

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda (b)*	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Dytiscidae								
Hydaticus dorsiger Aubé	—	—	—	1 *1*	—	—	—	—
Hydrocanthus sp.	—	3 *11*	—	—	—	—	—	—
Hydrovatus frater Rég.	—	1 *1*	—	—	—	—	—	—
Regimbartia ? *nilotica* Sap.	—	3 *12*	—	—	—	—	—	—
Cybister binotatus Klug	—	—	—	—	—	—	1 *1*	—
Cybister ? *natalensis* Whn.	—	—	—	—	—	2 *5*	—	—
Cybister senegalensis Aubé	—	—	2 *2*	—	—	—	—	—
Cybister ? *tripunctatus* Cast.	—	—	1 *1*	—	1 *1*	—	—	—
Cybister vicinus Zimm.	—	—	—	—	1 *1*	—	—	—
Cybister sp.	2 *2*	3 *3*	1 *1*	—	—	3 *3*	5 *9*	—
Gyrinidae								
Orectogyrus sp.	—	1 *1*	—	—	—	—	—	—
Indet.	—	1 *1*	—	—	—	—	—	—
Hydrophilidae								
Coelostoma sp.	1 *7*	1 *2*	—	—	—	—	—	—
Helochares sp.	—	1 *1*	—	—	—	—	—	—
Sternolophus angolensis Cast.	—	—	—	—	—	—	1 *1*	—
Sternolophus sp.	—	—	2 *2*	—	—	—	—	—
Hydrophilus aculeatus Sol.	—	—	—	—	1 *1*	25 *54*	11 *14*	—
Hydrophilus marginatus Lap.	—	—	1 *2*	—	—	—	—	—
Hydrophilus sp.	—	—	1 *3*	—	—	—	1 *1*	—
Hydrochara sp.	—	—	1 *1*	—	—	—	—	—
Amphiops senegalensis Cast.	—	2 *3*	—	—	—	—	—	—
Allocotocerus sp.	—	1 *1*	—	—	—	—	—	—
Tenebrionidae								
Adesmia sp.	—	—	—	1 *1*	—	—	—	—
Macropoda sp.	—	—	—	1 *1*	—	—	—	—
Peristeptus sp.	—	—	—	—	1 *1*	—	—	—
Gonocephalum simplex F.	1 *1*	—	—	—	—	—	—	—
Achrostus sp.	1 *1*	—	—	—	—	—	—	—
Indet.	—	2 *3*	—	—	—	—	—	—
Scarabaeidae								
Heliocopris ? *colossus* Bates	1 *1*	1 *1*	—	—	—	—	—	—
Heteroligus ? *gazanus* Arrow	—	—	—	—	—	—	1 *1*	—
Heteroligus meles Billb.	—	—	—	—	1 *8*	—	—	—
Heteronychus pauperatus Pér.	—	—	—	—	—	1 *2*	—	—
Heteronychus wilmsi Kolbe	—	—	—	—	—	—	1 *1*	—
Heteronychus sp.	—	—	2 *3*	1 *1*	—	10 *20*	4 *4*	—
Temnorhynchus coronatus F.	—	—	—	—	6 *6*	—	1 *1*	—
Temnorhynchus elongatus Arrow ..	—	—	—	—	—	—	1 *1*	—
Temnorhynchus sp.	—	—	—	—	8 *13*	—	2 *3*	—
Indet.	—	1 *1*	—	—	—	—	3 *3*	—
Cerambycidae								
Indet.	1 *1*	—	—	—	—	—	—	—
Curculionidae								
Indet.	—	—	—	1 *1*	—	—	—	—
Coleoptera indet.	1 *3*	4 *18*	4 *40*	1 *1*	29 *65*	21 *43*	36 *62*	—
HYMENOPTERA								
Apidae								
Apis mellifera Linn.	1 *2*	—	—	—	—	—	—	—

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Formicidae								
Bothroponera sp.	—	1 *1*	—	—	—	—	—	—
Odontomachus assiniensis Emery	2 *9*	—	—	—	—	—	—	—
Paltothyreus tarsatus Fab.	1 *4*	—	—	—	—	—	—	—
Psalidomyrmex sp.	1 *1*	—	—	—	—	—	—	—
Euponera sp.	1 *1*	—	—	—	—	—	—	—
Camponotus sp.	3 *10*	—	—	—	—	—	—	—
Myrmicaria sp.	1 *4*	—	—	—	—	—	—	—
Dorylus sp.	—	—	—	—	1 *1*	—	1 *1*	—
Indet.	2 *3*	1 *4*	—	—	3 *3*	—	—	—
DIPTERA								
Tachinidae								
Sturmia sp.	1 *2*	—	—	—	—	—	—	—
Otitidae								
Indet.	1 *1*	—	—	—	—	—	—	—
Anthomyidae								
Indet.	1 *1*	—	—	—	—	—	—	—
Diptera indet.	—	—	—	—	—	—	1 *1*	—
Insecta indet.	5 *7*	1 *1*	1 *2*	—	2 *2*	—	—	—
ARACHNIDA								
ARANEIDA								
Tetragnathidae								
Tetragnatha sp.	—	—	—	—	—	—	1 *2*	—
Pisauridae								
Dolomedes bistylus Roewer	—	—	—	—	—	1 *1*	1 *1*	—
Dolomedes lesserti Roewer	—	—	—	—	—	2 *2*	2 *2*	—
Dolomedes sp.	—	—	1 *1*	1 *4*	—	1 *2*	1 *1*	—
Thalassius sp.	—	—	—	—	—	—	2 *4*	—
Araneida indet.	5 *6*	5 *8*	—	1 *1*	1 *1*	2 *2*	4 *6*	—
CRUSTACEA								
BRACHYURA								
Potamonidae								
Potamonautes niloticus (M.-Edw.)	5 *6*	—	—	—	—	—	—	—
Potamonautes ? *bayonianus* (Capello)	—	—	—	—	—	—	48 *56*	—
Potamonautes sp.	11 *13*	—	2 *2*	—	—	23 *32*	18 *28*	—
MACRURA								
Atyidae								
Caridina nilotica de Man	1 *1*	—	—	—	—	—	—	—
Caridina sp.	—	1 *1*	—	—	—	—	—	—
MOLLUSCA								
GASTROPODA								
Ampulariidae								
Pila ovata (Olivier)	5 *60*	—	—	—	—	—	—	—
Lanistes ovum Peters	—	—	20 *1155*	13 *528*	6 *21*	26 *1610*	20 82	—
Viviparidae								
Bellamya unicolor Olivier	1 *8*	—	—	—	—	—	—	—
Hydrobiidae								
Gabbia tilhoi Germain	—	1 *1*	—	—	—	—	—	—

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda (b)*	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
PULMONATA								
Planorbidae								
Biomphalaria choanomphala V. Martens	—	1 *1*	—	—	—	—	—	—
Biomphalaria sudanica V. Martens ..	1 *1*	1 *4*	—	—	—	—	—	—
Segmentina angusta Limnaeidae ..	—	1 *1*	—	—	—	—	—	—
Limnaeidae								
Limnaea natalensis Krauss	—	—	—	—	—	2 *2*	—	—
Gastropoda indet.	6 *7*	—	29 *627*	—	—	2 *5*	10 *78*	—
LAMELLIBRANCHIATA								
Sphaeriidae								
Sphaerium sp.	—	1 *1*	—	—	—	—	—	—
Unionidae								
Parreyssia ? kunensis Mouss	—	—	—	—	—	1 *1*	—	—
Lamellibranchiata indet.	—	—	—	—	—	3 *3*	2 *2*	—
CHONDRICHTHYES								
SELACHII								
Shark, indet.	—	—	—	—	—	—	—	1 *2*
OSTEICHTHYES								
DIPNOI								
Lepidosirenidae								
Protopterus aethiopicus Heckel	7 *7*	—	—	—	—	—	—	—
ISOSPONDYLI								
Mormyridae								
Mormyrus caschive Linn.	—	1 *1*	—	—	—	—	—	—
Mormyrus sp.	3 *11*	—	—	—	—	—	—	—
Gnathonemus monteiri Blgr.	—	—	1 *1*	—	—	—	—	—
Gnathonemus macrolepidotus Peters ..	—	—	—	—	—	—	1 *4*	—
Indet.	—	—	—	—	—	—	1 *1*	—
OSTARIOPHYSI								
Characidae								
Hydrocyon lineatus Blgr.	—	—	1 *1*	—	—	—	—	—
Hydrocyon ? vittatus (Cast.)	—	—	—	—	2 *2*	—	1 *3*	—
Hydrocyon sp.	—	2 *3*	1 *1*	—	—	—	1 *1*	—
Hepsetus odoë (Bloch)	—	—	—	—	—	2 *2*	—	—
Alestes macrophthalmus Gunth. ..	—	—	—	1 *4*	—	—	—	—
Alestes sp.	—	2 *10*	—	—	—	—	—	—
Cyprinidae								
Barbus bynni Forsk.	—	1 *1*	—	—	—	—	—	—
Barbus eutaenia Blgr.	—	—	—	—	—	1 *1*	—	—
Barbus radcliffii Blgr.	3 *3*	—	—	—	—	—	—	—
Barbus sp.	1 *1*	—	—	—	—	—	—	—
Labeo sp.	—	1 *2*	—	—	—	—	—	—
Bagridae								
Auchenoglanis occidentalis C. & V. ..	—	3 *8*	—	—	—	—	—	—

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Schilbeidae								
Schilbe ? mystus Linn.	—	—	1 *1*	—	—	—	—	—
Eutropius banguelensis Blgr.	—	—	1 *2*	—	—	—	—	—
Clariidae								
Clarias mossambicus Peters	—	—	—	29 *42*	—	1 *1*	2 *2*	—
Clarias ? mellandi Blgr.	—	—	—	—	—	2 *2*	—	—
Clarias sp.	—	1 *1*	1 *1*	1 *1*	—	3 *3*	28 *34*	—
Mochocidae								
Synodontis schall Bl.-Schn.	—	1 *4*	—	—	—	—	—	—
Synodontis frontosus Vaill.	—	1 *1*	—	—	—	—	—	—
Synodontis nigromaculatus Blgr. ..	—	—	2 *2*	—	—	—	—	—
Synodontis zambesensis Peters	—	—	—	—	1 *1*	—	5 *6*	—
Synodontis sp.	—	2 *7*	2 *2*	—	—	—	11 *11*	—
Siluroidea indet.	—	—	—	—	2 *2*	2 *2*	—	1 *1*
APODES								
Anguillidae								
Indet.	—	—	—	—	—	—	—	1 *1*
MICROCYPRINI								
Cyprinodontidae								
Aplocheilichthys sp.	—	—	—	—	—	1 *1*	—	—
PERCOMORPHI								
Plectorhynchidae								
Pomadasys operculare (Playf.)	—	—	—	—	—	—	—	1 *6*
Centropomidae								
Lates sp.	—	1 *1*	—	—	—	—	—	—
Cichlidae								
Tilapia macrochir Blgr.	—	—	1 *1*	—	—	—	—	—
Tilapia sparrmani A. Smith	—	—	1 *2*	—	—	—	—	—
Tilapia andersonii Cast...	—	—	—	—	—	1 *1*	2 *2*	—
Tilapia mossambicus Peters	—	—	—	—	1 *1*	—	—	—
Tilapia melanopleura Dumeril ..	—	—	—	—	—	—	2 *2*	—
Tilapia sp.	1 *1*	2 *2*	2 *4*	—	—	3 *5*	13 *15*	1 *1*
Serranochromis angusticeps (Blgr.) ..	—	—	1 *2*	—	—	—	—	—
Serranochromis thumbergii (Cast.) ..	—	—	—	—	—	—	2 *2*	—
Serranochromis sp.	—	—	—	—	—	—	1 *1*	—
Sargochromis codringtoni Blgr. ..	—	—	—	—	—	—	1 *1*	—
Sargochromis mellandi (Blgr.)	—	—	1 *1*	—	—	—	—	—
Astatoreochromis alluaudi Pellegrin ..	1 *1*	—	—	—	—	—	—	—
Haplochromis moffattii (Cast.)	—	—	—	—	—	2 *4*	—	—
Haplochromis darlingi Blgr.	—	—	—	—	—	—	1 *1*	—
Haplochromis sp.	1 *1*	—	—	—	—	1 *1*	1 *1*	—
Indet.	—	—	—	—	1 *2*	1 *1*	2 *2*	—
Pisces indet.	13 *13*	1 *2*	32 *52*	3 *3*	1 *1*	18 *21*	30 *30*	5 *5*
AMPHIBIA								
ANURA								
Bufonidae								
Bufo regularis Reuss	1 *3*	—	—	—	6 *9*	—	1 *1*	—
Bufo sp.	1 *1*	—	1 *1*	—	2 *2*	—	—	—

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Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Ranidae								
Arthroleptis sp.	—	—	1 *1*	—	—	—	—	—
Phrynobatrachus natalensis (Smith)	—	—	—	—	1 *1*	—	—	—
Polypedatidae								
Hyperolius sp.	5 *6*	—	—	—	—	—	—	—
Brevicipitidae								
Hemisus mormoratum (Peters)	—	—	—	—	1 *1*	—	—	—
Anura indet.	8 *16*	1 *1*	1 *1*	—	6 *7*	2 *4*	3 *5*	—
REPTILIA								
CHELONIA								
Pelomedusidae								
Pelusios subniger (Lacépède)	—	3 *3*	—	1 *1*	2 *2*	2 *3*	7 *7*	—
Pelusios sinuatus (Smith)	—	—	—	—	1 *1*	—	—	—
Pelusios sp.	—	—	—	—	—	4 *4*	3 *3*	—
Indet.	—	—	—	—	—	—	6 *6*	5 *5*
CROCODILIA								
Crocodilidae								
Crocodilus niloticus Blgr.	9 *9*	1 *1*	—	3 *3*	2 *2*	—	2 *2*	1 *1*
Eggs	—	—	—	—	—	—	—	1 *82*
LACERTILIA								
Varanidae								
Varanus niloticus (Linn.)	—	1 *1*	—	—	3 *3*	1 *1*	3 *3*	1 *1*
OPHIDIA								
Boidae								
Python sebae (Gmelin)	—	—	1 *1*	—	—	—	1 *1*	—
Colubridae								
Natrix olivacea (Peters)	2 *2*	—	—	—	—	—	—	—
Boaedon lineatum (Dum. & Bib.)	—	—	—	—	1 *1*	—	—	—
Chlorophis hoplogaster (Günther)	—	—	—	—	—	4 *4*	—	—
Dasypeltis scabra (Linn.)	1 *1*	—	—	—	—	—	—	—
Naia melanoleuca Hallowell	1 *1*	—	—	—	—	—	—	—
Viperidae								
Bitis arietans (Merrem)	—	—	—	—	—	1 *1*	—	—
Ophidia indet.	—	—	1 *1*	—	2 *2*	1 *1*	—	—
AVES								
PELECANIFORMES								
Phalacrocoracidae								
Phalacrocorax lucidus (Licht.)	1 *1*	—	—	—	—	—	—	—
Phalacrocorax africanus (Gmel.)	—	—	2 *2*	—	—	2 *3*	—	—
Phalacrocorax sp.	2 *2*	—	—	—	—	1 *1*	6 *6*	—
Anhingidae								
Anhinga rufa (Lacépède & Daudin)	2 *2*	—	—	—	2 *2*	2 *2*	1 *1*	—
Pelecanidae								
? *Pelecanus* sp.	—	—	—	—	—	1 *1*	—	—
Pelecaniformes indet.	1 *1*	—	—	—	—	—	—	—

(*continued next page*)

Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Ranidae								
Arthroleptis sp.	—	—	1 *1*	—	—	—	—	—
Phrynobatrachus natalensis (Smith) ..	—	—	—	—	1 *1*	—	—	—
Polypedatidae								
Hyperolius sp.	5 *6*	—	—	—	—	—	—	—
Brevicipitidae								
Hemisus mormoratum (Peters)	—	—	—	—	1 *1*	—	—	—
Anura indet.	8 *16*	1 *1*	1 *1*	—	6 *7*	2 *4*	3 *5*	—
REPTILIA								
Chelonia								
Pelomedusidae								
Pelusios subniger (Lacépède)	—	3 *3*	—	1 *1*	2 *2*	2 *3*	7 *7*	—
Pelusios sinuatus (Smith)	—	—	—	—	1 *1*	—	—	—
Pelusios sp.	—	—	—	—	—	4 *4*	3 *3*	—
Indet.	—	—	—	—	—	—	6 *6*	5 *5*
Crocodilia								
Crocodilidae								
Crocodilus niloticus Blgr.	9 *9*	1 *1*	—	3 *3*	2 *2*	—	2 *2*	1 *1*
Eggs	—	—	—	—	—	—	—	1 *82*
Lacertilia								
Varanidae								
Varanus niloticus (Linn.)	—	1 *1*	—	—	3 *3*	1 *1*	3 *3*	1 *1*
Ophidia								
Boidae								
Python sebae (Gmelin)	—	—	1 *1*	—	—	—	1 *1*	—
Colubridae								
Natrix olivacea (Peters)	2 *2*	—	—	—	—	—	—	—
Boaedon lineatum (Dum. & Bib.) ..	—	—	—	—	1 *1*	—	—	—
Chlorophis hoplogaster (Günther) ..	—	—	—	—	—	4 *4*	—	—
Dasypeltis scabra (Linn.)	1 *1*	—	—	—	—	—	—	—
Naia melanoleuca Hallowell	1 *1*	—	—	—	—	—	—	—
Viperidae								
Bitis arietans (Merrem)	—	—	—	—	—	1 *1*	—	—
Ophidia indet.	—	—	1 *1*	—	2 *2*	1 *1*	—	—
AVES								
Pelecaniformes								
Phalacrocoracidae								
Phalacrocorax lucidus (Licht.)	1 *1*	—	—	—	—	—	—	—
Phalacrocorax africanus (Gmel.) ..	—	—	2 *2*	—	—	2 *3*	—	—
Phalacrocorax sp.	2 *2*	—	—	—	—	1 *1*	6 *6*	—
Anhingidae								
Anhinga rufa (Lacépède & Daudin) ..	2 *2*	—	—	—	2 *2*	2 *2*	1 *1*	—
Pelecanidae								
? *Pelecanus* sp.	—	—	—	—	—	1 *1*	—	—
Pelecaniformes indet.	1 *1*	—	—	—	—	—	—	—

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Table 21—*continuation*

	Uganda (a)	*Uganda (b)*	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
CICONIIFORMES								
Ardeidae								
Ardea purpurea Linn.	—	—	—	—	—	—	1 *1*	—
ANSERIFORMES								
Anseridae								
? *Anas sparsa* Eyton	—	—	—	—	—	—	1 *1*	—
Anas undulata Dubois	—	—	1 *1*	—	—	—	—	—
? *Sarkidiornis melanota* (Pennant) ..	—	—	—	1 *1*	—	—	—	—
Indet.	—	—	2 *2*	—	—	—	—	3 *4*
RALLIFORMES								
Rallidae								
Porphyrula alleni (Thomson)	—	—	—	1 *1*	—	—	—	—
Porphyrio alba (White)	—	—	—	—	—	1 *1*	—	—
COLUMBIFORMES								
Columbidae								
? *Streptopelia capicola* (Sundev.) ..	—	—	—	—	1 *1*	—	—	—
Indet.	—	—	—	—	1 *1*	—	—	—
CAPRIMULGIFORMES								
Caprimulgidae								
Caprimulgus fossii Hartlaub	—	—	—	—	—	—	1 *1*	—
PASSERIFORMES								
Ploceidae								
Estrildine sp.	—	—	—	—	1 *1*	—	—	—
Indet.	1 *1*	—	1 *1*	—	—	—	—	—
Aves indet.	4 *4*	—	2 *2*	—	3 *3*	7 *7*	5 *5*	1 *2*
MAMMALIA								
PHOLIDOTA								
Manidae								
Manis tricuspis Rafinesque	1 *1*	—	—	—	—	—	—	—
PERISSODACTYLA								
Equidae								
Equus asinus Linn.	—	—	—	—	—	—	—	1 *1*
Equus burchellii (J. E. Gray)	—	—	—	—	1 *1*	—	—	—
ARTIODACTYLA								
Hippopotamidae								
Hippopotamus amphibius Linn. ..	1 *1*	2 *2*	—	1 *1*	1 *1*	—	—	1 *1*
Suidae								
Potamochoerus porcus Linn.	—	—	—	—	—	—	—	2 *2*

(continued next page)

