GROWTH AND FEEDING ECOLOGY OF THE NILE CROCODILE *CROCODYLUS NILOTICUS* AT NGEZI, ZIMBABWE

By J. M. HUTTON

Department of Biological Sciences, University of Zimbabwe, Box MP 167, Harare, Zimbabwe

SUMMARY

(1) In a study of the population ecology of the Nile crocodile at Ngezi, Zimbabwe, animals were measured, and thermal and feeding data collected during a 3-year mark–recapture experiment.

(2) Juvenile growth was confined to the hot season and physical condition declined in the cool season. Large animals grew in irregular spurts.

(3) Low cool-season growth was attributed to the physiological affects of temperature on feeding. Juvenile body temperatures equilibrated with the water to which they returned at night and were therefore as high as 30 °C in the hot season, but fell to 15 °C in the cool. Animals of all sizes basked in the sun, but only for short periods in the cool season did body temperatures exceed 25 °C and therefore approach temperatures efficient for digestion. Juveniles were more often seen feeding and were more replete in the hot season. Hatchlings were able to grow at lower temperatures than older animals.

(4) On the basis of size, it was impossible to assign juveniles to accurate age-classes after 3 years, and growth curves resulting from the estimation of individual ages by skeletochronology were more accurate than those constructed from growth data.

(5) Because growth was slow, females took approximately 30 years to reach sexual maturity. The growth rate of males declined more slowly than that of females and thus they attained larger sizes.

(6) At a size of 600 mm snout–vent length, the diet of juveniles changed from a predominance of insects to fish and birds and a concurrent reversal of several important allometric relationships of the head was believed to be an adaptation for the efficient capture of prey of an increasing size. A fundamental change of home range behaviour also occurred in these animals and the abruptness of the dietary transition may partly reflect a change in prey availability.

INTRODUCTION

Life-history phenomena are scaled to body size (Peters 1983). Where growth rates are very variable, as in large ectotherms, demographic parameters are poorly related to age, and growth is of primary interest in an ecological study. In the Nile crocodile, *Crocodylus niloticus* Laurenti, growth appears to be indeterminate (Graham 1968), growth rates are very variable (Cott 1961; Graham 1968; Blake & Loveridge 1975) and survival is

Present address: Department of National Parks and Wildlife Management, P.O. Box 8365, Causeway, Harare, Zimbabwe.

size-related (Hutton 1984). There are, however, few detailed observations on growth and the factors which affect it in the wild.

This paper reports on growth of the Nile crocodile at Ngezi, Zimbabwe, between 1979 and 1982. Growth and feeding data were collected in a mark-recapture experiment in which every animal was measured. Wherever possible, the temperature of juveniles and their environment was recorded and their stomach contents removed. Climatic data were recorded. Growth is discussed in relation to thermal biology, apparent food intake and season.

STUDY AREA

Lake Ngezi, an artificial impoundment filled in 1948, lies at 1220 m above sea level between 30°20′/30°29′S and 18°39′/18°44′E. The area has a hot-rainy season between November and March, followed by a cool-dry season until September and a hot-dry season until the start of the rains (Fig. 1). Mean minimum air temperatures follow a regular pattern with a trough, in which temperatures may fall to 2 °C, at *c*. day 150, rising to a plateau of 15–20 °C between *c*. day 280 and day 85 of the following year. Water temperature follows a similar cycle with a plateau of 25–30 °C between *c*. days 300 and 80. Rainfall is variable, but most occurs between day 270 and day 100 of the following year. Water level is also variable, responding to down-river requirements, but is generally at its maximum for 7–9 months before falling towards a minimum at *c*. day 320, shortly after the start of the rains (Fig. 1).
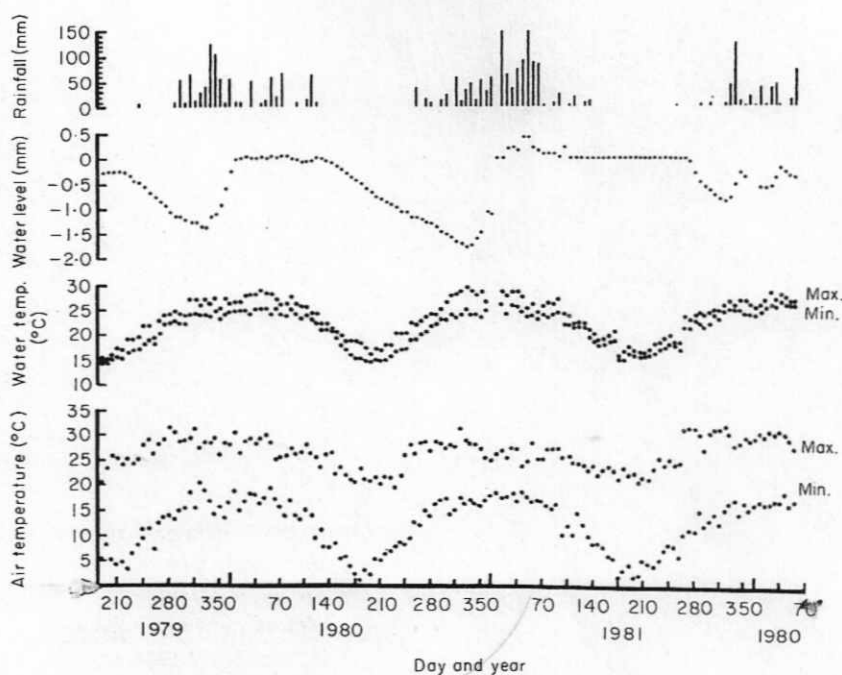

Fig. 1. Seven-day rainfall, 7-day mean maximum and minimum surface water temperatures, 7-day mean maximum and minimum air (screen) temperatures and water level measured at Ngezi over the study period.

The lake is narrow and irregularly shaped, closely following the course of the old river. When full, it covers 580 ha. The main body of water has gently shelving banks with wide beds of perennial hydrophytes such as *Echinochloa stagnina* (Retz.) Beav. and *Cyperus digitatus* Roxb. Over 30% of this area is less than 2 m deep and supports a dense growth of aquatic macrophytes, notably *Ceratophyllum demersum* L. The prevailing wind is south-easterly and the long, exposed north-west shore is characterized by rough water, particularly during the cool-dry season. The headwaters are confined within the steep, raised banks of the Ngezi River. Fringing hydrophytes occur in patches: *Phragmites mauritianus* Kunth predominates.

The shore-line, including both banks of the river, is approximately 32 km and crocodiles occur at a density of $3 \cdot 9$ km^{-1} and a biomass of 172 kg km^{-1}. They occur naturally and have been fully protected since 1967. Mortality is high and confined to animals less than 600 mm snout–vent length (SVL). As a result, recruitment is low. Size-classes are ecologically separated; adults and small juveniles co-exist in the headwaters, larger juveniles and sub-adults are confined to the main body of the lake (Hutton 1984).

MATERIALS AND METHODS

Crocodiles less than 600 mm SVL (juveniles) were captured by hand at night. Following Webb *et al.* (1978) their recapture was attempted every 60 days. Larger animals were captured and recaptured during frequent trapping exercises (Hutton 1984). Thirty physical parameters were recorded for each animal on each occasion of capture, and allometric growth was examined with particular reference to the shape of the head. The size and shape of each animal were quantified by:

   (i) total length (TL);

   (ii) snout–vent length (SVL), measured along the belly from the tip of the snout to the rear margin of the vent;

   (iii) trunk length (TR), the distance from a position equivalent to the rear of the skull to the posterior margin of the vent;

   (iv) body mass (BM);

   (v) head length (HL), measured from the tip of the snout to the rear of the supra-occipital;

   (vi) head width (HW), measured as the greatest width of the head at the posterior border of the quadratojugals;

   (vii) length of the head anterior to the eyes, measured from the tip of the snout to the anterior border of the orbit (SABO);

   (viii) length of the head behind the eyes, measured from the post-orbital border to the posterior margin of the cranial platform (POBECP).

Measurements were made to 1 mm in juveniles, but to 5 mm in large animals. As a consequence, last digits in the data were not normally distributed.