Table 21—*continuation*

	Uganda (a)	*Uganda* (b)	*Bangweulu*	*Mweru and Kalungwishi*	*Luangwa*	*Kafue*	*Zambesi*	*Zululand*
Bovidae								
Bos taurus Linn.	—	—	—	—	—	2 *2*	1 *1*	3 *3*
Ovis aries Linn.	—	—	—	—	—	—	—	1 *1*
Capra hircus Linn.	—	—	—	—	—	—	—	2 *2*
Redunca arundinum Boddaert	—	—	—	—	—	—	1 *1*	—
Kobus ellipsiprymnus (Ogilby)	—	1 *1*	1 *1*	—	—	1 *1*	1 *1*	—
Kobus leche J. E. Gray	—	—	1 *1*	—	—	2 *2*	—	—
Hippotragus niger (Harris)	—	—	—	—	—	—	1 *1*	—
Tragelaphus spekii Sclater	—	—	2 *2*	—	—	—	1 *1*	—
? *Cephalophus natalensis* A. Smith	—	—	—	—	—	—	—	1 *1*
Indet.	1 *1*	—	—	1 *1*	—	1 *1*	—	—
Carnivora								
Canidae								
Canis familiaris Linn.	1 *1*	—	—	—	—	1 *1*	2 *2*	3 *3*
Mustelidae								
Lutra maculicollis Licht.	—	—	—	1 *1*	—	—	—	—
Viverridae								
Atilax paludinosus (G. Cuvier)	—	—	2 *2*	—	—	—	—	—
Genetta sp.	—	—	—	—	1 *1*	—	—	—
Indet.	—	—	—	—	—	3 *3*	—	—
Rodentia								
Hystricidae								
Hystrix africaeaustralis Peters	—	—	—	—	—	—	—	1 *1*
Octodontidae								
Thryonomys swinderianus (Temm.)	—	—	2 *2*	—	8 *8*	—	4 *4*	3 *5*
Muridae								
Mastomys natalensis A. Smith	—	—	—	—	—	—	1 *1*	—
Dasymys incomtus (Sundevall)	—	—	—	—	—	1 *1*	—	—
Oenomys hypoxanthus Puch	1 *1*	—	—	—	—	—	—	—
? *Otomys* sp.	—	—	1 *1*	—	—	—	—	—
Indet.	—	—	—	—	4 *4*	—	—	—
Rodentia indet.	3 *3*	1 *1*	5 *9*	—	—	1 *1*	9 *9*	—
Primates								
Cercopithecidae								
Papio ursinus Kerr	—	—	—	—	—	—	—	2 *2*
Cercopithecus sp.	—	—	—	—	—	—	—	2 *3*
Hominidae								
Human remains	—	—	—	—	—	2 *2*	1 *1*	1 *1*
Mammalia indet.	4 *4*	1 *1*	3 *3*	1 *1*	4 *4*	7 *7*	4 *4*	—

Coleoptera—making up more than half of the total insect catch—represent the bulk of insects taken by crocodiles in the Luangwa, Kafue and Zambesi Rivers, but not in Uganda and Bangweulu Swamp. As might be expected, water-beetles are well represented—both Hydrophilidae (including various species of *Hydrophilus*) and Dytiscidae (such as the large predaceous *Cybister*) being prominent. But a surprising feature of the collection is the large number of terrestrial forms—notably Carabidae, Scarabaeidae and Cicindelidae. Land-beetles number 196 as compared with 148 water-beetles : most of the former must have been taken when crocodiles were feeding ashore or climbing in vegetation over shallows.

Hemiptera are well represented from most localities, giant water-bugs (Belostomatidae) being prevalent. Such bugs as *Hydrocyrius*, *Lethocerus* and *Limnogaster* are the largest insects available to crocodiles, and especially in Uganda, they make a substantial food source which juveniles have been ready to exploit.

Orthoptera include both long- and short-horned grasshoppers, crickets and mole-crickets ; but only in the Luangwa Valley can they be regarded as other than incidental captures. Luangwa juveniles had fed quite extensively upon *Gryllotalpa africana*. Orthopterous prey again provide indirect evidence of the terrestrial hunting habits of young crocodiles.

Odonata were mostly taken from stomachs examined in Uganda (58 of 74 specimens). There are only three records from Bangweulu, and only two were found in 303 stomachs containing other food, from the Kafue and Zambesi Rivers. Dr P. S. Corbet (15.6.55) has most kindly examined a sample of the Uganda material. His analysis is as follows :

Larvae, 24 :	pharate or exuviae, 23 ;	non-pharate,	1.
Adults, 7 :	immature, 4 ;	mature,	3.

In this sample of thirty-one specimens, at least twenty-seven (87 per cent.) were probably taken at the time of emergence. This suggests that the reptiles must have been taking their prey on, or near to, the shore ; and that—since the species here represented all leave the water prior to emergence soon after dusk—the crocodiles had captured most of their prey at night. Both of these conclusions, for which I am indebted to Corbet, are fully confirmed by field observation.

Araneida

At no time of life do spiders make a substantial contribution to a crocodile's diet. Of forty-four spiders recovered, all but seven were from juveniles less than one metre in length, and none were found in any crocodile over two metres in length. Most of the specimens identified are referable to *Dolomedes*, a genus of water-spiders which frequent floating vegetation, from which they make predatory sorties over the surface film.

Mollusca

One of the surprising facts here brought to light is the quite unexpected role of molluscs in crocodile ecology. Of 673 stomachs containing food of any kind from Uganda and Rhodesia, 145 (21·5 per cent.) contained molluscs. This food is taken by crocodiles of all length groups. In terms of the number of prey, molluscs far exceed all other food organisms, and account for nearly 70 per cent. of the total. Predation upon ampulariid water snails was especially heavy in Bangweulu Swamp, Mweru Wa Ntipa, and the Kafue Flats, where molluscs represent 89·1, 87·0 and 84·7 per cent. of all prey. The very high proportion of Gastropoda (4192) as compared with Lammellibranchiata (only 6) is remarkable. The former consist almost entirely of ampulariids—*Pila ovata*, a species common on rock surfaces just below water-line, in Uganda ; and *Lanistes ovum*, which is found submerged among water plants and on detritus in Rhodesian waters.

Crustacea

Remains of 137 crabs were recovered from 106 stomachs. The importance of crabs as food varied widely in different waters. None were found in stomachs examined in Bangweulu, Mweru Wa Ntipa, the Kalungwishi River or Luangwa Valley. On the other hand, in the Kafue and especially in the Upper Zambesi, crabs of the genus *Potamonautes* form a substantial element in the diet of crocodiles up to about 1·5 metres in length. In Uganda the prey species is *P. niloticus*, and in Rhodesia, apparently *B. bayonianus*.

Pisces

The percentage occurrence of invertebrates, fish, and other vertebrates throughout the life cycle is summarised in Fig. 36, from which it will be seen that the

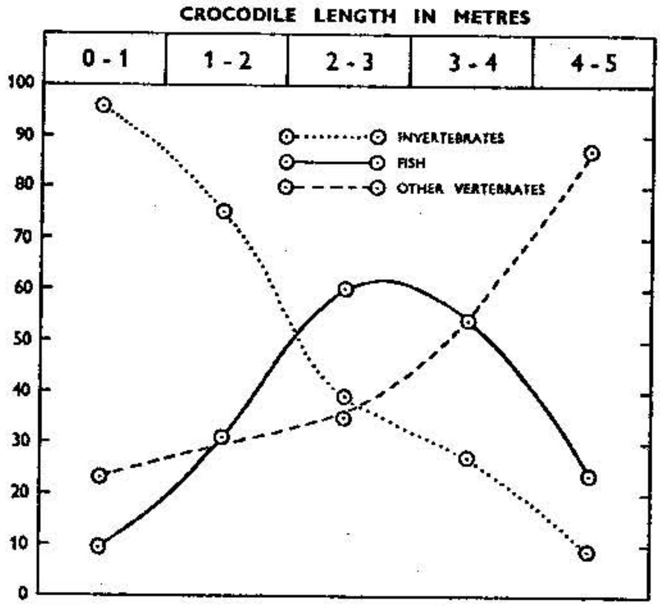

Fig. 36. Changes in the feeding pattern which accompany growth, with special reference to fish prey. Occurrences of three categories of food are expressed as a percentage of stomachs containing food of any kind.

relative importance of fish, as prey, changes markedly with age. It is only in the length range from about 2·0 to 3·5 metres that fish form the main food.

Wholly extravagant views as to the quantity of fish eaten have been held in the past. For example, Capt R. J. D. Salmon (1932), referring to crocodiles feeding below Murchison Falls, mentions 50 lbs. a night as an estimate. Nothing approaching this weight has been found in any crocodile examined by me. Remains of some 393 fish were recovered from 265 of the 851 crocodiles examined. In 701 stomachs containing food of any kind, the percentage occurrence of fish-prey is 37·8 ; and the number of fish per stomach only 0·56.

The proportions in which various genera are taken varies markedly according to locality. On Lakes Kioga and Kwania it appears from Hippel's investigation (1946) that *Protopterus* and *Barbus* together account for nearly two-thirds of the catch, the remaining genera, in order of importance, comprising *Tilapia, Clarias, Bagrus, Mormyrus* and *Haplochromis*. My own data from waters in Uganda above Murchison Falls agree in placing *Protopterus* and *Barbus* as the main prey (some of my *Mormyrus* records were from crocodiles that had been feeding on offal discarded near fish-camps).

The records from the Semliki River, Lake Albert and the Nile below Murchison indicate that *Synodontis, Alestes,* and *Auchenoglanis* are most frequently taken (in the order given).

Lake Bangweulu in Northern Rhodesia was the only locality in which catches of *Tilapia* were in excess of any other genera (seven specimens among a total of twenty-one fish identified). In Mweru Wa Ntipa crocodiles were feeding almost entirely upon *Clarias*. Prey records from the Upper Zambesi and Kafue include the following genera as most frequent : *Clarias,* 42 ; *Tilapia,* 25 ; *Synodontis,* 17 ; *Haplochromis* and allied genera, 14.

Amphibia

Frogs and toads are eaten during the first three or four years of life (up to 1·5 metres in length). Thereafter this prey almost disappears from the diet and no Anura were recorded from any crocodile exceeding 2·5 metres. The species most frequently taken, both in Uganda and Northern Rhodesia, is *Bufo regularis*.

Reptilia

Reptiles or their remains were found in seventy-seven stomachs, as follows : Ophidia, 16 ; Lacertilia, 9 ; Chelonia, 35 ; Crocodilia, 17. Most of the snakes were small riverine species such as *Natrix olivacea* and *Chlorophis hoplogaster* which could have been taken in the water : this also applies to a large Black Cobra (*Naia melanoleuca*) taken at Fajao. A surprising catch was a Puff Adder (*Bitis arietans*) from the Kafue Flats. Two crocodiles had eaten African Python (*Python sebae*). Three snakes were recovered from juveniles less than a metre in length, these being the smallest crocodiles to contain reptilian prey of any kind.

The Nile Monitor (*V. niloticus*)—the only species of lizard identified—is doubtless preyed upon in all localities where it associates with crocodiles, present records including Murchison (1), Luangwa (3), Kafue (1), Zambesi (3), Zululand (1). Most of the identified turtles were *Pelusios subniger*, a species very common in the muddy waters of the Kafue and Zambesi.

Cannibalism

Crocodiles are much addicted to cannibalism and this is doubtless one of the factors which accounts for their segregation in " age-groups " on the basking grounds and elsewhere. Evidence of cannibalism is afforded by (i) injured specimens, (ii) direct observations, and (iii) stomach contents. Injuries that may be attributed to cannibalistic assaults are not infrequent. Predatory attacks by one crocodile upon another have rarely been witnessed, though these are known to occur in captivity. Wajalubi told me (1952) that he had seen an old crocodile prey upon a young one in the Semliki River; and both Pitman (1935) and Poles (1956) give details of such attacks. But the main evidence is to be derived from stomach examinations. In 1952 N. H. Searle recovered a crocodile's tail from the stomach of another individual. In Zululand, P. H. Jackson found a crocodile measuring about one metre in the stomach of another four metres in length. In Uganda Hippel (1946) found crocodile remains in thirty-seven of 587 crocodiles examined; and he ascertained that these could not derive from carcasses caught by his organization. Of the seventeen occurrences of crocodile prey now recorded (Uganda 9, Mweru 3, Luangwa 2, Zambesi 2, Zululand 1) only two of the predators (both from Luangwa) measured less than 3 metres, and no fewer than eight were very large, ranging from 4·1 to 4·9 metres. Cannibalism thus appears to be a habit acquired with age.

Aves

Birds are preyed upon by crocodiles of all length groups, and the records show a more even distribution for avian than for any other type of prey. But at no period do they form an important food. Bird remains were found in sixty of 701 stomachs containg food of any kind. These figures are in general agreement with Hippel's recoveries of bird remains from thirty-eight of 587 stomachs (Hippel, 1946)—the percentage occurrence for the two series of observations being 8·6 and 6·5 respectively.

Much of the present material was too fragmentary for identification. So far as determination allows of analysis, the several orders are represented by specimens as follows: Pelecaniformes, 24; Anseriformes, 9; Passeriformes, 3; Ralliformes, 2; Columbiformes, 2; Ciconiiformes, 1; Caprimulgiformes, 1.

African records from many sources have been collected by Pitman (1957). While it is known that a very wide range of birds may be taken by the Nile Crocodile—from pelicans and Fish Eagle to weavers and swallows—it now seems clear that cormorants (*Phalacrocorax lucidus* and *P. africanus*) and darters (*Anhinga rufa*) make up the bulk of captures.

Mammalia

The frequency of occurrence of mammals rises with growth of the predator.

Various mammalian orders represented in the present material are as follows: Rodentia, 51; Artiodactyla, 33; Carnivora, 13; Primates, 9; Perissodactyla, 2; Pholidota, 1. Nearly half of the identified specimens were rodents; much hair listed in Table 21 as unidentified was certainly of rodent origin and seemed to be either *Dasymys*, *Otomys*, *Pelomys* or *Arvicanthis* (Ansell, 4.9.57). In Northern Rhodesia and Zululand the Cane Rat (*Thryonomys swinderianus*) is numerically the most important prey species.

Attacks upon game animals do not appear to be heavy, except perhaps in the Kafue near Lochinvar Ranch. From the whole series under review, remains of antelopes were found in sixteen of 323 stomachs of crocodiles larger than 2·0 metres, as follows: Waterbuck, 4; Lechwe, 3; Situtunga, 3; Sable, 1; Reedbuck, 1; Natal Duiker, 1; unidentified, 3. Evidence of predation upon domestic cattle was found in six stomachs, and of sheep or goats in three stomachs. The records from all areas also include six hippopotamus, and four human fatalities.

Food in relation to locality

Considerable differences have been found in the proportions and kinds of prey taken in different localities. Tables 22 to 27 give comparative data for the main categories. In these tables the occurrences are expressed, under each Length Group, as a percentage of stomachs containing food of any kind. Since many stomachs contained more than one kind of food, it has been necessary to adjust percentages in the comparative histograms (Fig. 37), where the occurrence of a particular food is expressed, within each Length Group, as a percentage of all occurrences.

Salient features in the diet of crocodiles in different localities are here briefly summarised.

TABLE 22

Number and percentage of stomachs containing various foods, by Length Groups: Uganda.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*	*4–5*
Number of crocodiles containing prey	49	25	13	19	18
Insecta ..	47 (96·0%)	16 (64·0%)	—	1 (5·3%)	—
Araneida ..	8 (16·3%)	2 (8·0%)	—	—	—
Crustacea ..	3 (6·1%)	11 (44·0%)	2 (15·4%)	—	—
Mollusca ..	4 (8·2%)	5 (20·0%)	3 (23·1%)	2 (10·5%)	—
Pisces ..	2 (4·1%)	10 (40·0%)	12 (92·3%)	15 (79·0%)	5 (27·8%)
Amphibia ..	11 (22·4%)	4 (16·0%)	1 (7·7%)	—	—
Reptilia ..	2 (4·1%)	2 (8·0%)	1 (7·7%)	3 (15·8%)	10 (55·6%)
Aves ..	—	4 (16·0%)	2 (15·4%)	4 (21·1%)	1 (5·6%)
Mammalia ..	2 (4·1%)	3 (12·0%)	2 (15·4%)	2 (10·5%)	7 (38·9%)

TABLE 23

Number and percentage of stomachs containing various foods, by Length Groups: Bangweulu.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*
Number of crocodiles containing prey ..	18	28	44	20
Insecta	12 (66·7%)	5 (17·9%)	1 (2·3%)	—
Araneida	1 (5·5%)	—	—	—
Crustacea	1 (5·5%)	1 (3·6%)	—	—
Mollusca	1 (5·5%)	11 (39·3%)	27 (61·4%)	10 (50·0%)
Pisces	5 (27·8%)	14 (50·0%)	17 (38·6%)	8 (40·0%)
Amphibia ..	1 (5·5%)	1 (3·6%)	—	—
Reptilia	—	—	1 (2·3%)	1 (5·0%)
Aves	2 (11·1%)	1 (3·6%)	3 (6·8%)	2 (10·0%)
Mammalia ..	—	2 (7·1%)	7 (15·9%)	7 (35·0%)

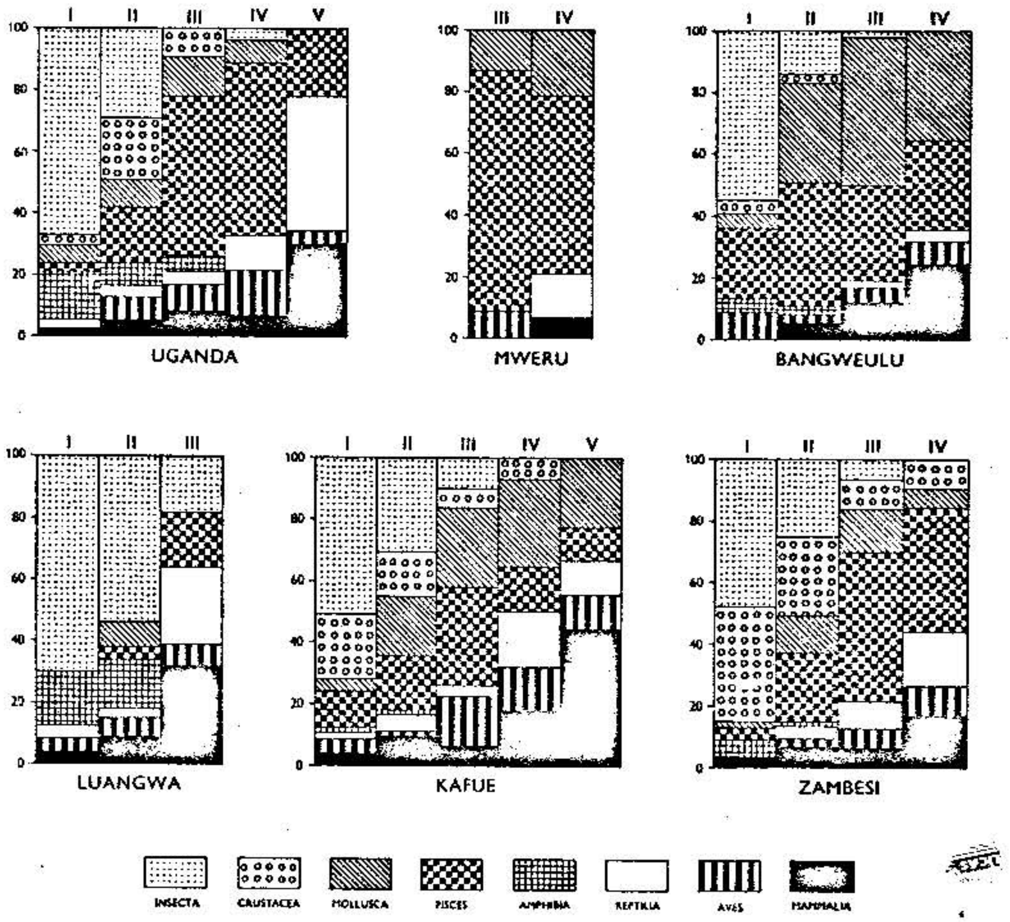

Fig. 37. Comparison of feeding habits of *C. niloticus* in six localities. The occurrences of each food category are expressed, for each Length Group, as a percentage of all occurrences.

TABLE 24

Number and percentage of stomachs containing various foods, by Length Groups: Mweru Wa Ntipa and Kalungwishi River.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*	*4–5*
Number of crocodiles containing prey	2	2	20	24	1
Insecta ..	2 (100·0%)	1 (50·0%)	—	—	—
Araneida ..	2 (100·0%)	—	—	—	—
Crustacea ..	—	—	—	—	—
Mollusca ..	2 (100·0%)	2 (100·0%)	3 (15·0%)	6 (25·0%)	—
Pisces ..	—	—	18 (90·0%)	16 (66·7%)	—
Amphibia ..	—	—	—	—	—
Reptilia ..	—	—	—	4 (16·7%)	—
Aves ..	—	—	2 (10·0%)	—	—
Mammalia ..	—	1 (50·0%)	—	2 (8·3%)	1 (100·0%)

TABLE 25

Number and percentage of stomachs containing various foods, by Length Groups: Luangwa Valley.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*
Number of crocodiles containing prey ..	17	49	20	1
Insecta	17 (100·0%)	41 (87·5%)	5 (25·0%)	—
Araneida	—	1 (2·0%)	—	—
Crustacea	—	—	—	—
Mollusca	—	6 (12·2%)	—	—
Pisces	—	3 (6·1%)	5 (25·0%)	—
Amphibia ..	4 (23·5%)	12 (24·5%)	—	—
Reptilia	1 (5·9%)	2 (4·1%)	7 (35·0%)	—
Aves	1 (5·9%)	5 (10·2%)	2 (10·0%)	—
Mammalia ..	1 (5·9%)	7 (14·3%)	9 (45·0%)	1 (100·0%)

TABLE 26

Number and percentage of stomachs containing various foods, by Length Groups : Kafue Flats.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*	*4–5*
Number of crocodiles containing prey	27	29	18	12	4
Insecta ..	25 (92·6%)	19 (65·5%)	3 (16·7%)	—	—
Araneida ..	3 (11·1%)	1 (3·4%)	—	—	—
Crustacea ..	10 (37·0%)	9 (31·0%)	2 (11·1%)	2 (16·7%)	—
Mollusca ..	2 (7·4%)	12 (41·4%)	8 (44·4%)	8 (66·7%)	2 (50·0%)
Pisces ..	5 (18·5%)	11 (37·9%)	10 (55·5%)	4 (33·3%)	1 (25·0%)
Amphibia ..	1 (3·7%)	1 (3·4%)	—	—	—
Reptilia ..	1 (3·7%)	3 (10·3%)	1 (5·5%)	5 (41·7%)	1 (25·0%)
Aves ..	2 (7·4%)	1 (3·4%)	5 (27·8%)	4 (33·3%)	1 (25·0%)
Mammalia ..	2 (7·4%)	6 (20·7%)	2 (11·1%)	5 (41·7%)	4 (100·0%)

TABLE 27

Number and percentage of stomachs containing various foods, by Length Groups : Zambesi.

Length in metres	*0–1*	*1–2*	*2–3*	*3–4*	*4 –5*
Number of crocodiles containing prey	31	78	65	37	1
Insecta ..	25 (80·6%)	29 (37·2%)	6 (9·2%)	—	—
Araneida ..	7 (22·6%)	—	—	—	—
Crustacea ..	20 (64·5%)	31 (39·8%)	9 (13·8%)	5 (13·5%)	1 (100·0%)
Mollusca ..	1 (3·2%)	14 (17·9%)	13 (20·0%)	3 (8·1%)	—
Pisces ..	2 (6·5%)	26 (33·3%)	46 (70·8%)	21 (56·8%)	—
Amphibia ..	3 (9·7%)	1 (1·3%)	—	—	—
Reptilia ..	—	5 (6·4%)	8 (12·3%)	9 (24·3%)	—
Aves ..	—	3 (3·8%)	6 (9·2%)	5 (13·5%)	—
Mammalia ..	2 (6·5%)	8 (10·3%)	6 (9·2%)	9 (24·3%)	—

Uganda

The composition of insect food is remarkable for the high proportion of Hemiptera and Odonata : especially prominent are the giant water-bugs *Hydrocyrius columbiae* and *Limnogeton fieberi*, and the smaller *Sphaerodema nepoides*, as food of young crocodiles. The Uganda material shows a higher rate of predation on fish (Length Group III, 92·3 per cent.; Length Group IV, 79·0 per cent.) than has been found elsewhere, except in Mweru Wa Ntipa.

Bangweulu

A unique feature is the heavy intake of gastropods of the genus *Lanistes*. These large water snails were found in crocodiles of all length groups examined and—whether considered by bulk, by number of prey taken, or by occurrences—comprise the main food. The mean content per stomach containing food of any kind is 16·2 gastropods, as compared with 0·7 fish. Surprisingly, this local habit is shared even by the largest crocodiles. Thus : No. 127 (3·68 metres and the largest shot) contained no food other than 90 *Lanistes* ; No. H.64 (3·55 metres) contained 150 *Lanistes* ; and No. 124 (2·55 metres) had its stomach distended with 820 *Lanistes* and remains of two fish. Notable deficiencies from the diet of these swamp crocodiles are crabs (2 only), anura (3 only) and turtles (none).

Mweru Wa Ntipa

Nothing is known of the feeding habits of the young. Those of the adults are specialised, and indeed crocodiles living in the highly opaque, alkaline waters of this shallow lake appear to be almost monophagous. Thirty-seven of fifty-one crocodiles over 2·5 metres contained food, and of these thirty had been feeding on *Clarias mossambicus*. No *Tilapia* were recovered. Occurrences of other prey were limited to molluscs (4), crocodile remains (3), birds (1) and mammals (2).

Luangwa Valley

The food of crocodiles in the Lunsemfwa and Luangwa Rivers again shows certain distinctive features. Beetles are preyed upon more extensively than elsewhere and the insectivorous habit persists longer in life. Prominent are various terrestrial insects, notably *Gryllotalpa africana, Cicindela dongalensis, Scarites aestuans* and *Temnorhynchus* spp.; while surprisingly few water beetles (Dytiscidae, Hydrophilidae) were found. Other notable deficiencies in the diet are crabs (none), molluscs (6 occurrences) and fish (only 8 occurrences in 87 stomachs containing food). Anura and reptiles occur frequently, and in greater variety than elsewhere ; and rodents, especially cane rats, are the main mammalian prey.

Kafue and Zambesi Rivers

Beetles are the most frequent food of the young, *Hydrophilus aculeatus* being an important prey species. In certain other respects the diet differs markedly from that in the Luangwa Valley. Fresh water crabs, *Potamonautes*, were taken by crocodiles of all sizes, including the largest, and appear to form the bulk of all food of juveniles up to about 1·2 metres in the Kafue and up to about 1·5 metres in the Zambesi. Anura were rarely taken (only six occurrences in 303 stomachs containing food). Both molluscs and fish become important prey in adult life, the former especially in the Kafue and the latter in the Zambesi.

Feeding behaviour

The Nile Crocodile is remarkable for the wide variety of prey taken in the course of its life. Victims range from terrestrial and aerial to wholly aquatic forms ; and in size from small organisms such as spiders, ants and termites, up to the great mammals and including African Buffalo (Andersson, 1856 ; Pitman, 1936, 1949), Lion, Black Rhinoceros (Selous, 1908 ; N.R. Journal, 1950), and Camel (Owen, 1951).

Its methods of hunting, capture and disposal of prey are as varied as the habits of its victims. Thus no general statement regarding feeding techniques is admissible, though it may be said that nearly always stealth, surprise, and a sudden final burst of speed are involved.

Methods of attack

The method of attack depends upon circumstances : the approach may be (a) from water to land ; (b) from water to air ; (c) on land ; and (d) under water.

(a) Adult crocodiles often lurk off-shore near game trails and watering places. On sighting an animal that has come down to drink, the reptile quietly submerges, and cruises under water to the precise spot from which it can make its fatal upward rush. The prey is seized by the nose or leg, dragged back into the water, and drowned.

(b) The under-water approach is also used when crocodiles are feeding upon flocks of weavers at their overhanging nests (Baker, 1871), or in attacks upon *Quelea* during their evening drinking ritual (Attwell, 1954). The speed of the final assault is instantaneous. At Jinja I have seen a swimming crocodile take a dragonfly on the wing, the jaws closing over the insect like a sprung gin. On the Zambesi a crocodile has been seen to catch a leaping tigerfish (*Hydrocyon*) in mid-air (Voigt, 6.10.56).

(c) The habits of young crocodiles when feeding on land are similar to those of an insectivorous lizard : either the animal snaps at insects that pass or alight within reach—sometimes jumping into the air to do so ; or else it scrambles in search of beetles and other more sluggish prey.

When feeding ashore, adults often lie in ambush near trails or beside dried-up water courses that are used by waterbuck and other game coming to drink. It is under such circumstances that the deadly tail-stroke or sledge-hammer head-blow take effect—to throw the victim, break its leg, or fling it into the water.

(d) Two main methods of fishing—passive and active—have been observed. When feeding on small fish in-shore, crocodiles will lie submerged and motionless, with the mouth open and awash, and snap up prey as the shoals swim within reach (Stevenson-Hamilton, 1954 ; Holloway, pers. comm.).

Crocodiles have often been observed fishing in open water (Carpenter, 1928 ; Hubbard, 1927 ; Pitman, 1929 ; Graham, 1929 ; Salmon, 1932, and others) ; and further evidence that they take actively swimming fish is afforded by their seizing the plug-baits of anglers (Kinloch, 1956). The various accounts agree as to the procedure : the crocodile disappears under the water, hurls itself at its prey with a sudden plunge. It then surfaces, thrusting its head out of the water and smacks its jaws to kill and manipulate the fish until it can be swallowed head first.

Disposal of prey

The popular belief that crocodiles store bulky prey in "larders," and that they prefer their meat when it is partly decomposed, does not appear to be generally true. And despite what has often been said to the contrary, crocodiles are well able to feed from a large, fresh carcass.

According to Major W. E. Poles (1951), who watched crocodiles feeding on a hippopotamus in the Luangwa, the initial penetration is effected with an upward and sideways slash delivered with the lower jaw, the fourth tooth of which is admirably adapted for a spear thrust. Once the jaws are locked, the crocodile executes a slow roll, and so tears off a portion. Sometimes the reptile will roll right round half a dozen times in succession to detach a piece of meat. Smaller mammals are speedily dismembered in this fashion.

Food is always brought to the surface to be swallowed. Sometimes, as reported by Percival (1928) a large siluroid may be taken ashore and battered to death on a rock. Anderson (1950) saw crocodiles take catfish from pools of the Ibba onto a sand bank, where they ripped the flesh of the back and tail from the still living prey.

Scavenging

As scavengers, crocodiles fill the same niche as that occupied by vultures, marabou and hyaenas in the economy of nature. They readily assemble, especially at night, to feed on a carcass, and have frequently been observed in the water dismembering buffaloes, zebra, waterbuck or the carcasses of crocodiles discarded by skinners. Savidge (*in litt.*, 27.4.57) saw a crocodile feeding at the carcass of a lion that had been killed by buffaloes above Murchison Falls.

If the carcass is on shore, the reptiles often drag it into the water, where they can more readily, and in greater safety, dispose of it. Pitman (1939) reports that crocodiles he had shot were sometimes dragged to the lake through 30 or 40 yards of forest. But often these scavengers will come inland to feed from a kill (Attwell, 1959) ; and in the Semliki Valley Mr A. M. Henley once found four crocodiles feeding at the carcass of an elephant that had died half a mile from the river.

Enemies

Being the master predator in its environment, the adult crocodile has little to fear from any aggressor—except man. But various enemies take a heavy toll of both eggs and young.

Egg predators

The most important enemy is undoubtedly the Nile Monitor (*Varanus niloticus*) (Plate 7, fig. 2). In Uganda, wherever crocodiles are found in the breeding season, there the monitors are in active attendance. And on almost every nesting ground their scrapes and the surrounding litter of discarded egg-shells tell the tale of destruction. Mitchell (5.6.57) records that in Northern Rhodesia monitors appear to take the majority of clutches laid ; and Player (3.2.60) also reports heavy predation by *V. niloticus* in Zululand.

When foraging for eggs, the lizards show little fear of the crocodile, often walking close alongside to make exploratory scrapes within a few feet of its flanks (Plate 8, fig. 1). Sometimes they employ a ruse to entice a guardian crocodile from her eggs. Pitman (1931) on more than one occasion saw a monitor provoke a female to chase it into the water, while its mate speedily excavated the nest, later to be joined by the individual that had lured the crocodile away. Hippel (25.4.52) tells me he has also seen monitors working thus in pairs—which he believed to be the male and female—near Bugonda, Lake Kioga. However, their best chance of booty comes when the crocodiles have been disturbed. At such times half-a-dozen or more of the lizards will appear from nearby cover, to conduct on the deserted grounds a persistent search for eggs.

Defence of the eggs by the crocodile is mainly passive—each female lying over her clutch. But Mr Douglas Jones told me he once saw crocodiles go into action against the marauders. As his launch drew near one of the beaches at Fajao, the crocodiles walked into the water : however, while the monitors were taking advantage of their absence, several returned and sent the lizards scurrying from the site. Such counter-attacks have rarely been witnessed : but the presence of monitors in crocodiles' stomachs—from Murchison, Uganda (No. 36), the Luangwa, Kafue and Zambesi Rivers, Northern Rhodesia (Nos. 254, 259, 265, 374, V. 21), Upper Zambesi, Barotseland (Nos. 481, 510), and the Usutu River, Zululand (No. Pl. 1)—indicate that the egg thieves are often caught unawares.

The Marabou (*Leptoptilos crumeniferus*) is known to eat the eggs. In 1955, at two places below Murchison Falls, Douglas Jones watched these carrion-feeders gorge themselves on clutches that had been uncovered by monitors. Goldsmith (1805) states that vultures watch the crocodile laying, and later tear up the eggs : Ellis (1838) also refers to egg-eating by vultures in Madagascar.

Mammalian egg thieves include mongooses, baboons and hyaenas. Many early writers refer to the mongoose's hostility to the crocodile. In Egypt the culprit would presumably be *Herpestes ichneumon* (Anderson 1898). According to Stevenson-Hamilton (1954) the Water Mongoose (*Atilax paludinosus*) is one of the most deadly enemies in southern Africa. Mitchell (1946) records that many nests are dug out by the Spotted Hyaena (*Hyaena crocuta*) in Nyasaland ; and in Uganda this habit has been confirmed by Pitman (27.5.59).

Olive Baboons (*Papio anubis*) often visit the crocodile beaches when on their way to water, and have opportunity to steal unguarded eggs. Mr John Savidge (12.2.57) tells me that at three separate places in one day he has seen baboons sitting close beside crocodiles : as soon as the reptiles had been frightened into the water, the baboons scrambled to the place where they had been lying to dig up and eat the eggs.

According to Lavauden (1934) eggs are also taken by Warthogs and Bush-pigs.

Enemies of the young

The newly-hatched young are relatively defenceless, and they doubtless fall victims to a variety of enemies both on land and when first launched upon life in the shallows.

From the evidence of stomach contents, and from observations on captive specimens, it would appear that older crocodiles are an agent of infantile mortality. Again, monitors certainly do not confine their attentions to the eggs. Anderson (1898) states that when the young make from the nest to the water, they fall a prey to *V. niloticus*. Charles Magala assured me that he had himself seen the lizards preying upon recently-hatched young ; and Mr R. M. Bere (17.5.56) refers to the heavy toll taken by both monitors and marabou, below Murchison Falls, when the eggs are hatching.

According to various early accounts from Egypt (Sonnini, 1800 ; Borderip, 1852 ; Burton, in Anderson, 1898) a turtle called Thirse—which is presumably *Trionyx triunguis* (Flower, 1933)—also takes heavy toll when the newly-hatched young repair to the river. Both at the Magungu and Fajao crocodile grounds these large turtles were often seen, and they were found breeding at the former site. From the Congo, Hoier (1950) reports predations by catfish.

Mr I. H. Player tells me that both he and Mr L. Trollope have seen baby crocodiles taken by the Fish Eagle (*Cuncuma vocifer*) in Zululand. Livingstone (1865) had previously recorded that fish-hawks make havoc among the young. Marabou also take their toll at hatching time (Bere, 17.5.56). Finally, Mr John Savidge (27.4.57) sends me circumstantial evidence from Murchison that the Ground Hornbill (*Bucorvus abyssinicus*) must be numbered among their enemies.

Enemies of the adult

The animal with which adult crocodiles are most likely to come into conflict is the hippopotamus. The species often meet and intermingle, both on land and in the water, and their relations are those of armed neutrality. On land, the hippopotamus is the acknowledged master and the reptiles readily give ground before them, sometimes hissing remonstrance as they retreat. At Fajao in 1952 Major Roy Wyndham saw two males—which were about to fight—first clear the arena by pushing all the crocodiles from their basking place. Stevenson-Hamilton

(1954) states that at calving time either the mother or others of the school will drive all the crocodiles out of the pool in which they happen to be lying. When protecting her calf in the water, a female will snap viciously at any crocodile that ventures too close. Sometimes the attack is pressed home and the crocodile is seized and bitten in half. Evidence of such an assault is reported from the Pafuri River by Stevenson-Hamilton (1954) ; and on 26th July, 1956, near Paraa, I saw a crocodile lying in the shallows in two pieces—its body completely severed just in front of the hind limbs. Further evidence of such encounters is given by Poles (1953) and by Mr J. E. Tully (personal communication).

The only other animals that are known to kill adult crocodiles are the Lion, Leopard and African Elephant. Crocodiles are quick to take advantage of another animal's kill, and Stevenson-Hamilton (1954) heard one reliable instance of a crocodile being killed by lions in such an encounter. A remarkable incident is recorded by Cameron (1877) in which a crocodile interfered in a lion and buffalo fight—all three animals eventually perishing.

It is an indisputable fact that lions sometimes deliberately prey upon the reptiles. Salmon (1932) described such an occurrence—the first recorded from Uganda—at Butiaba, where in August 1931 a lion, having killed a large crocodile measuring 11 feet, 7 inches, consumed the neck, shoulder and flanks. Pitman (1942) also reports that one afternoon visitors to the Murchison Falls saw a lion stalk and kill a crocodile on the opposite bank : the creature was so hungry that it continued to feed even when the launch crossed the river to afford a closer view. According to Thomas & Scott (1949) lions have been known to kill and devour crocodiles on the Lake Albert flats. Salmon (*ibid.*) also states that crocodile killing by lions "has been recorded as quite a normal occurrence on the western shore of Lake Rudolf."

Mr R. I. G. Attwell tells me that in the Luangwa Game Reserve, in June 1957, a crocodile moving from one drying pan to another was killed by a leopard, which later returned and ate half the tail.

According to Maberly (1959) there are several records of elephants having attacked and killed crocodiles—especially when the reptiles had been encountered travelling overland. In the Rufiji, elephants are reported to have placed their crocodile victims up in trees (Barker, 1953).

Injuries

Injuries of various kinds—wounds, scars, fractures and amputations—were frequently observed in the specimens examined (Plate 6, figs. 1 to 4). Data under this heading are recorded for 548 crocodiles : of these, 113 (about 20 per cent.) had sustained 127 injuries varying in severity from minor damage to serious mutilations. As might be expected, injuries are more frequent in older than in younger animals. This cumulative effect is shown in the following tabulation :

Length Group	*I*	*II*	*III*	*IV*	*V*
Number examined	119	178	156	84	11
Number injured ..	8	25	36	37	7
Per cent. injured	6·7	14·0	23·1	44·0	63·6

In the collections from each of the seven localities listed in Table 28, the tail is the part most often damaged. For the whole series, injuries are distributed as follows : tail, 89 (70·1 per cent.) ; limbs, 18 (14·2 per cent.) ; head, 14 (11·0 per cent) ; body, 6 (4·7 per cent.).

Direct evidence as to the agents responsible for the damage is generally wanting. Several crocodiles from the Upper Zambesi (Nos. 419, 420, 439, 454 and 468) had one or more of the barbed pectoral or dorsal fin spines of *Synodontis* firmly fixed in the palate or tongue. In other cases, it is probable that most of the injuries were inflicted by crocodiles, either in inter-male combat (see p. 267) or in the course of attacks by potential cannibals (see p. 296). The latter may account for many of the caudal lesions. If, on the other hand, injuries are received in combat between males, this would be reflected in their higher incidence among mature males than among mature females. Comparative data for the sexes (see Table 28) support the view that much of the damage is sustained in this way. The upper graphs in Fig. 38 show, for the sexes separately, the percentage with injuries. (In the absence of knowledge concerning the growth rate in adults, the comparison has here to be made in terms of length rather than age. When

TABLE 28

Incidence of injuries, in relation to sex and crocodile length.