Growth curves were constructed from measured growth in two ways. Juveniles were assigned ages by comparison with N11, the most rapidly-growing animal (Hutton 1984), and a growth curve was constructed as if they comprised a cohort. There were insufficient data to extend this to large animals. For crocodiles of all sizes a logistic growth curve was calculated from the relationship between growth rate and size following the method of Webb, Buckworth & Manolis (1983). Periods between recaptures spanned different proportions of the growing and non-growing seasons and thus contained different numbers

TABLE 1. Mean monthly air (screen) temperatures in the Ngezi area (Kadoma, over 16 years) and Hwange National Park (over 2 years)

Month	Mean maximum temp. (°C)		Mean minimum temp. (°C)	
	Kadoma	Hwange	Kadoma	Hwange
Jan.	28·7	32·1	17·7	20·6
Feb.	28·1	31·8	17·6	20·3
Mar.	27·8	31·9	16·6	19·8
Apr.	27·1	32·0	14·2	18·1
May	25·7	30·1	9·3	13·8
Jun.	23·4	27·3	8·5	10·9
Jul.	23·5	27·5	8·1	10·6
Aug.	26·1	29·7	9·2	14·4
Sep.	30·6	33·9	13·1	18·7
Oct.	31·7	36·6	16·8	22·2
Nov.	30·6	35·3	17·4	21·7
Dec.	28·2	33·4	17·7	21·0

of growing days (GD). The mean daily growth rate of each animal was calculated from the amount that the individual's HL was expected to increase over a full 150-day growing season, divided by 365 ([HL −HL/GD × 150]/365). Recapture intervals of ten or less GD were omitted. The best linear relationship between growth rate and size was calculated for each sex and solved to derive growth curves by:

$$S(t) = (S_m - S_0)[1 - \exp(-t/Y)],$$

where $S(t) =$ mm HL at time t in days, S_m is the theoretical maximum size (mm HL) when growth ceases (calculated directly as the intercept/slope of the growth rate–size relationship), S_0 is the initial size (mm HL) and Y is the time constant (calculated directly as the inverse of the slope of the growth rate–size relationship) (Webb *et al.* 1978).

Growth curves were also constructed from ages estimated by skeletochronology (Hutton 1986). The growth of Ngezi crocodiles was compared with that of 'Beadle', the only free-living adult Nile crocodile for which complete growth data are available. Beadle hatched in 1935 and was soon introduced into Hwange National Park, Zimbabwe, where the climatic seasons are similar to those of Ngezi, but with higher mean temperatures (Table 1). The early growth of Beadle was reported by Cott (1961).

A relative condition factor (RCF), a simple index of fatness, was established for juveniles. Taylor (1979) used this RCF in a study of estuarine crocodiles, *Crocodylus porosus* Schneider, and considered it a measure of the success of the individual under prevailing environmental conditions. Derivation of RCF at Ngezi required evaluation of the exponent b from the relationship between BM and SVL for juveniles, which has the form: BM $= a$SVL^b and the value BM $= (4·08 × 10^{-5})$ SVL$^{2·89}$. The relative condition of each individual was evaluated and the mean condition of the population in the growing and non-growing seasons compared.

The behaviour was recorded of every animal seen during forty-eight spotlight counts (Hutton 1984). Data on the frequency of feeding were extracted and those of the growing and non-growing season compared.

The stomach contents of crocodiles less than 1000 mm SVL were removed using a modification of the technique of Taylor, Webb & Magnusson (1978). Briefly, a hard plastic cylinder was secured between the jaws of the animal to allow safe access to the oesophagus and a self-loading syringe was used to pump 25–40 ml of water into the stomach. The animal was then inverted over a fine mesh gauze (those larger than 600 mm SVL were

immobilized with gallemine triethiodide) and a scoop, lubricated with vegetable oil, was gently pushed into the stomach to mix and remove its contents. Scooping was repeated until no further material collected on the gauze. The process was efficient in all individuals larger than 300 mm SVL. Samples were preserved in 70% alcohol. In the laboratory they were filtered, washed and air dried for 30 min before weighing ($0 \cdot 1$ g). The mass of the component parts (gastroliths, parasites and prey fragments) was then measured separately. The volume of the air-dried contents was measured by displacement of water in a measuring cylinder.