Locality	*Crocodile length in metres*									
	0·3–1·0		1·0–2·0		2·0–3·0		3·0–4·0		4·0–5·0	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Uganda	2	1	2	2	2	1	3	4	4	–
Bangweulu	–	–	0	1	2	1	2	1	–	–
Mweru Wa Ntipa ..	–	–	–	–	2	1	5	1	0	–
Kalungwishi R. ..	–	–	0	1	0	1	2	0	–	–
Laungwa Valley ..	0	1	3	2	3	1	0	1	–	–
Kafue Flats	1	2	3	1	3	2	3	5	3	–
Upper Zambesi	1	0	5	5	8	9	6	4	–	–
No. examined	55	46	85	92	71	85	45	39	11	–
No. injured	4	4	13	12	20	16	21	16	7	–
Per cent.	7·3	8·7	15·3	13·0	28·2	18·8	46·7	41·0	63·6	–
No. seriously injured ..	2	1	4	1	5	0	6	3	4	–
Per cent.	3·6	2·2	4·7	1·1	7·0	0·0	13·3	7·7	36·4	–

allowance is made for the fact that females attain maximum growth over a size range that is at least one metre below that of fully-grown males, the divergence in the proportions of injured adult males and females will be greater than appears from the data as here presented.) The discrepancy becomes far more striking if account is taken only of severe casualties (see Table 29 and lower graphs, Fig. 38) : among twenty-six crocodiles showing evidence of more or less disabling mutilations, no fewer than twenty-one (about 81 per cent.) were males.

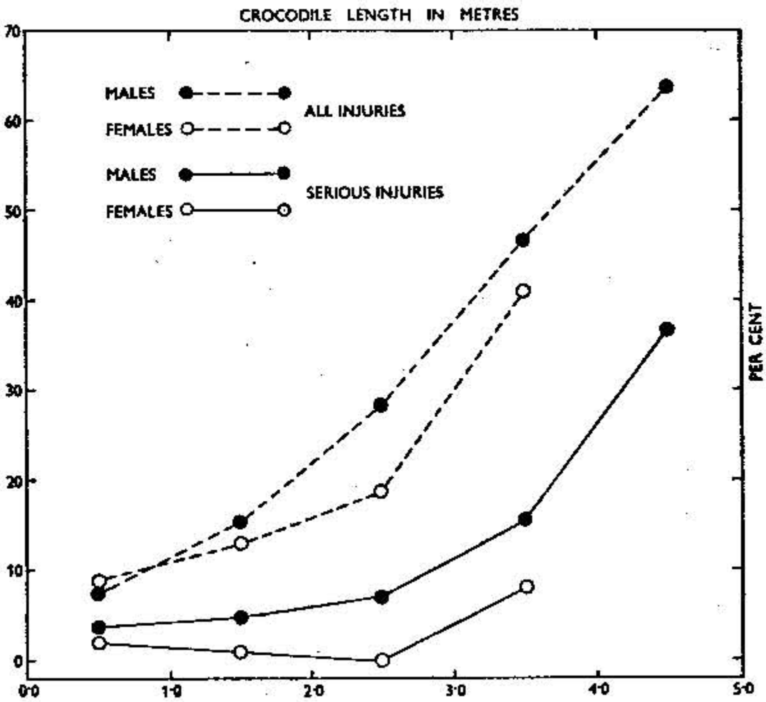

Fig. 38. Injuries, in relation to sex and length.

Table 29

List of serious (more or less disabling) injuries.

Serial No.	*Locality and Date*	*Length in mm.*	*Sex*	*Nature of injury*
1	Jinja, L. Victoria ; 9.1.52	c.1110	♂	distal half of tail missing ; wound healed with regenerated cornification.
17	Ntoroko, L. Albert ; 17.6.52	2750	♂	wound in groin.
27	Ripon Falls, Nile ; 8.7.52	3117	♀	right fore limb amputated at shoulder ; injury healed with pad of regenerated scales. (Plate 6, 2).
44	Buluba, L. Victoria ; 22.8.52	c.690	♀	distal half of tail missing behind penultimate paired caudal scutes.
124	Bangweulu Swamp ; 23.8.56	2550	♂	distal rami of lower jaw amputated at level of 5th tooth in upper jaw ; injury healed ; anterior teeth of upper jaw recurved. (Plate 6, 3).
178	Mweru Wa Ntipa ; 14.9.56.	c.3820	♂	tail amputated behind 7th median scute.

(continued next page)

Table 29—*continuation*

Serial No.	*Locality and Date*	*Length in mm.*	*Sex*	*Nature of injury*
180	Mweru Wa Ntipa ; 14.9.56	3520	♂	deep gash at base of left rear limb.
190	Mweru Wa Ntipa ; 14.9.56	2860	♂	distal rami of lower jaw amputated at level of 4th tooth in upper jaw ; dental abnormalities (Plate 6, 4).
193	Mweru Wa Ntipa ; 15.9.56	3380	♂	abnormal growth of snout resulting from serious injury in the nasal region (Plate 6, 1).
223	Magungu, Victoria Nile ; 2.1.57	4220	♂	a long open festering wound, infested with leeches, at base of tail, dorsally ; several median dorsal tail scutes missing ; tail tip amputated.
S.1	Magungu, Victoria Nile ; 23.4.57	c.4460	♂	four scars of old wounds, from 9 to 17 cms. long, on tail ; 4 scars on belly ; end of tail missing ; 4th digit of left fore limb fractured.
229	Rufunsa, Lunsemfwa R. ; 2.8.57	c.1030	♂	tail amputated behind 9th median scute.
273	Rufunsa, Lunsemfwa R. ;	c.2800	♂	tail amputated behind 8th median scute ; caudal scutes missing ; wound scars dorsally above hind limbs, and at base of tail.
299	Beit Bridge, Luangwa R. ; 11.8.57	950	?	rami of lower jaw amputated at level of 6th tooth in upper jaw ; regenerated with new symphysis.
305	Ndevu, Luangwa R. ; 13.8.57	c.1500	♀	tail amputated behind 3rd median scute.
337	Chimwajila, Kafue R. ; 24.8.57	4350	♂	tail tip missing ; upper jaw injured with many anterior teeth missing ; 10 cm. gashes on side of tail and behind right shoulder ; deep wound on right side of neck.
343	Chimwajila, Kafue R. ; 25.8.57	4270	♂	long gash dorsally at base of tail ; left fore limb fractured and deformed.
386	Iyeshya, Kafue R. ; 30.8.57	3540	♂	scars of two severe gashes, beneath throat and behind vent.
398	Iyeshya, Kafue R. ; 31.8.57	c.1370	♂	tail fractured at mid-length ; amputated behind 13th median scute ; 5 median dorsal scutes missing.
410	Iyeshya, Kafue R. ; 1.9.57	775	♂	severe regenerated injury at base of tail behind vent.
416	Mongu, Upper Zambesi; 10.9.57	c.3040	♂	end of tail amputated ; severe gashes ventrally in mid sector of tail.
428	Mongu, Upper Zambesi ; 10.9.57	885	♂	scars of severe bites ventrally at base of left hind limb.
450	Mongu, Upper Zambesi ; 13.9.57	3120	♀	lower jaw broken at symphysis ; injury regenerated but jaws closing asymmetrically.
481	Mongu, Upper Zambesi ; 15.9.57	c.3490	♂	tail amputated behind 10th median scute.
483	Mongu, Upper Zambesi ; 15.9.57	2910	♂	severe caudal injury, with large festering sore.
519	Mongu, Upper Zambesi ; 16.9.57	1890	♂	segment of muzzle missing, right side.
532	Mongu, Upper Zambesi ; 18.9.57	3130	♀	wedge-shaped portion of muzzle missing anteriorly, right side.

Parasites

Tsetse flies

In Uganda the tsetse fly *Glossina palpalis* is a common parasite of the crocodile. Both in Lake Victoria and along the Murchison reach of the Nile the flies were frequently observed settled, and feeding, on the thin skin between the scutes and on the tongue and mucosa (see Plate 2, fig. 2).

At Entebbe, Hoare (1929) experimentally carried the crocodile trypanosome, *T. grayi*, through its entire life-cycle, from naturally infected flies to the crocodile and from the crocodile to the flies again. Hoare (1931) also found that the degree of infection among " wild " tsetse flies compared closely with that among experimental flies that had fed only on crocodiles ; hence he inferred that in Lake Victoria the blood of the crocodile is the main food of the fly.

That the tsetse prefers reptilian to mammalian blood is also indicated by the fact that where crocodiles are abundant, as at Magungu, *G. palpalis*, though plentiful, is hardly troublesome to man. On the other hand, Marlier (1954) has stated that in areas of the Ruzizi basin where crocodiles were scarce, tsetse flies were less numerous but attacked man more vigorously.

The intimacy of the association between *G. palpalis* and *C. niloticus* is further shown by the fact that this fly is also the intermediate host of another crocodile blood parasite—the haemogregarine *Hepatozoon pettiti* (Hoare, 1932).

Leeches

Crocodiles are commonly infested, in some degree, with leeches. From samples, collected, the following have been identified : *Placobdella fimbriata*, from Jinja, Buluba (L. Victoria), Ripon Falls (Victoria Nile), and Kigi Is. (L. Kioga) ; ? *Helobdella conifera*, from Jinja ; and *Placobdella jaegerskioeldi*, from Mweru Wa Ntipa, and L. Chali (Bangweulu).

Leeches were present on 174 out of 506 crocodiles for which data are available. Table 30 summarises the information collected.

Table 30

Occurrence of leeches, in relation to crocodile length, for different localities.

Locality	*Crocodile length-groups*									
	I		II		III		IV		V	
	No. examined	*No. with leeches*	*No. examined*	*No. with leeches*	*No. examined*	*No. with leeches*	*No. examined*	*No. with leeches*	*No. examined*	*No. with leeches*
Uganda	39	5	17	4	10	6	12	10	6	6
Bangweulu Swamp ..	10	0	9	3	17	13	7	5	—	—
Mweru and Kalungwishi R.	2	0	2	1	24	6	32	18	2	1
Luangwa Valley ..	14	0	51	7	20	0	1	1	—	—
Kafue Flats	31	0	30	2	15	7	11	5	3	3
Upper Zambesi	11	0	53	21	59	40	18	10	—	—

The main point that emerges from this study is that infestation tends to increase progressively throughout the crocodile's life: this is true both as regards occurrence (see Fig. 39) and degree of infestation (see below). In their first year, the young are entirely free: the percentage occurrence rises from 4·7 per cent. in Length Group I, to 90·9 per cent. in Length Group V. This trend was generally similar for all the localities studied, except the Luangwa Valley (see Fig. 40).

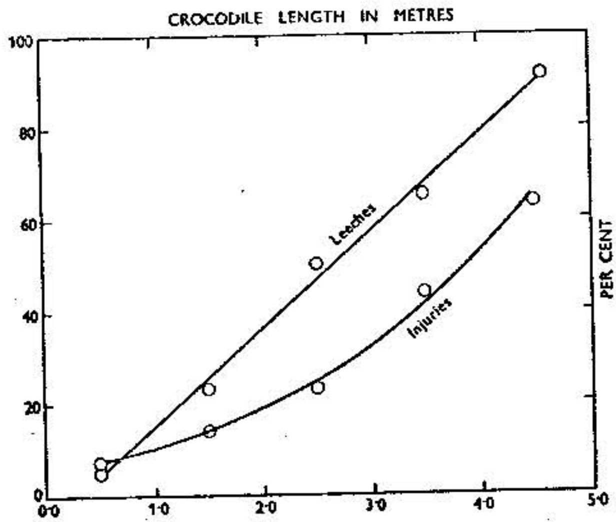

Fig. 39. Changes in the percentage of crocodiles carrying leeches, and with injuries, in relation to growth.

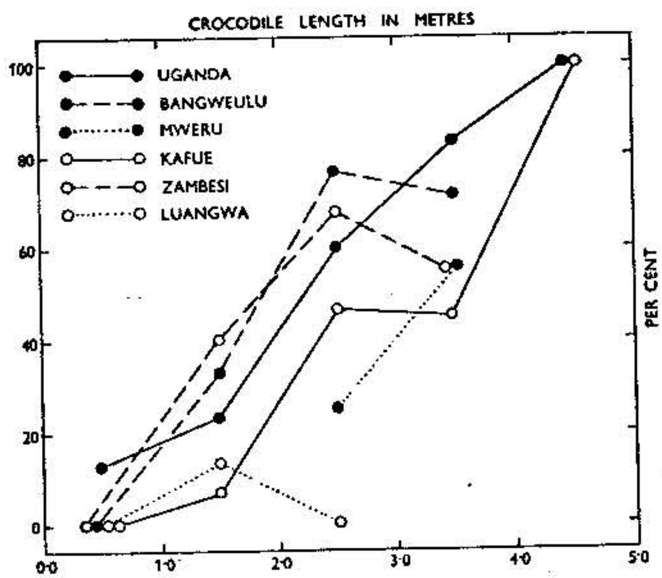

Fig. 40. Leech infestation: showing percentage of crocodiles carrying leeches in different localities, and in relation to crocodile length.

The incidence rate was exceptionally low (9·3 per cent.) in the Luangwa; and highest in Bangweulu (48·8 per cent.) and the Upper Zambesi (50·4 per cent.).

Three degrees of infestation are here recognized: light—from one, to a cluster of about ten leeches; moderate—two or more clusters; and heavy infestation—for example, No. 112 carried about 150 leeches. Occurrences, in different degrees of infestation, are summarised below, and shown graphically in Fig. 41.

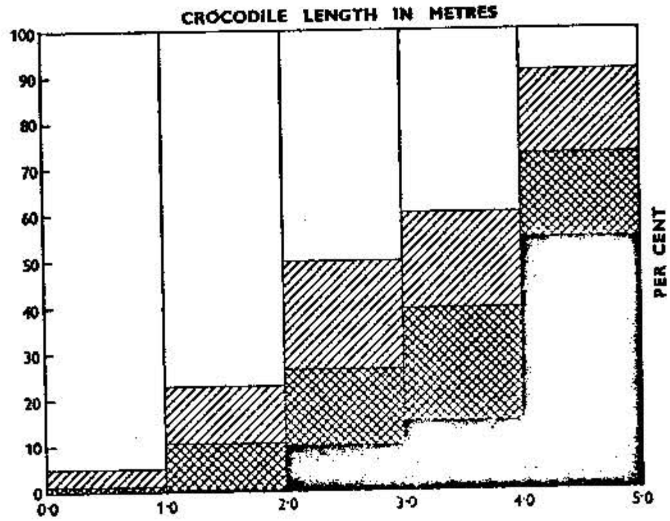

Fig. 41. Histogram showing percentages of different degrees of leech infestation in relation to crocodile length. Black—heavy; cross-hatched—moderate; diagonals—light; white—nil.

Length Group	*I*	*II*	*III*	*IV*	*V*
Number examined	107	162	145	81	11
Light infestation	4	21	34	17	2
Moderate infestation	1	16	24	20	2
Heavy infestation	0	1	14	12	6

Leeches may be found attached to any part of the body. Large concentrations were often present on the site of old scars, festering sores, and in dental sockets (Plate 6, fig. 4). Occurrences (in any degree of infestation) were distributed as follows: muzzle, head and nuchals, 3; shoulder, dorsal scutes and flanks, 32; fore limb, 24; armpit, 27; hind limb, 87; groin, 37; tail, 12; cloaca, 29; ventral shields, 28; gular shields, 14; tongue, teeth and mucosa, 23. In relation to the surface available for attachment, inaccessible parts, such as the cloaca, groins and armpits were far more heavily infested than the large exposed surfaces of the head, back, flanks and tail. It is not improbable that the leech-gathering activities of commensal birds (see p. 315) may account, in part, for the very uneven distribution observed.

Nematodes

Conditions under which the field work was carried out did not permit of a routine study of internal parasites; and information under this head is meagre. The commonest obvious parasites were nematodes. These were found in forty-four of sixty-six stomachs examined in Uganda, and in this sample were distributed in length-groups as follows:

Length Group	*I*	*II*	*III*	*IV*	*V*
Number examined	33	17	7	7	2
Number with nematodes ..	25	10	3	4	2
Occurrence per cent.	76	59	43	57	100

Two species are represented: *Multicaecum agile*, from Jinja and Namasagale; and *Dujardinascaris dujardini*, from Jinja, Buluba, Damba and Kaiso.

Nematodes recovered from stomachs in other localities include *D. dujardini*, from Iyeshya (Kafue R.); and *Contracaecum* sp., from Chimwajila (Kafue R.). Mr W. G. Inglis, who examined the material, tells me that the specimens of *Contracaecum* were almost certainly derived from fish: both the other nematodes are specific to the crocodile.

COMMENSAL BIRDS

Birds of many kinds—including darters, herons, egrets, duck, plovers, waders, skimmers and wagtails—frequent the basking and breeding grounds; and in such places become casually associated with the crocodile. Thus, at Magungu, Goliath Heron (*Ardea goliath*), Little Egret (*Egretta garzetta*) and Egyptian Goose (*Alopochen aegyptiacus*) were often found close to the reptiles. Below Murchison Falls, White-Collared Pratincole (*Galachrysia nuchalis*) and Pied Wagtail (*Motacilla aguimp*) frequented the rock islets when these were covered with crocodiles. At Ntoroko, on the Semliki, I have seen crocodiles closely attended by Hadada (*Hagedashia hagedash*) and Sacred Ibis (*Threskiornis aethiopicus*), Goliath and Great White Heron (*Casmerodius albus*), besides the more regular companion birds—Spur-Winged Plover (*Hoplopterus spinosus*) and Water Dikkop (*Burhinus vermiculatus*). On the Paraa-Fajao reach of the Nile, certain shelving mudbanks were often covered with White-faced Duck (*Dendrocygna viduata*) resting among lines of crocodiles: some of these banks were also the resort of African Skimmers (*Rynchops flavirostris*).

In such cases the association is fortuitous, the birds and reptiles merely sharing a common resting place. When lying ashore the crocodiles seem never to interfere with their companions; and the birds approach these potentially dangerous predators on the most familiar terms. For example, Chapman (1921) observed a large flock of Crowned Cranes (*Balearica pavonina*) placidly sleeping among crocodiles. On a mudbank in Lake Albert, Eggeling saw a crocodile surrounded by Knob-bill Geese (*Sarkidiornis melonotos*)—four of which were actually perched on its back (Pitman 1935). And Player (19.7.55) tells me that in Zululand he has observed White-faced Duck walking all over the bodies of crocodiles. This tolerance shown by basking crocodiles (which in other circumstances habitually prey upon waterfowl) throws indirect light upon the special associations next to be considered.

The classical account of a bird which was supposed to attend the crocodile in Egypt, as given by the early natural historians, is well known. In Pliny's version of the narrative, the crocodile-bird was said to take scraps of food that remained sticking to the reptile's teeth. Herodotus is more explicit: ". . . the crocodile . . . is in the habit of lying with its mouth wide open, facing the western breeze: at such times the *Trochilos* goes into his mouth and devours the leeches. This benefits the crocodile, who is pleased, and takes care not to hurt the *Trochilos*" (Rawlinson's trans.).

The identity of the Trochilos was much debated in the last century. St. Hilaire (1827), Taylor (1859, 1867), von Heuglin (1869), Dresser (1871–81), and Newton (1893–96) were among those who sustained the claim for the Egyptian Plover (*Pluvianus aegyptius*). Others, including Broderip (1852), Adams (1864), Smith (1868), Cook (1892) and Butler (1905) adduce evidence that the crocodile's benefactor is the "Zic-zac" (*H. spinosus*). Those who have disputed the rival claims of these birds all assume that the classical authors referred to one particular species. In the light of what is now know from other parts of Africa (see below) it is probable that *P. aegyptius* and *H. spinosus* were both associated with the crocodile in Egyptian waters.

For a long time the story was put down as one of the old Greek myths; and despite observations of St. Hilaire, Brehm, Cook and Burton—all of whom claimed to have seen plovers take food from the crocodile's mouth, some authorities, including Anderson (1898), Flower (1908), Bannerman (1930–51), and Cave & MacDonald (1955) have remained sceptical. For example, Bannerman states: "The popular belief . . . does not find much favour amongst competent naturalists at the present day."