Using low-power magnification, prey were identified and counted. Stomach contents were quantified, prey and parasites by their number and gastroliths by their mass as a percentage of that of the animal. Size-related diet was examined by a principal components analysis of the relative frequency of gastroliths, parasites and different prey in crocodiles of different sizes.

The number of prey items in stomachs (the number of whole prey estimated from fragments) and relative mass of prey fragments ($\log_{10}$ body mass/prey mass) were used as indices of repleteness and compared between seasons.

A crocodile was considered to be basking if it was lying at the waters edge with more than 50% of its body exposed. The basking behaviour of crocodiles of all sizes was routinely recorded. That of juvenile and adults was analysed on a seasonal basis.

Air (shade), water and cloacal temperatures were measured with a mercury thermometer ($0 \cdot 1$ °C) within 2 min of capture.

Maximum and minimum air (shade) and water (20 mm depth) temperatures (°C), rainfall (mm) and water level (m) were recorded daily throughout the study.

RESULTS

Of 102 marked animals, fifty were recaptured on at least one occasion. A disproportionate number of juveniles were recaptured; larger crocodiles rapidly learnt to avoid traps. SVL was the standard measure of length both in large animals (it was more accurately measured than TL and was not affected by tail-tip amputations) and juveniles (the length of the tail was commonly found to decrease during the cool season). In some circumstances, the use of HL was preferred as it further reduced measuring errors. Each parameter is used in this paper as appropriate, important relationships between them are:

$$TL(mm) = 1 \cdot 799 \; SVL(mm) + 84 \cdot 981, \; r = 0 \cdot 995, \; n = 218,$$
$$TL(mm) = 7 \cdot 559 \; HL(mm) - 49 \cdot 143, \; r = 0 \cdot 997, \; n = 218, \; and$$
$$SVL(mm) = 4 \cdot 185 \; HL(mm) - 74 \cdot 038, \; r = 0 \cdot 996, \; n = 218.$$

Seasonal growth

Hatchlings grew throughout their first year, but their growth rate declined from $0 \cdot 869 \pm 0 \cdot 117$ ($\pm$S.E.) mm day^{-1} to $0 \cdot 063 \pm 0 \cdot 020$ ($\pm$ S.E.) mm day^{-1} in the cool-dry season. Growth in older animals was confined between c. 21 October and 15 March (day 290 until day 75), a period of 150 growing days (GD) (Fig. 2). Thus, growth was stepwise, animals in a cohort attaining a size of 175–225 mm SVL at the end of their first growing season, 250–325 mm SVL at the end of their second and so on (Fig. 3). There is a paucity of growth data for animals larger than 600 mm SVL, but those of 600–1000 mm SVL grew in
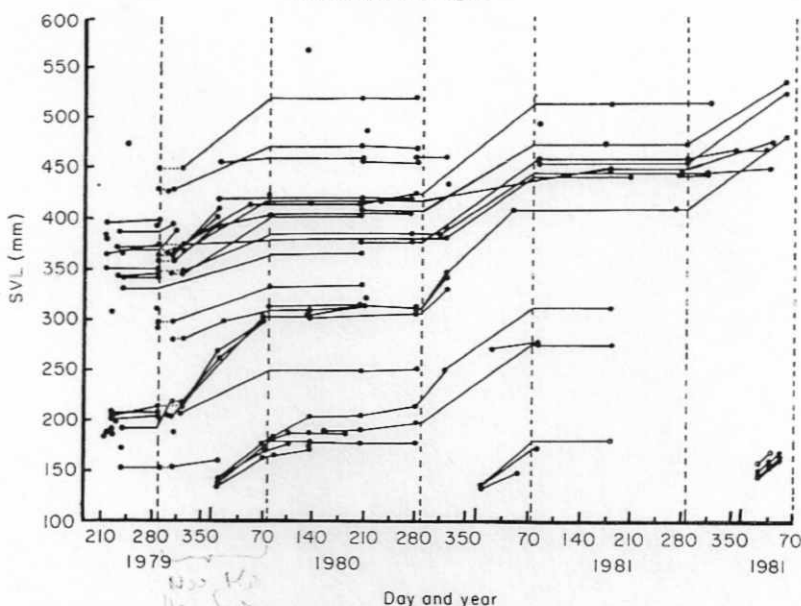
FIG. 2. Growth of small crocodiles over the study period. Some hatchlings continued growing during their first cool season, but juvenile growth was confined to the hot season between days 290 and 75.
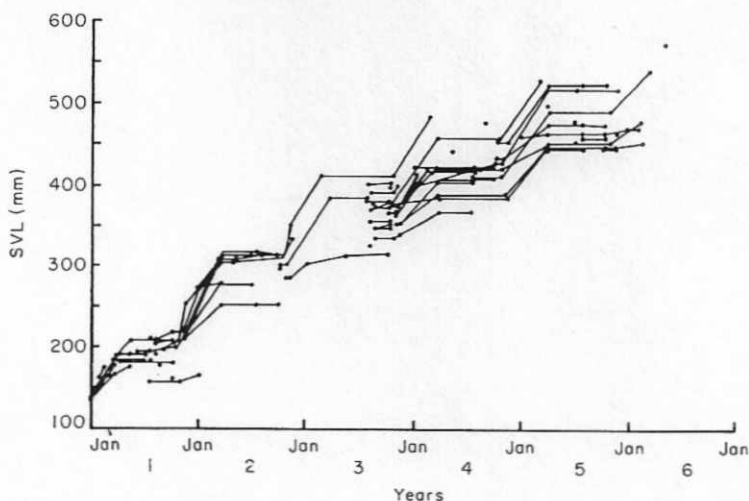