Turning to present observations: in Uganda, *H. spinosus* is the crocodile's constant companion on all the favoured basking grounds on the shores and islands of Lake Victoria, along the Victoria Nile, and in Lake Albert and the Semliki River. The birds live on terms of intimacy with their partners and may constantly be seen running from one reptile to another, flitting over the sprawled bodies, and foraging or standing beside them (Plate 9, figs. 1 and 2). I have seen a pair standing within a foot of the gaping jaws. At Magungu, and elsewhere, the plovers are probably attracted by tsetse flies (*G. palpalis*) which depend mainly upon the crocodile for their blood supply. There is no reason to doubt that the agile and ever-alert *Hoplopterus* can, with impunity, snap at flies and leeches from the mucosa. Mr J. D. Kelsall assured me that in southern Lake Victoria he once observed a "crocodile-bird" (unidentified) jump from the ground to take something from the upper jaw of a gaping crocodile; and Hobley (1919) states that on the Nzoia River near Mumias he saw a Grey Wagtail walking about inside the open mouth. In this connexion, it is relevant to note the closely-parallel and well-authenticated association in small tropical fish (*Elacatinus oceanops*) which enter and clean the mouth cavity of the grouper *Epinephelus* (Eibl-Eibesfeldt, 1955).

Another bird that habitually feeds from basking crocodiles is the Common

Sandpiper (*Actitis hypoleucos*). During long periods in the hide at Magungu I frequently observed this habit. To cite one example, the following is taken from my journal, 30.12.56 : " At 0945 hrs. a large crocodile waded boldly out of the river and planted itself squarely on the foreshore. . . . Almost immediately it had settled, a common sandpiper ran up to it and ran along beside its tail, starting from the hind limb and working towards the tail-tip, snapping at insects (probably tsetse flies) as it went (see Plate 9, fig. 3). Once it jumped from the ground to catch an insect otherwise out of reach. . . . This sandpiper returned on at least four occasions to work round the crocodile." The birds usually paid particular attention to crocodiles which had just come ashore : on one morning a sandpiper hurried up to four or five crocodiles in turn, while each was still wet from emergence.

In Zululand I. H. Player and K. Tinley have independently made similar observations, which both confirm and extend my own. On different occasions at Lake Nyamiti, Ndumu Game Reserve, sandpipers were seen—to peck at something in a crocodile's mouth ; to stand on the upper jaw ; to remove a leech from the gular scutes ; and to stand on the lower jaw and take a leech from the mucosa (Player, 24.3.55). Player and Tinley have also seen a Common Sandpiper run up to a turtle that had just come ashore and pick leeches off the neck and other exposed parts of skin (Player, 27.12.54).

In Borneo, sandpipers are reported to be similarly associated with *C. porosus* (Beccari, 1904 ; Hose, in Shelford, 1916).

While the commensal birds rid the crocodile of some ecto-parasites, these and other species play a far more important role in giving timely warning of danger. On countless occasions, while concealed in the hide, I have noted the reptile's immediate response to the alarm signal of birds which, of course, become aware of an approaching man or boat before their sleeping companions. The shrill call of a Spur-winged Plover or Water Dikkop is sufficient to send most of the crocodiles stampeding into the water, while others, often the largest on the beach, will delay their departure—raising their heads and looking for the cause of alarm, before following in retreat. Even the craning of a goose's neck, or the flurry of a sandpiper, provides a sufficient stimulus ; and all the crocodiles are at once alert and ready to leave.

In the capacity of watch-dog, *H. spinosus* takes pride of place in Uganda. While other species fly from the grounds when alarmed, the plovers will often remain, fluttering over the reptiles' backs and uttering the urgent notes—" quick, quick, quick "—as though to ensure that their charges are awake. Curzon (1849) saw one of these plovers dash itself two or three times against the head of a sleeping crocodile that he had surprised at close range. Such behaviour might appear incredible, were it not known that under similar circumstances oxpeckers react in the same way towards the rhinoceros—even attempting to arouse an animal that has been shot (Cumming, 1850).

The Water Dikkop is another regular associate on the sunning beaches and breeding grounds, and, especially in the season when the crocodiles are covering their eggs, one or more pairs of birds are nearly always to be found in the vicinity. On Buvu Island in early November, 1952, Lester and I found only two crocodile nests (hunters having been active in the area) : within 12 feet of one, and 13 feet of the other, a Water Dikkop was sitting on freshly-laid eggs. At the time of this discovery of a possible nesting association and synchronization of breeding cycles in the crocodiles and birds, I was unaware that Pitman (1950) had already noted the same phenomenon : he speaks of the birds' " definite association with crocodiles " and states that where the crocodiles breed there too will be found the eggs of *B. vermiculatus* " often . . . within a few feet of the brooding saurian." Player (7.2.55, 17.3.55) has observed the same habit in Zululand. It is not clear whether the partners derive mutual benefit from this nesting association. The birds undoubtedly serve the reptiles well as watchmen : it is also possible that from the habit of nesting beside the guardian crocodiles they may gain some adventitious protection against egg-eating enemies.

Ecological status

Population dynamics

The Nile Crocodile has no clearly defined mode of subsistence. Being a versatile opportunist, it maintains itself and meets varying circumstances with extreme flexibility of behaviour. Its ability to thrive, as an adult, upon prey ranging from crustaceans, molluscs and fish, to waterfowl, reptiles and large mammals, and upon carrion, gives it a unique status in its environment. Apart from the general role it plays as master predator, it occupies no single niche, but rather many niches—both on land and in the water. Thus it seems unlikely that food shortage can normally be an important factor in limiting its numbers. Should one food become temporarily scarce, the crocodile can turn to another, and in so doing it will exercise a differential pressure upon the shore and fresh water community. Moreover, the marked divergence in prey, feeding habits and habitat of young and old crocodiles—which is even more marked than that often found in a group of congeneric species (Gause's principle)—must tend to reduce intraspecific competition.

While the crocodile's place at the head of an elaborate system of food chains is unquestioned, heavy mortality, due to predation, nevertheless takes effect in the egg, newly-hatched young and adolescent stages. The maturing population also contains its own internal means of regulation, through cannibalism. Cannibalism also provides an explanation of the segregation of age-groups, for the habit tends to keep the young away from open water and basking grounds, in among weedy shallows.

In studies of the food habits of other animals, and especially of birds, attempts have often been made to evaluate the activities of particular species as " harmful " or " beneficial." The difficulties involved in attempting any such assessment have been discussed by Ritchie (1931) and Hartley (1948). The concept rests upon the assumption, rarely proved, that the predator is in fact a major factor in controlling the density of a prey species that is injurious, or useful, to agriculture, fishery or other other economic interests.

Even were it known that the crocodile exercised a controlling function upon the numbers of certain food organisms, it would not be possible to estimate its capacity for good or ill merely by comparing the proportion of " harmful " and " beneficial " food organisms eaten, when these are themselves so diverse in kind and habit, and so variously interconnected in a complex food web.

The web of food relationships in which the crocodile plays an essential part, is broadly outlined in Figs. 42 and 43, which indicate links in the chains: (a) which have been observed in the locality concerned (continuous lines); (b) which are known to obtain elsewhere (broken lines); and (c) which are unconfirmed but probable (dotted lines).

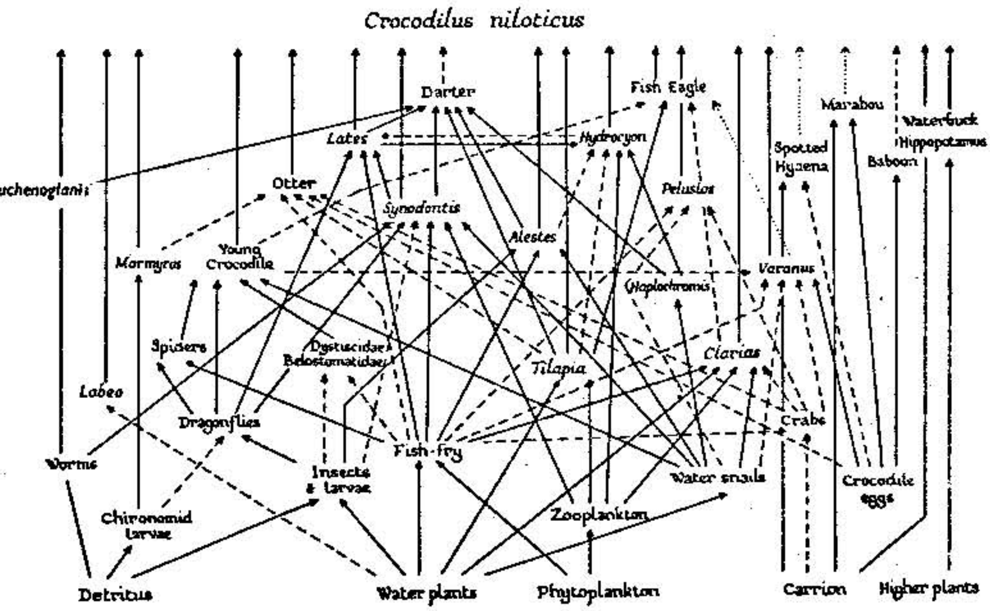

Fig. 42. Diagram showing the food relations of *C. niloticus* to various other members of the fauna: Uganda below Murchison Falls.

Examination of that part of the food web which primarily concerns reptiles and amphibia alone reveals sufficient complications, including cases of inter-specific competition and reciprocal predation. Thus, the turtle *Pelusios nigricans* and the monitor *Varanus niloticus* both feed extensively upon ampulariid gastropods such as *Lanistes* and *Pila*, which in some localities form a main item in the crocodile's menu at all ages. These three reptiles also prey upon the fresh water crab *Potamonautes*. Young crocodiles, and monitors, also eat toads and frogs, and the turtle takes tadpoles, while *Potamonautes* almost certainly includes anura in its generalised diet. Various snakes such as *Naia melanoleuca* and *Chlorophis hoplogaster*, themselves frog-eaters, are also preyed upon by the crocodile. The crabs and crocodile are both scavengers, readily feeding upon carcasses including those of the crocodile itself. *Varanus* destroys crocodile eggs wholesale, also despoiling the nest of *Trionyx* and (presumably) of *Pelusios*. *Trionyx* is reputed to prey upon crocodile eggs and newly-hatched young. The crocodile in turn preys upon its enemy *Varanus*, and upon *Pelusios* and *Trionyx* : it also eats the eggs both of the turtles and of its own kind. And it rounds off these activities as a cannibal. Part of the food web is indicated in Fig. 44.

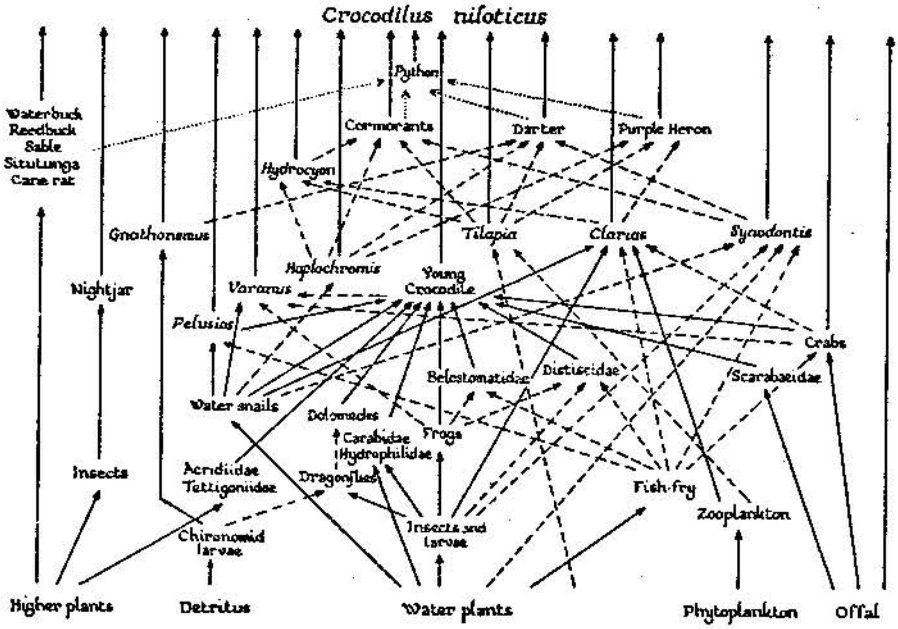

Fig. 43. Diagram showing the food relations of *C. niloticus* to various other members of the fauna : Upper Zambesi, Barotseland.

Similar complexities are seen at all levels of the food web. Thus, the feeding habits of young crocodiles reveal an intricate network of relationships—the reptiles preying extensively upon secondary predators such as belostomatid bugs and dytiscid and hydrophilid beetles, which in turn take tertiary predators such as dragonfly nymphs, young frogs and fish-fry. Young crocodiles also take pisaurid water-spiders whose victims include fish-fry and dragonflies—including *Crenigomphus rennei* and *Brachythemis leucosticta*—as observed at Kaiso, Lake Albert. These Odonata are themselves predatory upon other members of the insect fauna ; and the situation is further complicated by the crocodile's penchant both for larval and adult dragonflies.

In other food chains there are but two steps between the supply of plant material and the end-point—for instance, where herbivorous mammals form the intermediate link. But even where the predator's habits are thus simply defined, it is not easy to assess the effect upon the prey species. For predation is not necessarily harmful in its long-term effects, and indeed a predator may indirectly benefit the species preyed upon—either by keeping the population in better adjustment to its own food supply, or by removing weakened or abnormal individuals. A dramatic example of the former effect is given by Leopold (1943); and examples of the latter by Rudebeck (1950) and Dobben (1952).

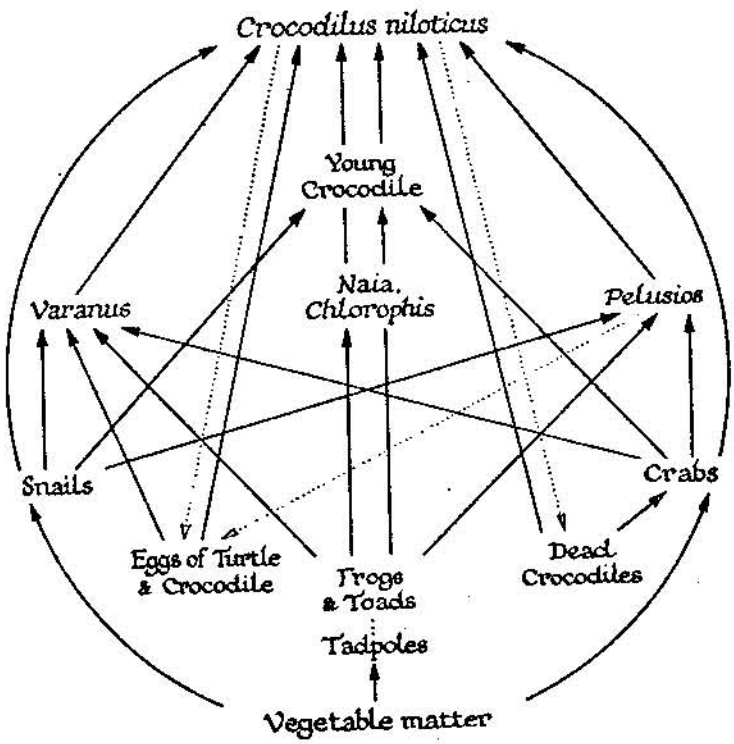

Fig. 44. Food relations of crocodiles to various other reptiles (see p. 317).

In this connexion, it is worth referring briefly to the crocodile's relation to the Hippopotamus in Uganda. Before the introduction of firearms, natural increase in the population was doubtless balanced by the activities of native hunters, by inter-male combat, and by the removal of old or injured individuals, and calves, by crocodiles. Today, under protection, the species has increased enormously in the Queen Elizabeth Park, and as a result over-grazing and land-erosion is evident over wide areas (Bere, 1955, 1959). The hippopotamus is also plentiful along the Victoria Nile in the Murchison Falls Park. But here no such excess has been reported. And it is perhaps significant—though quantitative proof is lacking—that these waters support a thriving population of crocodiles which are known to prey upon the hippopotamus; whereas the Queen Elizabeth Park lacks this predator.

Crocodiles and fisheries

Crocodiles and fish prey

In most of the localities with which this investigation is concerned, comparatively worthless, or second-class fish (compared with the commercially desirable *Tilapia, Serranochromis* and *Sargochromis*) predominate among prey eaten. Only in Bangweulu Swamp were catches of *Tilapia* found to be in excess of other genera. In Lakes Kioga, Kwania and Victoria, *Protopterus* and *Barbus* appear to be the main fish prey. Records from the Semliki River, Lake Albert and Murchison Nile indicate that *Synodontis, Alestes* and *Auchenoglanis* are the most important genera taken. Out of 119 fishes identified from stomachs in the Kafue and Zambesi Rivers, sixty-one were siluroids (*Clarias* and *Synodontis*) : Jackson (27.1.58) informs me that this is certainly a higher proportion than occurs in the natural population. In Mweru Wa Ntipa crocodiles were found to be feeding almost entirely upon *Clarias.*

Several of the above-mentioned genera together with other fishes less often included in the diet—*Protopterus, Barbus, Clarias, Synodontis, Bagrus, Alestes, Hydrocyon, Lates* and various species of *Haplochromis*—are themselves at some stage predatory on fish, fry or fish-eggs. Thus it appears that the destruction of crocodiles would be unlikely to benefit fishery interests, and might well be harmful.

The wisdom of killing crocodiles in Hunyani Poort Dam, near Salisbury, has been questioned by L. H. Stewart, Secretary of the Natural Resources Board of Southern Rhodesia (Anon, 1952) : and it was suggested that crocodiles should be maintained to limit the numbers of unwanted cannibal fish, such as barbel (*Heterobranchus*). Douglas Hey (*ibid.*), Director of Land Fisheries in the Union of South Africa, reported that where crocodiles had been reduced in the Belgian Congo, barbel rapidly multiplied.

Again, referring to the marked recent decline of crocodiles around Mwanza, Mr Lucas informs me (9.9.55) that the number of *Protopterus* appears to have increased, and that this is having an adverse effect upon the *Tilapia* fishery—as shown by the increase in the number of *Tilapia* mutilated in gill nets. R. S. A. Beauchamp (24.9.55) confirms that *Protopterus* mutilate fish in the nets.

Otters (*Lutra maculicollis*) are also causing an increasing amount of damage to netted *Tilapia* (E.A.F.R.O. Report, 1954–55) in Lake Victoria ; and the destruction of crocodiles in Lake Mweru has also been followed by similar damage. The crocodile is known to prey upon the otter : two specimens, each bitten in half, were found in the stomach of a large crocodile in the Semliki River (Kinloch, 1951) ; and a freshly-killed specimen of *L. maculicollis* was recovered from a crocodile in the Kalungwishi River.

The importance of the crocodile in relation to the *Tilapia* fishery is clearly seen in the conditions at present obtaining in Mweru Wa Ntipa, where the reptiles are very plentiful and strictly protected. In this lake they tend to be monophagous, feeding extensively upon *Clarias mossambicus*, but apparently not upon *Tilapia*, which is the main producer of animal protein from vegetable matter, and the important commercial fish. *Clarias* preys heavily upon *Tilapia* ; and in so far as the crocodile keeps *Clarias* in check there can be little doubt that it is beneficial. If, owing to a change of policy, unrestricted hunting were to be permitted, crocodiles would speedily be exterminated, and the consequences might well be disastrous to the fishery.

Young crocodiles and invertebrate predators

On the evidence available, it is also reasonable to suppose that young crocodiles play a useful role in the fresh-water economy. During the early years of life crocodiles prey extensively upon giant waterbugs (Belostomatidae), adults and nymphs of dragonflies (Gomphidae, Libellulidae), voracious water beetles (Dytiscidae, Hydrophilidae), fresh water crabs (*Potamonautes*) and upon aquatic spiders (*Dolomedes*). All these invertebrates feed, either as larvae or adults, upon fish fry. Mr K. Morris tells me (21.5.54) he has on several occasions seen dytiscid beetles attack fry. Mr P. H. Greenwood tells me (15.12.56) that near Napoleon Gulf he has seen water spiders stalk and seize *Protopterus* fry as they surfaced. The Belostomatidae are formidable enemies ; and here again the beneficial role of crocodiles may be presumed, especially in Uganda, where genera such as *Hydrocyrius* and *Limnogeton* are destroyed wholesale. The omnivorous crabs, which form an important part of the crocodile's diet in the Kafue and Upper Zambesi Rivers, also take their toll of fish: Mr A. D. Fraser informed me that in parts of Southern Rhodesia where crocodiles have been shot out of existence, crabs (*Potamonautes*) appear to have increased and are reported to be feeding in the nests of *Tilapia*. Fryer (1959) states that in Nyasaland *Potamonautes* " will readily feed on fishes entangled in gill nets—to which it sometimes causes considerable damage."

Crocodiles and fish-eating birds

Fish-eating birds, notably *Phalacrocorax lucidus*, *P. africanus* and *Anhinga rufa* play their part in the food web. In 1952 a large series of stomachs was examined in Uganda, and the following brief statement of results is relevant to the present discussion. Table 31 contains an analysis of prey, by genera, recovered from 246 of these birds which were shot in the same waters from which crocodiles were also examined. The figures in Table 32 provide a striking commentary upon the relative importance, as fish predators, of the birds and of crocodiles, respectively.

Bearing in mind the fact that crocodiles feed mainly upon fish only during part of their life-cycle and that even then many other foods are also taken, we are left with the surprising conclusion that the overall average daily fish-consumption of an individual crocodile is less in bulk than that of a White-breasted Cormorant (which consumes at least one kilogram of fish per day). Estimated in terms of occurrence, fish were found in only about one third of the crocodiles which contained food of any kind : the birds are almost exclusively fish eaters. The mean number of fish per stomach is ten times greater in *P. lucidus* and *A. rufa* than in the crocodile. In the light of these observations, it must be remembered that cormorants and darters themselves constitute the main avian prey of the crocodile in most waters where the reptile's habits have been studied.

TABLE 31

Prey of White-breasted Cormorant, Pigmy Cormorant and African Darter, in Uganda—(a) Lake Victoria and Victoria Nile above Murchison Falls ; (b) Lake Albert and Victoria Nile below Murchison Falls.

	P. lucidus		*P. africanus*		*A. rufa*		Total
Locality	*a*	*b*	*a*	*b*	*a*	*b*	
No. of stomachs	87	—	61	48	40	10	246
Protopterus ..	—	—	1	—	—	—	1
Mormyridae	11	—	—	—	1	3	15
Hydrocyon ..	—	—	—	2	—	—	2
Alestes ..	—	—	—	8	—	5	13
Barbus ..	4	—	—	1	—	—	5
Labeo	2	—	—	1	—	—	3
Engraulicypris	355	—	7	6	—	—	368
Discognathus	—	—	—	—	1	—	1
Bagrus ..	—	—	2	3	—	3	8
Auchenoglanis	—	—	—	2	—	1	3
Clarias ..	—	—	—	—	1	—	1
Synodontis ..	3	—	—	12	—	2	17
Lates ..	—	—	—	13	—	6	19
Tilapia ..	2	—	—	5	13	7	27
Haplochromis	398	—	139	159	293	47	1,036
Astatoreochromis	1	—	—	—	—	—	1
Mastacembulus	—	—	1	1	—	—	2
Total ..	776		363		383		1,522

TABLE 32

Comparison, in terms of occurrence and number of prey, of the fish-eating habits of water birds and crocodiles.

Locality	*Predator*	*Stomachs containing food of any kind*	*Stomachs containing fish*	*Per cent. stomachs containing fish*	*No. of fish prey*	*No. of fish prey per stomach*
Uganda	*P. lucidus*	87	87	100·0	776	8·92
Uganda	*P. africanus*	109	109	100·0	363	3·33
Uganda	*A. rufa*	50	50	100·0	383	7·66
	Total	246	246	100·0	1522	6·19
Uganda	*C. niloticus*	124	44	35·5	81	0·65
N. Rhodesia ..	*C. niloticus*	549	212	38·6	296	0·54
Zululand ..	*C. niloticus*	28	9	32·1	16	0·57
	Total	701	265	37·8	393	0·56

EXPLOITATION AND DECLINE

Causes of decline

In most parts of Africa where it was once abundant, *C. niloticus* has within recent years been drastically reduced in numbers. From wide areas the species has already vanished : from others it is fast disappearing.

Various factors have contributed to its decline. While the crocodile is affected by the general threat to all wild life which results from disturbance of natural habitats, its survival is also threatened more directly.

In the first place, the reptile suffers from a bad reputation, and is generally unpopular. It has never been scheduled as a species meriting protection under Game Laws ; but rather, has been officially classified as vermin. It is the only large animal for which permits are issued to regularise hunting by (otherwise) illegal methods of snaring, and shooting at night. In various territories campaigns have been authorised for its extermination. Thus for many decades, indiscriminate slaughter by every means available has been encouraged, in the supposed interests of humanity.

In more recent years the high profits to be made from hunting have led to a renewed and intensified onslaught, until in some territories the trade in belly-skins has become almost a major industry. Accurate figures for the toll taken are unobtainable, since there is a good deal of inter-territorial traffic—much of it by canoe, and by poachers. The following data (mainly based on the number of export permits obtained from the Department of Commerce) supplied by Mr D. H. Rhodes (23.5.56) give some indication of the crop taken from Uganda : 1953, 15,000 skins valued at £100,000 ; 1954, 7,900 skins valued at £44,553 ; 1955, 8,000 skins at £40,000. The value of the crop taken from other East African territories in the year 1954, as published in *East Africa and Rhodesia* (17 January 1957) was : £39,000 from Kenya, and £146,206 from Tanganyika. The number of crocodiles shot in East Africa that year was stated to be about 60,000. The report concludes with the laconic comment : " In Kenya the numbers are falling and traders are alarmed." Similar exploitation is taking place in Central Africa. For example, J. Nieuwoudt, a hunter operating in Northern Rhodesia, reported to the Department of Game and Tsetse Control (6.8.54) that between 1st January and 15th July, 1954, he handled a total of 5,721 skins, representing a turnover of about £20,000.

Modern hunting methods

The main immediate threat to the crocodile's survival comes from the techniques now employed by professional hunters. Working at night in fast motor boats, these men easily locate their quarry in the beam of a powerful spot-light, approach at speed, shoot at point-blank range, and gaff the dying animal before it can sink. Against this form of attack the crocodile has virtually no defence.

The crocodile population is especially vulnerable : (a) in waters that lack marginal swamps and lagoons difficult of access to the hunter ; (b) during the dry season when the reptiles have returned from inundated areas to the main bodies of open water ; and (c) in the vicinity of breeding grounds where, after the disturbance of nesting females, the eggs are left an easy prey to monitors.

As a result of this irrational exploitation for immediate gain, the crocodile has been almost shot out of existence in many areas where it was once abundant (Cott, 1954 a ; 1957). Meanwhile, the hunters attempt to justify their activities on the grounds that they are performing a public service in eradicating a dangerous animal ; or they meet criticism with the contradictory assertion that the supply is inexhaustible.

The high prices paid for skins provide a powerful incentive to poachers. Working from canoes, and using snares or baited hooks, or harpoon and light in night operations, these men easily escape detection. And, as the supply fails elsewhere, the crocodiles that remain hitherto preserved in reserves and national parks offer an irresistible attraction. For example, Bere (1958) reports the disturbing news that commercial hunting has been a regular occurrence near and inside the Murchison Falls Park. The spectacular congregation of crocodiles at Magungu, which I had the good fortune to observe and photograph in the undisturbed state in 1956, has already been extirpated ; and Bere informs me (2.1.60) that native poachers have recently pressed home their attack upon the main headquarters of the reptiles at Fajao, below the Falls, and that numbers in this last stronghold in Uganda have been reduced.

Hunting and population structure

Since profits are related to belly-width of the skins, hunters shoot larger in preference to smaller crocodiles. Hunting is indiscriminate as regards the sexes which (except for the largest males) cannot be distinguished in the field. Hence the animals first sacrificed are the breeding stock of both sexes. Subsequently the smaller size groups—immature specimens and juveniles—are successively exploited. This process eventually includes crocodiles in their second and third year of life.

The changes in the depleted population which result from this traffic are apparent in every locality where commercial hunting has proceeded unchecked. For example, Mr P. H. Greenwood tells me (8.8.54) that in 1954 a Czech hunter, equipped with a large motor boat, a European assistant, two Sikh gunners, a crew of fourteen Africans and three powered canoes, accounted in six weeks for about 1,000 crocodiles in and around Buvuma Channel, L. Victoria. Very few of these were more than four feet in length. The average length of sixty shot in one night in Napoleon Gulf was again about four feet. Similar changes in the population structure are shown by a comparison of the length frequency distribution of reptiles, examined during the present survey, from waters : (a) which had previously been much shot over—Luangwa Valley and Kafue Flats ; (b) where hunting had been discouraged for a number of years—Upper Zambesi in Barotseland : and (c) where crocodiles have hitherto enjoyed complete protection—Mweru Wa Ntipa (see Table 33 and Fig. 45).

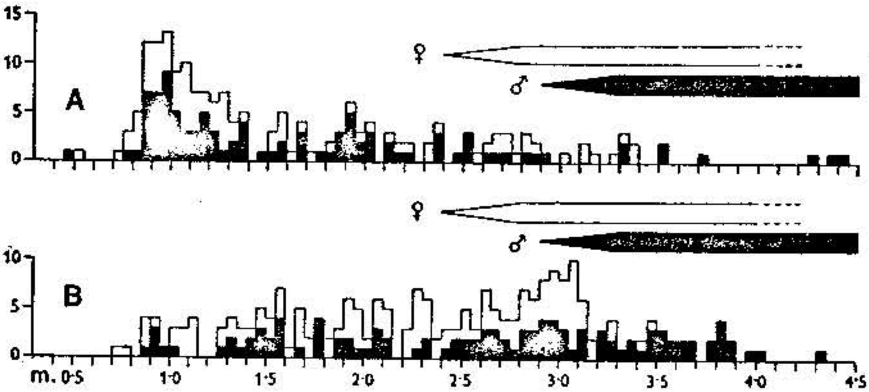

Fig. 45. Comparison of length frequency distribution of crocodiles shot : A—in areas where hunters had already been at work (Luangwa Valley and Kafue Flats) ; and B—in areas not previous exploited. The wedges indicate the onset of breeding maturity ; black—males ; white—females.

TABLE 33

Showing the distribution, by sexes, of immature and adult crocodiles collected in four localities in Northern Rhodesia. The threshold for maturity is here based upon a length of 3·0 metres for males, and 2·5 metres for females.

Locality	*Males*			*Females*			*Total*			*Mean length*
	No.	*Imm.*	*Ad.*	*No.*	*Imm.*	*Ad.*	*No.*	*Imm.*	*Ad.*	
Luangwa Valley	55	55 100%	0 0%	39	34 87%	5 13%	94	89 95%	5 5%	1·54 m. (5ft. 0½in.)
Kafue Flats ..	44	36 82%	8 18%	48	35 73%	13 27%	92	71 77%	21 23%	1·71 m. (5ft. 7ins.)
Upper Zambesi	78	61 78%	17 22%	106	72 68%	34 32%	184	133 72%	51 28%	2·17 m. (7ft. 1½ins.)
Mweru Wa Ntipa	31	9 29%	22 71%	20	0 0%	20 100%	51	9 18%	42 82%	3·18 m. (10ft. 5ins.)

In Mweru Wa Ntipa, where crocodiles had not previously been hunted, 82 per cent. of the catch was of mature size, and the mean length was 3·18 metres (or about 10 feet 5 inches). Only 5 per cent. of the specimens taken in the Luangwa Valley were mature, and the mean length of the catch was 1·54 metres (or about 5 feet).

CROCODILE PROTECTION

Status in relation to man

Nothing has come to light from the present survey which would justify the classification of the Nile Crocodile as vermin. On the contrary, whether considered from the point of view of ecology, economics or zoology, it is a valuable and important member of the African fauna.

Ecological status

On the ecological side, the conclusion may be reached that crocodiles are not detrimental to fishery interests, except in so far as, in certain localities, they damage gear. On the other hand, there is evidence that their presence is directly or indirectly beneficial to the industry.

In general, relatively few fish are eaten except in the middle years of life (see p. 294); and, in various localities, a large proportion of fish prey are either of secondary value or are predatory species (see p. 320). Juvenile crocodiles, representing the most numerous and voracious age group, account for many enemies of fish, fry and eggs (see p. 321). Adults take their toll of otters, cormorants and darters.

The reptiles also play their part as important scavengers of inland waters; and on this account alone they merit the consideration that is accorded to vultures and Marabou which, as I am informed by Pitman (20.10.59), are protected by law throughout British Africa for their value as carrion feeders.

Finally, the specious argument that the Nile Crocodile merits persecution because it endangers human life will impress no one who is familiar with the species in the field today. Its depredations have often been grossly exaggerated, as by Hubbard (1927) and Siggins (1931). In all areas known to me in Uganda, Northern Rhodesia and Zululand, human fatalities appear, from inquiries made, to be rare. This conclusion is fully supported by the observations of Lang (in Schmidt, 1919) from the Belgian Congo.

Commercial status

There are two grounds for regarding the crocodile as a commercial asset. Firstly, it is a producer of high-quality leather. But hitherto intensive hunting has been carried out irrationally, on a mining rather than a cropping basis. Already in many parts of Africa the hunters and their agents are showing concern at the reduced yield. Under rational management, the reptiles could provide a sustained yield of skins to the trade. But if the industry is to be saved, it will be necessary to check the present uneconomic slaughter.

The species has a subsidiary, but by no means negligible value, as a tourist attraction. Speaking of game in general, Simon (1957) has stated: " Quite apart from any other consideration, the future of East Africa's tourist trade is irretrievably linked with our wild fauna. Visitors come from all over the world to observe and admire the unrivalled variety of wild animals, and as a result of this the Exchequer benefits to the tune of over six million pounds per annum. This ranks third in the list of revenue earners." To this end, crocodiles undoubtedly make their contribution.

Scientific status

Crocodilians also merit protection in their own right. Crocodiles essentially like the modern species existed in Jurassic times and were contemporaries of the dinosaurs. As the only remaining members of the archosaurian stock which have survived the age of reptiles, they are of quite exceptional scientific importance, not least from the indirect light which studies of anatomy, physiology, ecology and behaviour can throw upon the biology of ancestors long extinct. It would be a grave loss to science and research, and to posterity, if these saurians—which have survived for over a hundred million years—were now to be sacrificed to the demands of uninformed public opinion, and subordinated to a passing fashion in leather goods.

Conservation and control of hunting

The speed at which the Nile Crocodile is losing ground almost everywhere in Africa presents a challenging conservation problem that demands urgent attention. Intensive hunting, as at present practised, is taking toll of all sizes, young and old ; breeding stock, is being killed out ; and potential breeders are shot years before they would reach adolescence. The inroads now being made upon the population provide a classic example of exploitation and mismanagement of a valuable asset.

If conservation is to become effective, measures must be framed with regard : (a) to modern hunting procedure (see p. 323) ; and (b) to the slow growth of the crocodile (see p. 245). In waters where hunting has reduced the population down to young animals in their third and fourth year, the species needs a long rest—for a period of at least fifteen years.

To allow for recovery, complete cessation of commercial hunting is advocated. Half-measures, such as the prohibition of hunting at night, or the introduction of a close season, are likely to be ineffective because they could not be enforced over vast areas of difficult terrain. The ease with which poachers can evade detection is sufficiently illustrated by recent exploits of African harpooners who have been operating in the heart of the Murchison Falls Park.

Protection can best be achieved only by depriving the hunter of his market for a prescribed period—through control of the import and export of skins. Strong opposition to such measures can be expected from the traders, and from hunters, on the grounds of interference with their means of livelihood. But in this respect the crocodile hunter should be regarded no differently from the hunter who wishes to make a living by the sale of game-meat or rhinoceros horn or ivory.

The general problem of the Nile Crocodile's relation to man is a very old one: and in the Book of Job the question is asked : " Shall the bands of fishermen make traffic of him? Shall they part him among the merchants? " It is hoped that the authorities concerned will now reconsider this question in the light of recent events and research, and so take appropriate steps before it is too late to save this unique and valuable member of the African fauna.

Summary

The results here reported and discussed are based upon observations of free-living crocodiles, and upon the examination of 576 freshly-killed specimens, during the years 1952, 1956 and 1957. The field observations mainly derive from the Murchison Falls National Park, Uganda. Study material was obtained in Uganda—from Lakes Victoria, Kioga and Albert, the Lower Semliki and Victoria Nile; and in Northern Rhodesia and Barotseland—from Bangweulu Swamp, Mweru Marsh, and the Luangwa, Kafue and Upper Zambesi valleys (pp. 215–217).

Studies in Uganda have shown that crocodiles observe a general diurnal rhythm of activity. The night is spent in the water. The haul out to land begins in the hour before sunrise. There are two main basking periods, between 0700 and 0930 hrs. and between 1430 and 1730 hrs. In the heat of the day there is a secondary return to the water, or into shade. Counts made at 15-minute intervals of crocodiles seen ashore and afloat throughout the day are considered in relation to environmental factors and to the reptiles' thermal requirements (pp. 217–224).

Cloacal temperatures of crocodiles shot at different hours of the day and night point to a remarkable degree of thermal control. The mean temperature is 25·6° C. with observed fluctuations from the mean of +3·4° C. and —2·6° C. Records of diurnal movements and observations on the habit of mouth gaping, indicate that thermal control is effected both by habitat selection and behavioural adaptation (pp. 225–229).

The methods of locomotion on land are described. There are three distinct gaits: the high walk is the method of progression used when hauling out and in unhurried movement overland; the belly run is generally seen when the crocodile is making its escape downhill; the gallop has very rarely been observed and only in juveniles when surprised in sleep at close range. Crocodiles have exceptionally been encountered many miles from the nearest water; and in certain localities aestivation appears to be a regular dry season habit (pp. 229–232).

An account is given of aquatic behaviour. Swimming is effected by the tail, the limbs being closely applied to the flanks. Experiments with specimens restrained under water, and observations on diving times in free individuals, indicate that diving endurance increases with crocodile length. Specimens less than one metre long can remain submerged for at least 44 minutes; and the maximum dive for an adult is believed to be far in excess of the one-hour period that has been observed (pp. 232–235).

The occurrence and weight of stomach stones has been recorded for 507 crocodiles. Stones are first ingested at some period after the first year of life: they are invariably present in the adult. The growth stage at which the whole population becomes stone-bearing is considered in relation to habitat. The weight of stones increases with growth until maturity: adults of both sexes carry a mean standard load amounting to about one per cent. of the body weight. Strong circumstantial evidence suggests that stones are deliberately swallowed; and several classes of facts, which are discussed in detail, indicate that the stones subserve hydrostatic functions (pp. 236–245).

The available data on growth rate in wild and captive crocodiles are assembled.

Growth is most rapid in early life, showing a mean annual increment during the first seven years of about 10·4 inches (or 265 mm.). Thereafter the growth rate decreases progressively, to about 1·4 inches (or 36 mm.) per annum at twenty-two years of age. Records of exceptionally large crocodiles are given for East and Central Africa. The maximum size attained differs widely according to locality. On reliable evidence specimens appear to attain a maximum length of at least 20 feet. Longevity is discussed (pp. 245–251).

An even sex-ratio—324 males and 327 females—is recorded for the combined collections. The sexes are also about equal in the lower length groups. The changing constitution of the population as it ages is discussed. Sexual maturity is attained by the male at a length of about 2·9 to 3·3 metres, and by the female at a length of about 2·4 to 2·8 metres. Present knowledge of the growth rate indicates that females do not attain sexual maturity until they are at least 19 years old (pp. 251–258).

Observations made on the ovarian condition and on nest eggs show that the breeding season differs in different localities. Eggs are laid in Northern Rhodesia and Barotseland in September ; in Lake Albert and the Victoria Nile below Murchison in early January ; and in northern Lake Victoria in August and again in December. The relation of the breeding season to environmental factors is discussed. It is shown, in each locality for which data are available, that laying occurs when water levels are falling, that the incubation period coincides with the phase of lowest water, and that hatching takes place after the onset of the rains. The biological advantages of this synchronization are considered (pp. 258–266).

Large males are known to defend a territory, which may be a basking or feeding place. Little is yet known of territorial behaviour in the breeding season. The very unequal incidence of serious injuries found in the sexes indicates that inter-male rivalry finds expression in combat. Different kinds of vocalization are reported. Roaring by males has only been heard in the breeding season : the full roar, which may be a mating call, is described. An account is given of a pre-nuptial display in the female and of the preliminaries to copulation—which takes place in shallow water (pp. 267–269).

The requisite conditions for the nest site are discussed. Colonial nesting grounds on the southern shore of Lake Albert are described and it is suggested that the habit of breeding in colonies—today only seen where crocodiles are entirely free from disturbance—may formerly have been normal for the species. Data are given of clutch sizes : observations suggest that there may be a correlation between the number (but not the size) of eggs laid and the size of the parent. Earlier statements that the incubation period is about 90 days have been confirmed (pp. 269–275).