FIG. 3. Variation in growth within a theoretical cohort of juvenile crocodiles at Ngezi.

the same seasons and at similar rates to juveniles. At approximately 1000 mm SVL growth was reduced, and that of adults occurred in irregular spurts (Hutton 1984).

Growth curves

The relationship between growth rate and size, derived by the method of Webb, Buckworth & Manolis (1983), was significant for females ($r = 0.446$, $n = 44$, $P < 0.005$), but not for males ($r = 0.273$, $n = 22$, $P > 0.1$). It predicts that Ngezi females will attain a
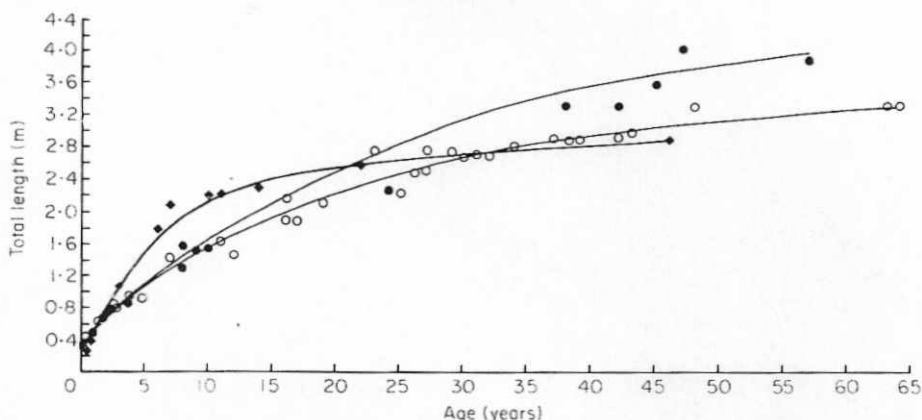
FIG. 4. The measured growth of 'Beadle' from Hwange National Park (♦) and that of Ngezi crocodiles (● males , ○ females) as determined from skeletochronology and the measurement of juvenile growth.

maximum size of 3050 mm TL in 17 years, but growth curves constructed from the estimation of individual ages by skeletochronology shows that they take approximately 35–40 years (Fig. 4). The growth of Ngezi animals is notably different to that of the Hwange animal. Beadle grew rapidly as a juvenile, reaching 1500 mm TL in only 5 years. This rate (approximately 286 mm year^{-1}) was maintained until a size of 2100 mm TL, then markedly declined to a steady 130 mm year^{-1}. Ngezi females grew less rapidly, reaching only 900 mm TL at 5 years. Their growth rate gradually decreased as they approached adult sizes. The growth rate of males decreased more slowly than that of females after a size of approximately 2300 mm TL (Fig. 4).

Allometric growth

In Ngezi crocodiles up to 200 mm SVL, HL grew relatively faster than HW, the trend being reversed in animals over 250 mm SVL, tending towards isometry at 1750 mm (Fig. 5a). This confirmed the observation that a crocodile at hatching has a relatively short head which rapidly lengthens, relative to its width, in the first weeks of life. However, this relative growth between HL and HW was itself the result of allometric growth between the length of different portions of the head; SABO grew proportionally much faster than POBECP until animals attained a size of 600 mm SVL when they began to grow isometrically (Fig. 5b). Thus, although HW was increasing at a more rapid rate than HL from the time that SVL reached 250 mm, in fact, the length of SABO was growing proportionally faster than HW until animals attained a size of 600 mm SVL when the trend was dramatically reversed (Fig. 5c).

The allometric growth between SABO and HW was the result of both parameters altering their rate of growth. When TR was taken as the fundamental unit of the animal rather than SVL (which includes the head and trunk, which may not be growing isometrically) then it was found that neither SABO nor HW grew isometrically with TR; SABO increased at a proportionally faster rate than TR until a size of 600 mm SVL when the trend was reversed (Fig. 5d), while the relationship between HW and TR traced exactly the opposite curve (Fig. 5e). Neither relationship was particularly marked, but the allometry was in opposite directions amplifying the relative growth between SABO and HW.
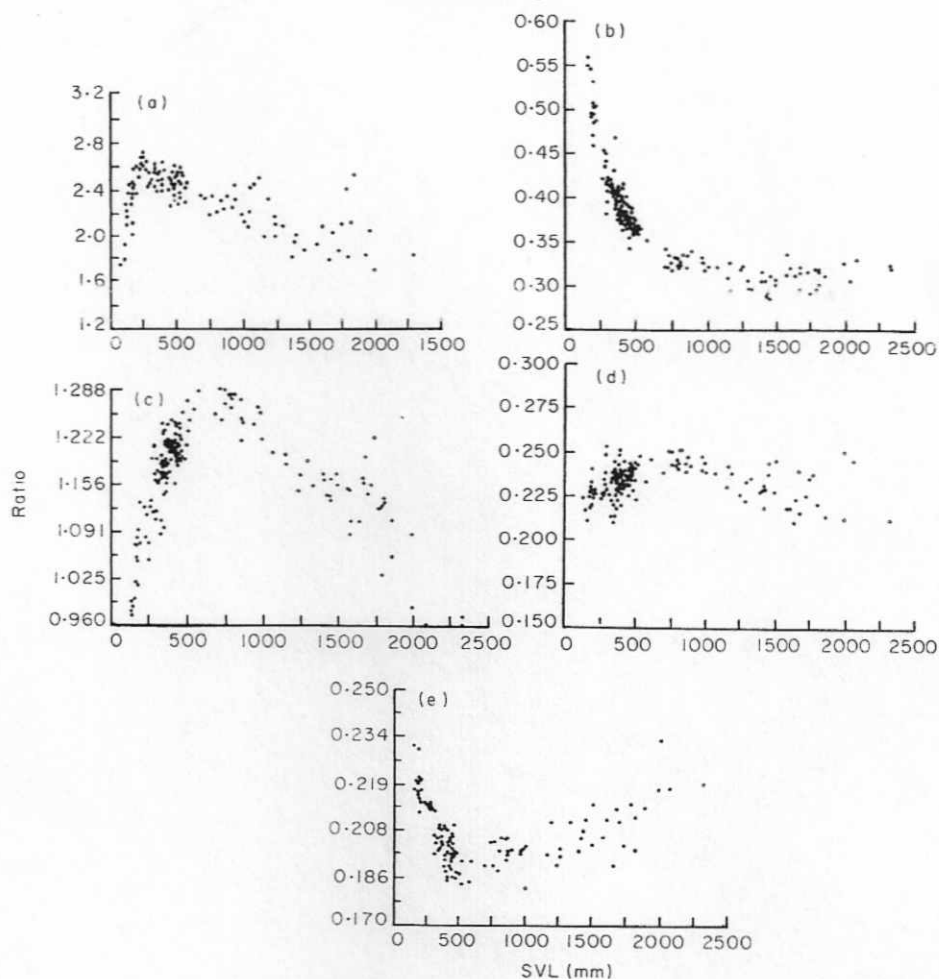
FIG. 5. Allometric growth of Ngezi crocodiles; relationships between parts of the body with increasing body size. (a) HL:HW (b) POBECP:SABO (c) SABO:HW (d) SABO:TR (e) HW:TR (see text).