Throughout the incubation period the female guards the nest, either lying over the eggs or in nearby shade. At this time females may become torpid and reluctant to leave the grounds even when approached. The young croak as hatching time approaches : they cannot emerge until liberated. Eye-witness accounts, and the appearance of the shallow nest craters after hatching, indicate that the eggs are uncovered by shovelling movements of the parent's belly and not by the feet. An account is given of parental care of the newly-hatched young, and of the crocodile's habits in early life (pp. 275–278).

A detailed account is given of the food and feeding habits, based upon field observations and upon the stomach contents of 851 crocodiles. It is shown that the diet is extremely varied, and that it changes markedly and progressively with the predator's age. The young feed in shallows and ashore on insects, spiders and frogs ; in middle life underwater prey, notably crabs, gastropods and fish, form the main food ; old crocodiles feed increasingly upon reptiles and mammals. Data are presented relating to the quantity of food eaten by wild and captive crocodiles. Prey organisms recovered from stomachs are tabulated systematically and in relation to localities. The crocodile's methods of hunting, capture and disposal of prey are described (pp. 278–303).

Among enemies that take a toll of the eggs, the Nile Monitor, *Varanus niloticus*, is far the most destructive. Other egg-predators include Marabou, *Leptophilos cruminiferus*, Water Mongoose, *Atilax paludinosus*, Spotted Hyaena, *Hyaena crocuta*, and Olive Baboon, *Papio anubis*. Records of predation upon newly-hatched young are briefly reviewed, and instances are given of attacks upon adults by hippopotamus and elephant, and of predation upon adults by lion and leopard (pp. 304–306).

Data relating to the occurrence, site and nature of external injuries are recorded for 548 crocodiles examined. Injuries are more frequent in older than in younger animals, and in males than in females. Evidence is given to suggest that most injuries result from the habits of cannibalism and inter-male combat. Particulars of more or less disabling wounds and amputations in twenty-seven specimens are tabulated (pp. 306–309).

In Uganda the tsetse-fly *Glossina palpalis* is a common parasite of the crocodile. Reference is made to blood parasites transmitted by the fly. Crocodiles are frequently infested with leeches—*Placobdella fimbriata* in Uganda and *P. jaegerskioeldi* in Northern Rhodesia. Data relating to occurrence, site and degree of infestation are given for 506 crocodiles. Infestation tends to increase progressively with age, first-year crocodiles being entirely free of these parasites. Nematodes, which include *Multicaecum agile* and *Dujardinascaris dujardini*, were found in forty-four stomachs in a sample of sixty-six examined in Uganda (pp. 310–313).

Birds of many kinds, including darters, herons, egrets, duck, dikkops, plovers, waders, pratincoles, skimmers and wagtails, frequent the basking grounds. Crocodiles tolerate their presence and react to their alarm signals. Such fortuitous relationships grade into those of true commensalism, which have been observed in the Spur-wing Plover (*Hoplopterus spinosus*), Common Sandpiper (*Actitis hypoleucos*) and Water Dikkop (*Burhinus vermiculatus*). The relations between these birds and the crocodiles are described. In Uganda, *H. spinosus* and *B. vermiculatus* habitually feed on the grounds and give the reptiles timely warning of danger. In Uganda and Zululand *A. hypoleucos* has been observed ridding crocodiles of ectoparasites. And from both localities there is evidence of a nesting association between *B. vermiculatus* and *C. niloticus* (pp. 313–316).

The status of the crocodile in the bionomics of inland waters is discussed. The young are shown to be ecologically separated from the adults. Attention is drawn to the complex web of food relationships in which *C. niloticus* plays a part as

master predator, cannibal and scavenger. The crocodile's relation to commercial fisheries is considered. The young feed extensively upon belostomatid bugs, dragonflies, dytiscid and hydrophilid beetles, and crabs—all of which prey upon fish fry. In most localities with which the investigation is concerned, a large proportion of the fish prey of adults are either comparatively worthless or predatory species. The relations between crocodiles and fish-eating birds is discussed. Various harmful effects, apparently resulting from crocodile destruction, are noted (pp. 316–322).

The Nile Crocodile has within recent years been drastically reduced in numbers : the causes of its decline are reviewed. The main immediate threat to its survival comes from modern methods employed by professional hunters. Examples are given of the effect of hunting upon the population structure. The reptile's status in relation to man is reassessed. Evidence is given to show that from the points of view of ecology, economics, and zoology, *C. niloticus* is a valuable member of the African fauna. Recommendations are made for its conservation (pp. 323–327).

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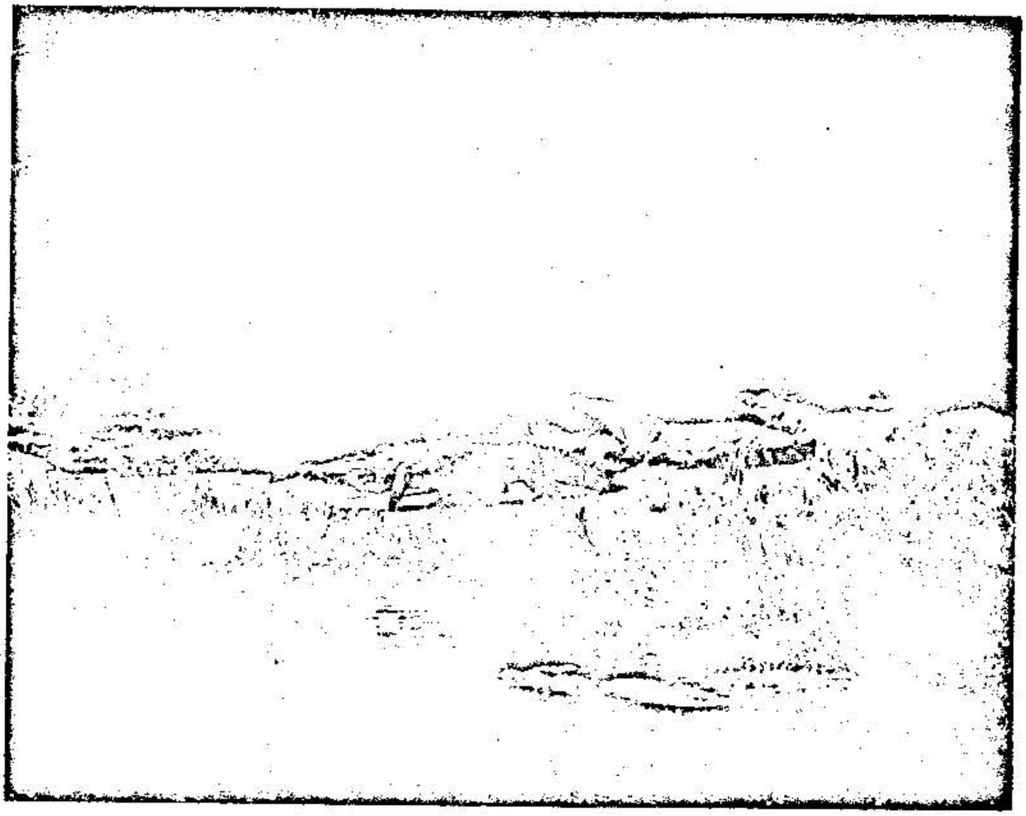
PLATE 1

Fig. 1. Congregation of crocodiles on the grounds at Magungu, Victoria Nile. The reptiles have become aware of the approach of a launch. Several can be seen in the typical alert attitude, with head raised and tail flexed. One, in the centre, is leaving at the high walk. Two, in the foreground, are already afloat. July 1952.

Fig. 2. A sector of the rock islet below Murchison Falls, as seen from Murchison Observation Post. The photograph shows twenty-three large crocodiles basking ashore, many with the jaws widely gaping ; five lie partly in the water, with the tail trailing. Several others can be seen floating in the lee of the rock, and one is keeping station in the rapid current. 12th July, 1956.



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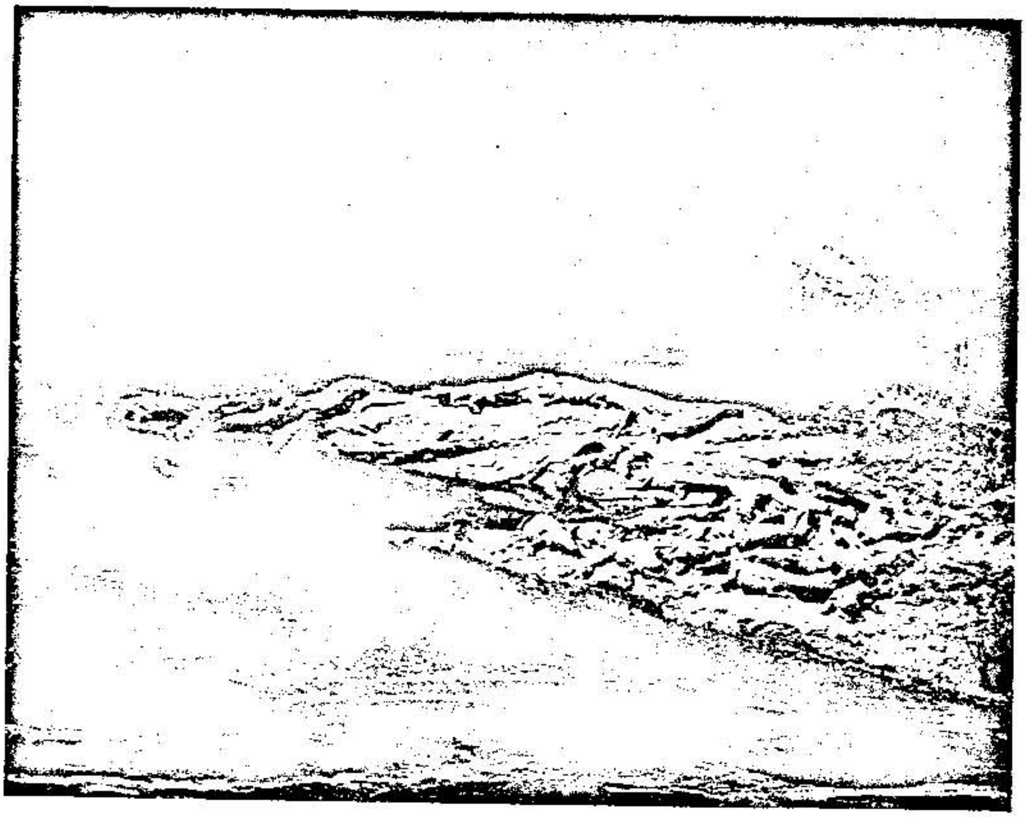
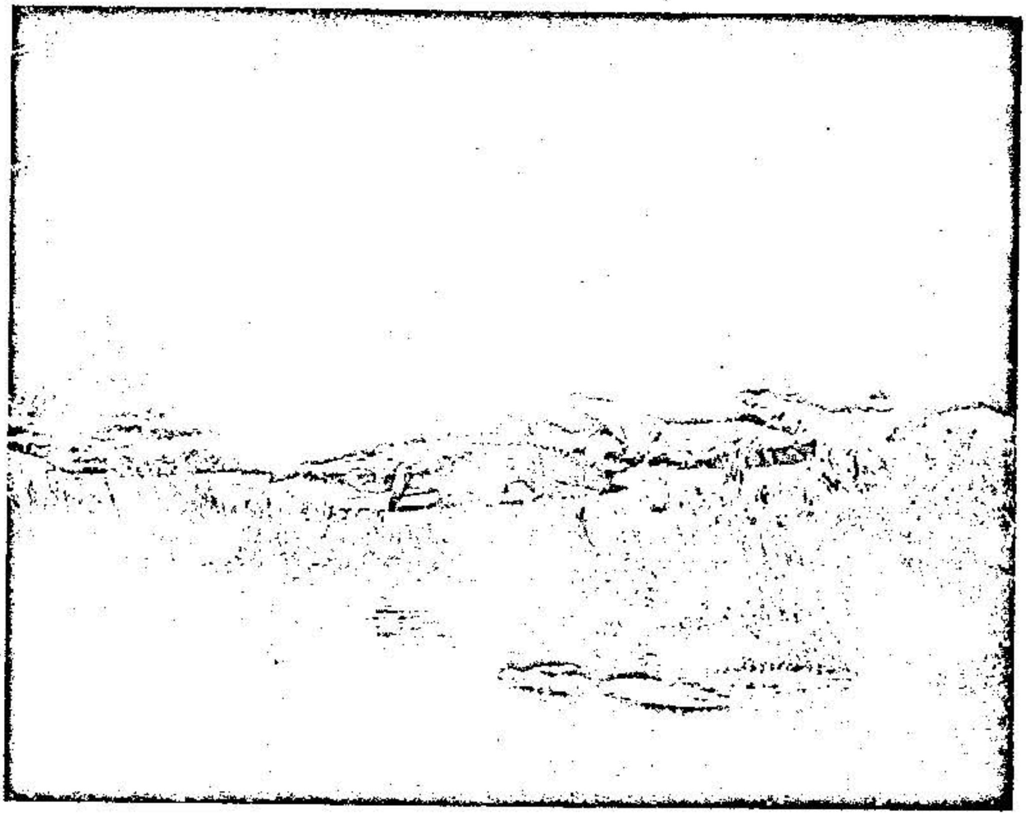


2

The Nile Crocodile in Uganda and Northern Rhodesia.



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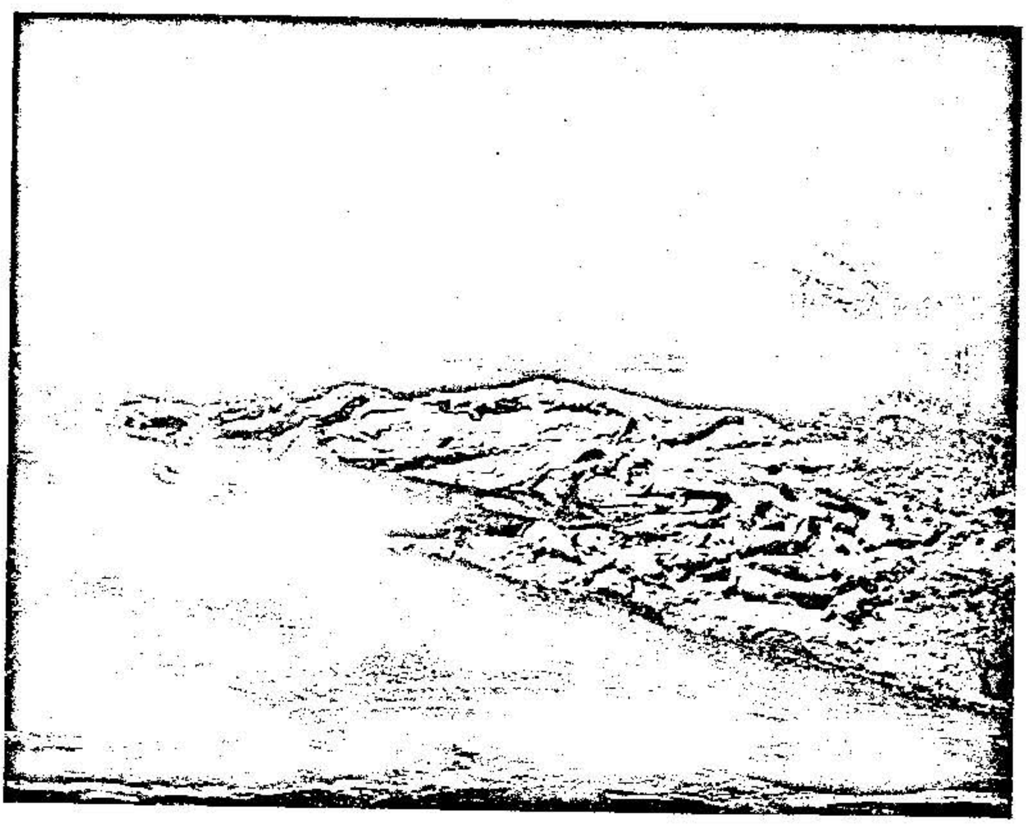


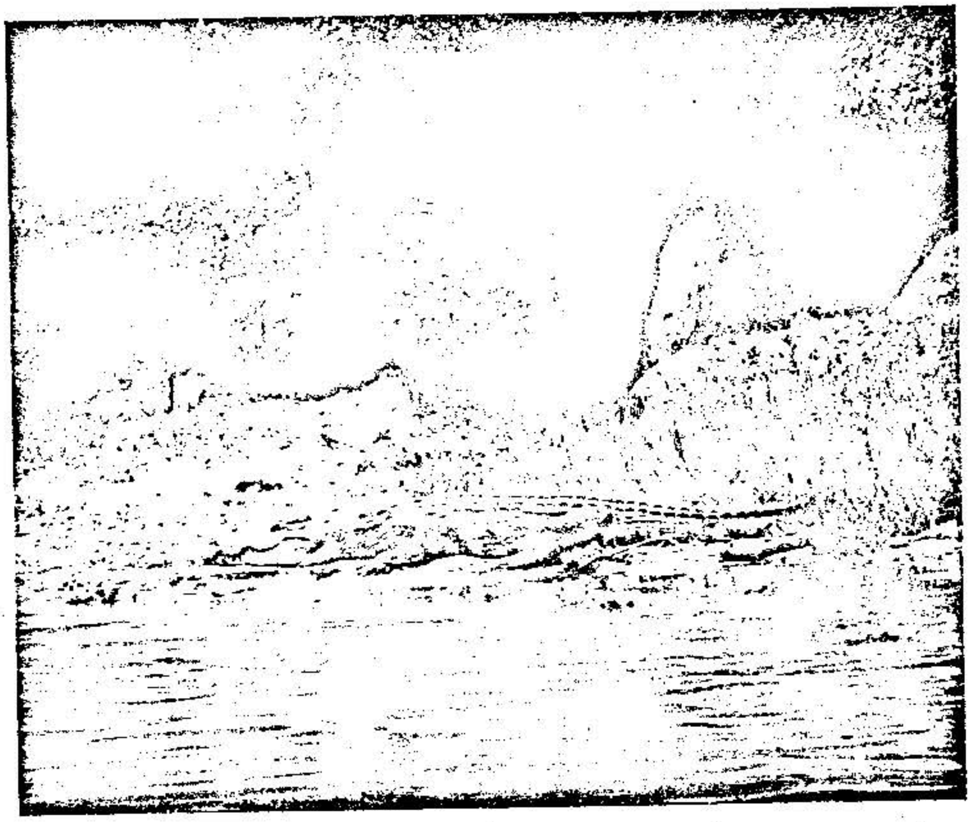
2

The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 2

Fig. 1. A crocodile has left the water to bask in the early morning sun. Note the closed jaws. Near Paraa, Victoria Nile. 5th July, 1956.

Fig. 2. Lateral study, at close quarter, of a mouth gaping crocodile. Several tsetse flies, *Glossina palpalis*, can be seen feeding between the scales on the head and jaws. Near Nansika confluent. 5th July, 1956.



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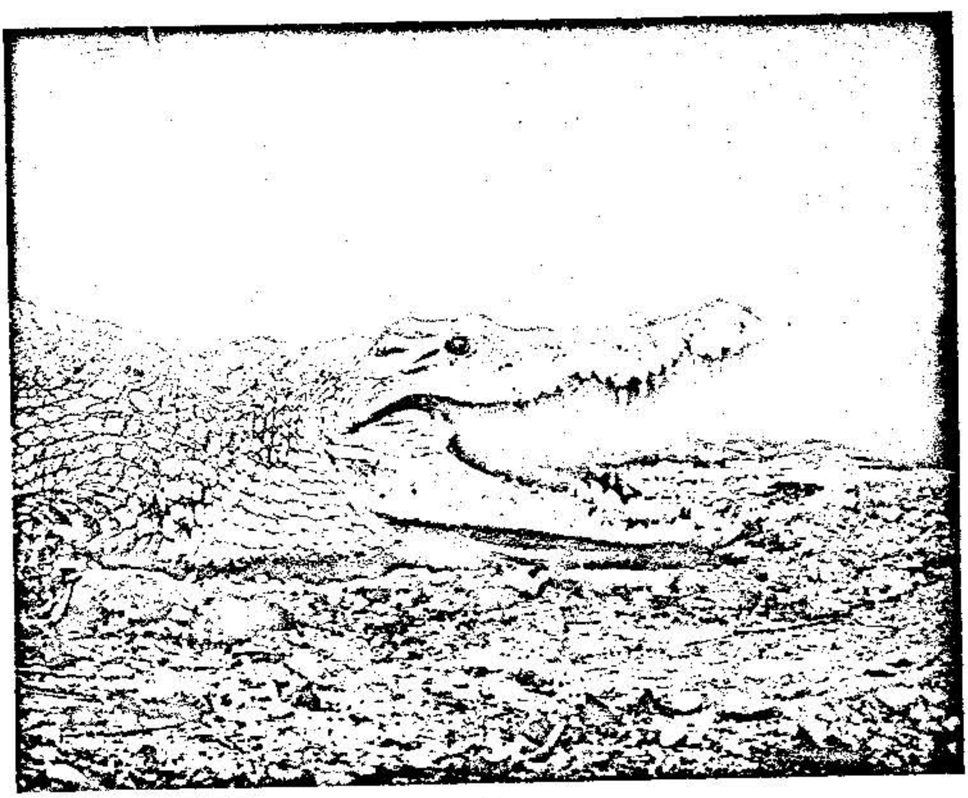

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The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 3

Fig. 1. The crocodile in the centre has just emerged from the river, and laboriously hauls itself up the beach. The belly is raised high off the ground : the hind limbs bear most of the weight while the fore limbs serve as props to support the head and shoulders. The animal photographed is about to swing forward the left hind and right fore limbs, while the weight is carried on the opposite diagonal pair. Magungu. 31st December, 1956.