Body temperature and thermoregulation

Body temperature data fell into three groups, those from animals captured in the water at night during the growing (hot-wet) season ($n = 23$), those from animals similarly captured during the non-growing (cool-dry) season ($n = 9$) and those from animals captured while basking during the day in the non-growing season ($n = 19$). In both the hot and cool seasons, body temperature (T_b) was significantly different from air temperature (T_a) (paired sample t-tests, $t = 10 \cdot 63$, $P < 0 \cdot 001$ and $t = 7 \cdot 343$, $P < 0 \cdot 01$, respectively. In all cases, T_a was lower than T_b. However, T_b was not significantly different from water temperature (T_w) at night in either the hot or cool seasons ($t = 1 \cdot 622$, $P > 0 \cdot 1$ and $t = 1 \cdot 082$, $P > 0 \cdot 3$, respectively). Thus, T_b conforms to T_w at night, maintaining body temperature above the ambient air temperature. In the nineteen juveniles sampled while basking during the cool season, T_b was significantly higher than T_w ($t = 4 \cdot 719$, $P < 0 \cdot 001$). In fact, there was no correlation between the two ($r = 0 \cdot 339$, $P > 0 \cdot 1$), T_b increasingly
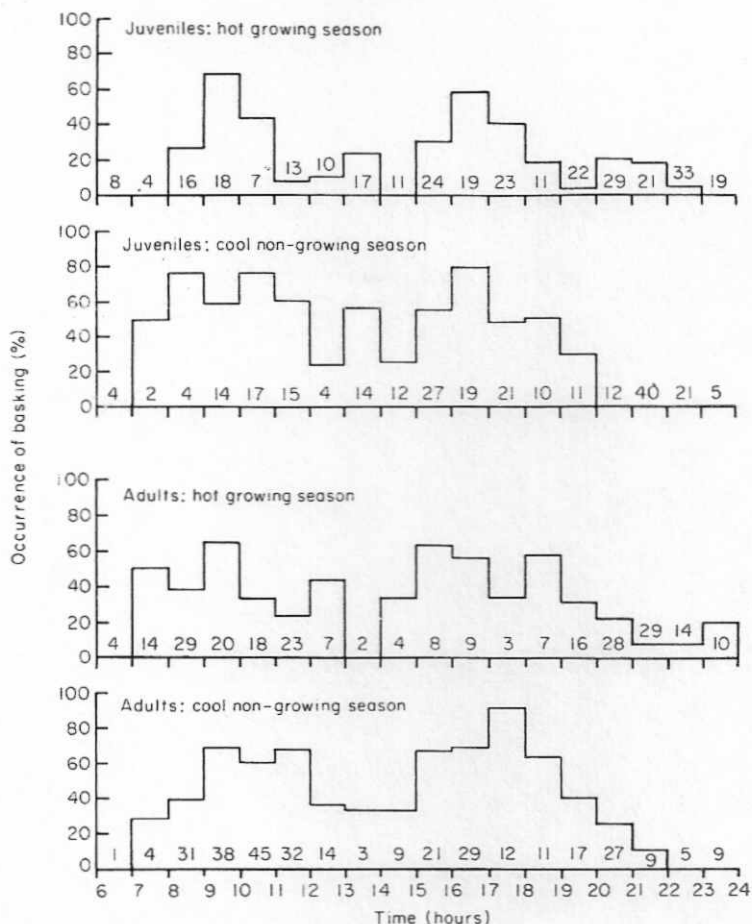
FIG. 6. Diurnal patterns of basking of juvenile and adult crocodiles in the hot, growing and cool, non-growing seasons at Ngezi. The sample size in each interval of time is given.