Fig. 2. Photograph showing the belly run, which is the gait normally adopted when the crocodile is hastily seeking refuge in the water. These reptiles have been alarmed and are tobogganing downhill at speed. The limbs are splayed sideways and used as oars. Murchison. 25th July, 1956.

1

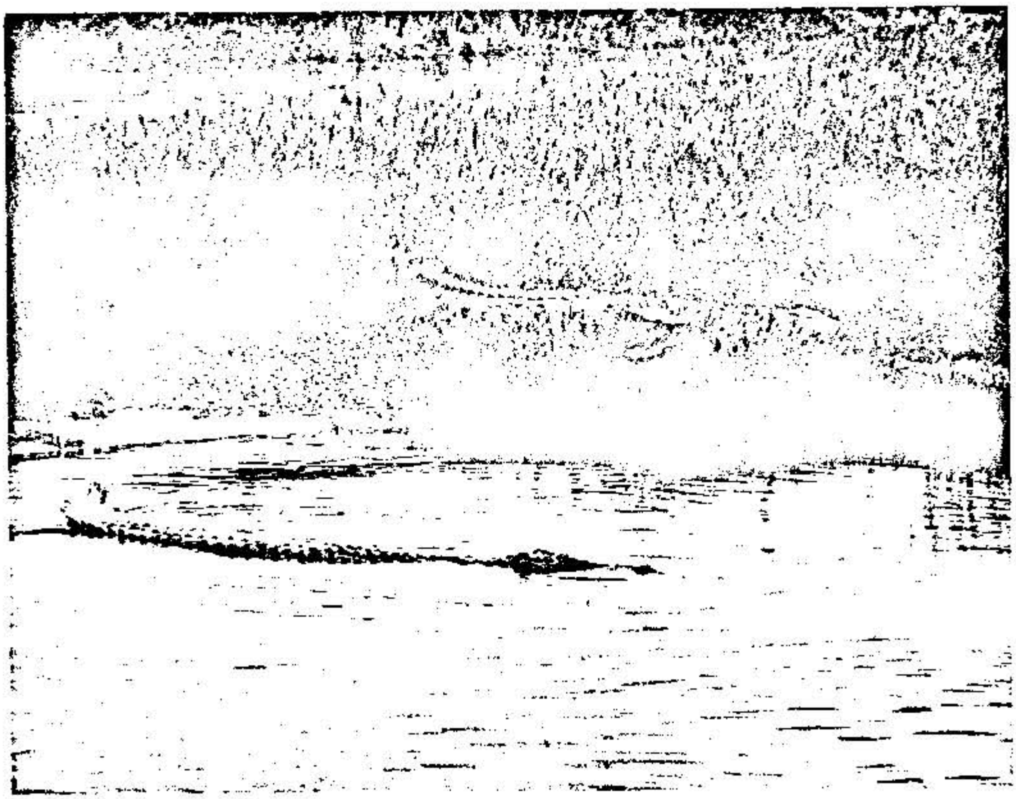
2

The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 4

Fig. 1. A crocodile has just taken to the water and is seen cruising. Only the nasal disc, top of the head, and mid dorsal scutes appear above the surface. Note the flexure of the tail, which alone drives the animal forward : the limbs are applied to the flanks and take no part in propulsion. Paraa. 26th July, 1956.

Fig. 2. The most powerful demonstration of a crocodile's vocal repertoire is the full roar, which is often heard in the breeding season. The photograph shows a large male in the act of roaring. It is looking across the river, its gular shields raised high off the beach, with head inclined upwards and jaws widely gaping. Magungu. 31st December, 1956.



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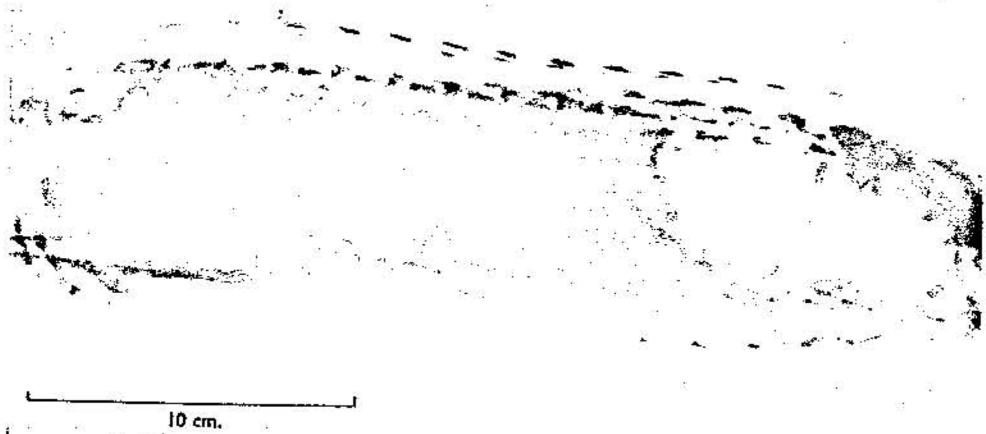
The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 5

Fig. 1. X-ray (lateral view) of a specimen measuring 1·1 metres (total length) showing the position of stomach stones low in the body.

Fig. 2. The same (vertical view). The author is indebted to Mr B. L. Mitchell (Department of Game and Tsetse Control) who supplied the negatives, and to Mr J. A. F. Fozzard (Anatomy School, University of Cambridge) who prepared the prints.



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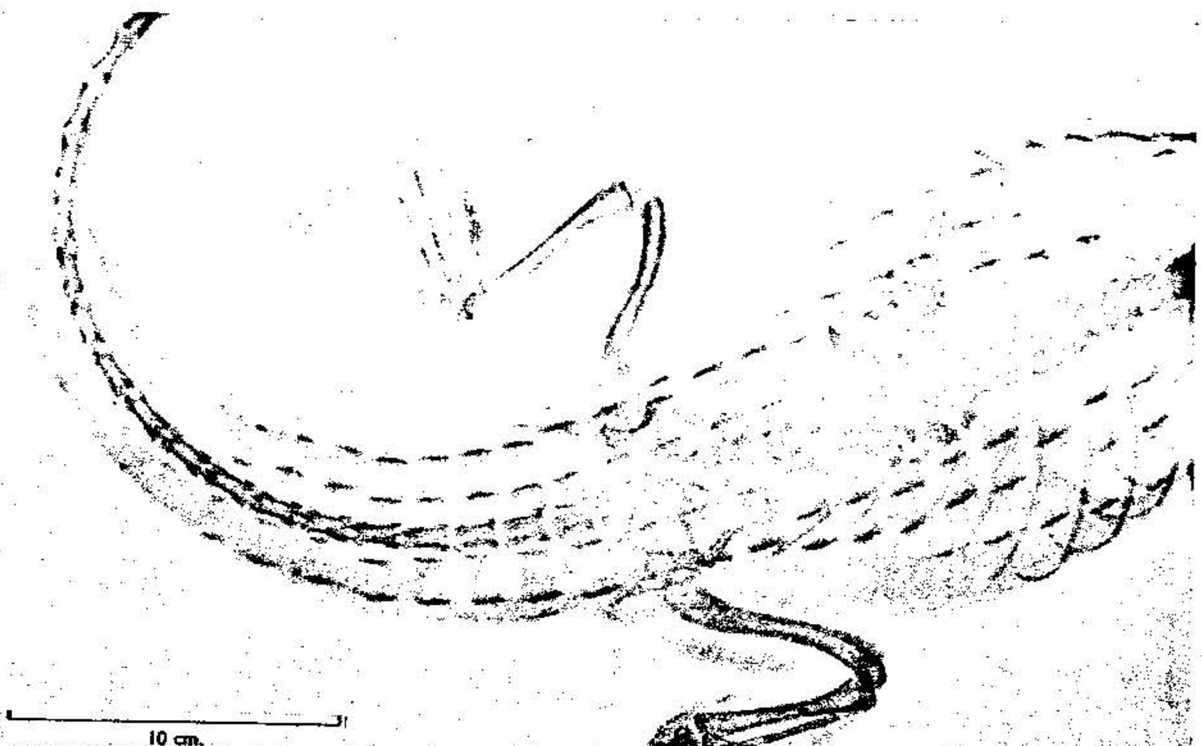

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The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 6

Fig. 1. Head of crocodile No. 193, a male measuring 3·38 m. total length, showing abnormality of snout resulting from serious injury. Mweru Wa Ntipa. 15th September, 1956.

Fig. 2. Crocodile No. 27, a female measuring 3·12 m. total length, showing site of amputated fore-limb, with pad of regenerated scales. Ripon Falls. 8th July, 1952.

Fig. 3. Head of crocodile No. 124, a male measuring 2·55 m. total length, showing amputation at lower jaw, healed injury, and recurved anterior teeth of upper jaw. Bangweulu Swamp. 23rd August, 1956.

Fig. 4. Head of crocodile No. 190, a male measuring 2·86 m. total length, showing amputation at lower jaw, dental abnormalities, and clusters of leeches in dental sockets. Mweru Wa Ntipa. 14th September, 1956.

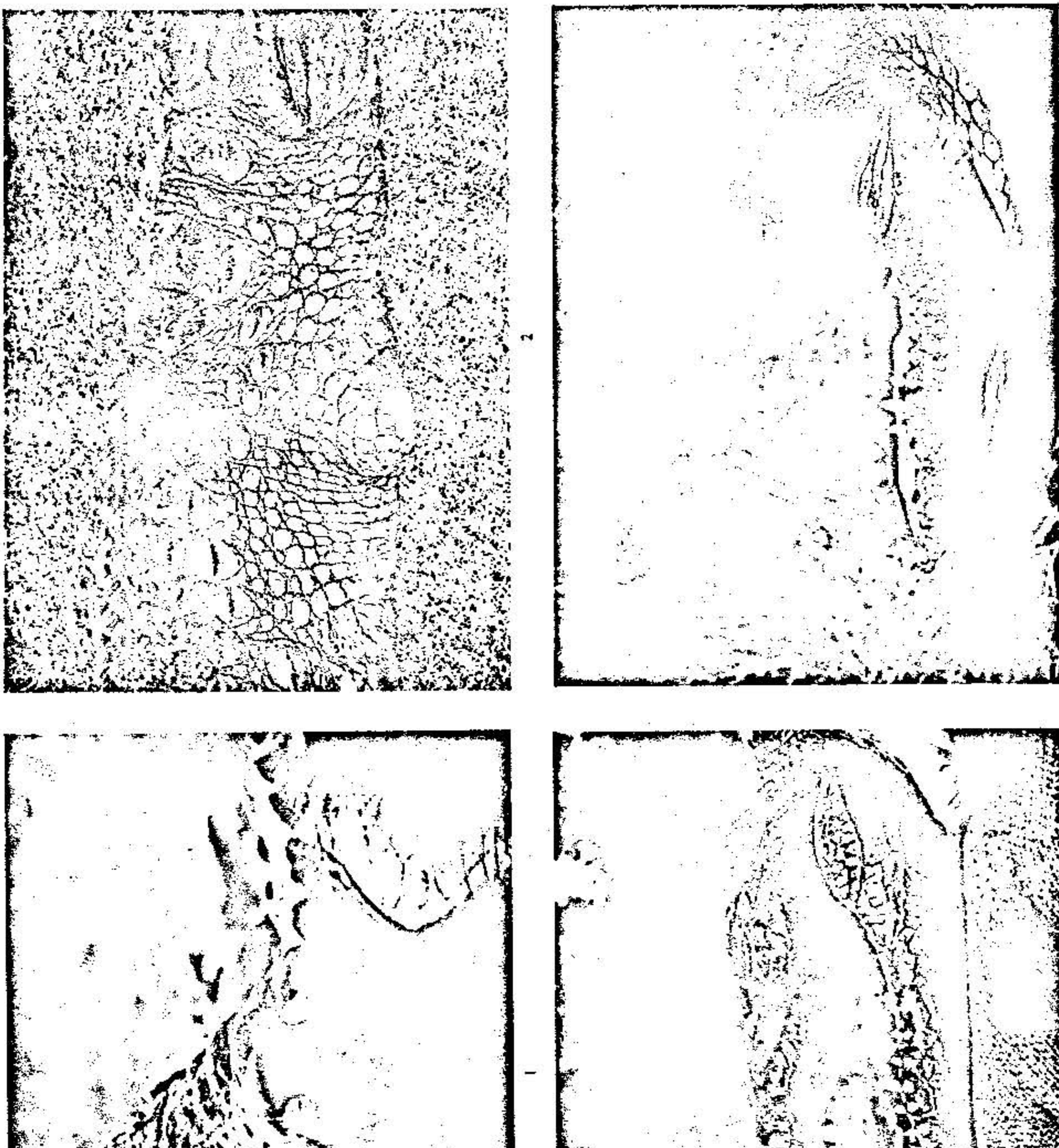

PLATE 7

Fig. 1. Female guarding her nest on a steep river bank site, about fifteen feet above the water. Near Paraa. 27th December, 1956.

Fig. 2. The same site after the female had been disturbed. Two Nile Monitors, *Varanus niloticus*, are seen searching for the eggs. 8th January, 1957.

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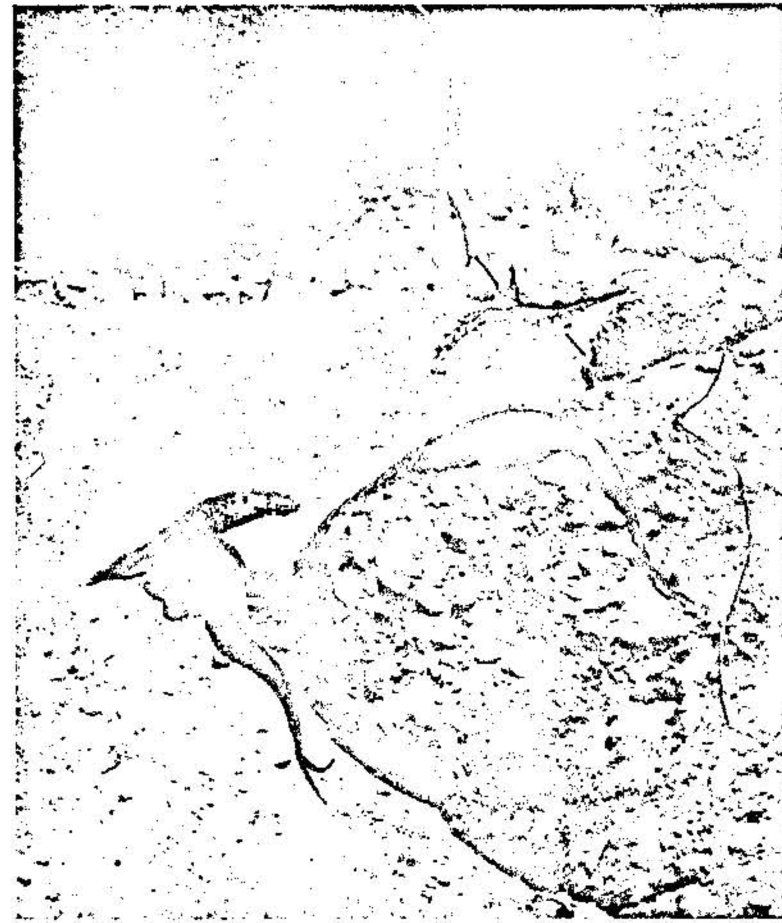


2

The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 8

Fig. 1. The photograph shows a basking crocodile closely attended by a monitor, with an Egyptian Goose nearby. The monitor is one of several which frequented the Magungu grounds, and which in the breeding season were constantly searching for eggs of *C. niloticus* and *Trionyx triunguis*. 31st December, 1956.

Fig. 2. Typical early morning scene on the Magungu grounds. Several large crocodiles are ashore, some lying across the bodies of their companions. 4th August, 1956.

1

2

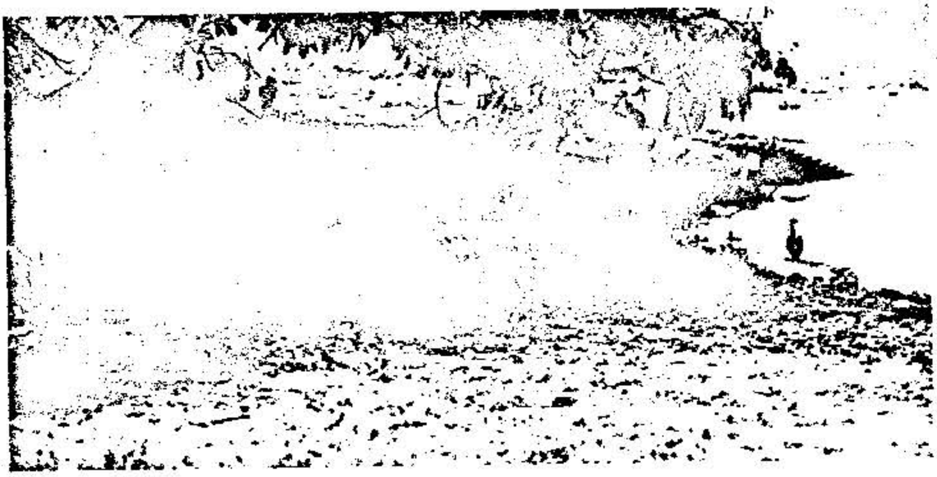
The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 9

Fig. 1. The Spur-winged Plover, *Hoplopterus spinosus*, is a constant companion of the crocodile at Magungu. Three of the birds are seen close to the gaping jaws of an animal in the foreground. 31st December, 1956.

Fig. 2. Another typical scene on the Magungu grounds. The large crocodile in the centre is lying with the tail trailing in the water and with jaws agape. On the right a crocodile is cruising inshore prior to hauling out on the beach. The animal on the left is attended by a Spur-winged Plover, and a Common Sandpiper is seen close to the tail. 1st January, 1957.

Fig. 3. A large male looks across the river from the Magungu grounds, while a Common Sandpiper takes a tsetse fly or leech from the base of the tail. 30th December, 1956.



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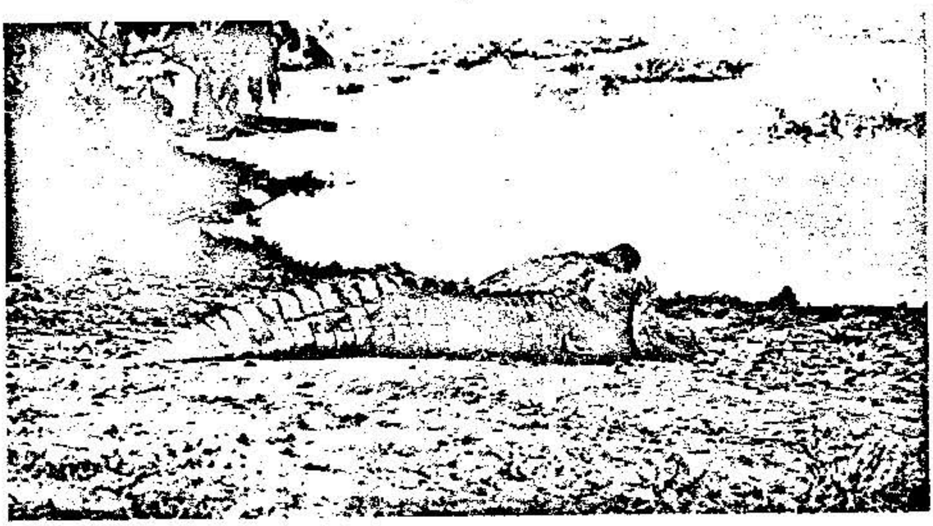

3

The Nile Crocodile in Uganda and Northern Rhodesia.