deviated from T_w as time progressed ($[T_b - T_w]°C = 3·123$ h $- 29·882$, $r = 0·872$, $P <$ 0·001). T_b and T_a were also significantly different in these animals ($t = 6·557$, $P < 0·001$) but were positively correlated ($r = 0·830$, $P < 0·001$). T_a increased steadily with time ($T_a°C = 2·868$ h $- 13·510$, $r = 0·836$, $P < 0·001$) and thus, the divergence between T_b and T_w widened as the air temperature rose. In both seasons, basking commenced after 07.00 hours and followed a bimodal daily pattern, broadly corresponding with the patterns observed by Cott (1961) and Loveridge (1984). Both adults and juveniles basked longer into the night in the hot-growing season (Fig. 6), but the proportion of occasions on which they were seen basking was greatest in the cool non-growing season (Table 2).

Feeding and physical condition

The mean relative condition of juvenile crocodiles during the growing period was significantly higher than during the non-growing season. They were also more frequently seen feeding and were more replete; both the number of prey items and the relative amount of food in stomachs were significantly higher than in the non-growing period (Table 2).

Crocodile at Ngezi

TABLE 2. Crocodiles at Ngezi: seasonal differences in the frequency of basking of juveniles and adults, mean relative condition, frequency of feeding and number of prey items and relative food mass in juvenile stomachs

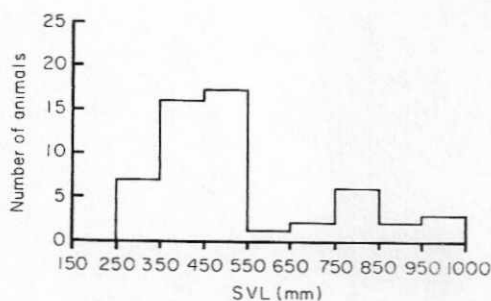|	Growing season (21 Oct.–15 Mar.)	Non-growing season (16 Mar.–20 Oct.)	Significance
Basking frequency			
juveniles	22%, $n = 305$	37%, $n = 252$	$\chi^2 = 9 \cdot 93$, $P < 0 \cdot 01$
adults	31%, $n = 244$	53%, $n = 311$	$\chi^2 = 10 \cdot 56$, $P < 0 \cdot 01$
Mean relative condition	4·012	3·808	$t = 2 \cdot 83$, d.f. $= \infty$, $P < 0 \cdot 01$
Feeding frequency	8%, $n = 169$	1%, $n = 392$	$\chi^2 = 16 \cdot 15$, $P < 0 \cdot 001$
Mean no. prey items	8·0	2·5	$t = 2 \cdot 55$, d.f. $= 35$, $P < 0 \cdot 02$
Mean $\log_{10} \dfrac{\text{mass croc.}}{\text{mass food}}$	2·151	2·592	$t = 2 \cdot 49$, d.f. $= 35$, $P < 0 \cdot 02$

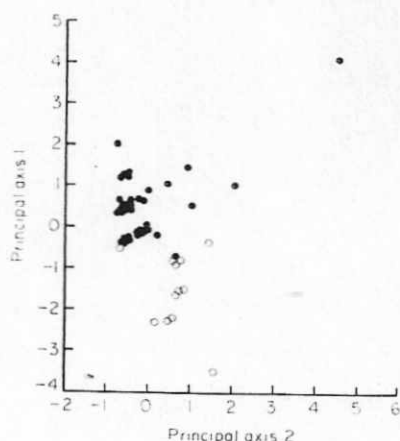FIG. 7. The size distribution of crocodiles sampled for feeding analysis.

FIG. 8. Principal components analysis of crocodile stomach contents relative to body size in the range 150–900 mm SVL: (●) animals < 600 mm SVL, (○) animals > 600 mm SVL.

Although individuals of 350–550 mm SVL predominated in the sample (Fig. 7), principal components analysis illustrated that there was a dichotomy in the distribution prey types in stomachs, a marked change occurring when crocodiles v approximately 600 mm SVL (Fig. 8). The frequency of insects decreased while that of

and birds increased. However, crabs were scarce in the smallest and largest individuals whereas mammals occurred only infrequently and were not characteristic of any size. Parasitic nematodes *Dujardinascaris dujardini* Travassos appeared throughout the size range and gastroliths were ubiquitous amongst animals larger than 350 mm SVL.

DISCUSSION

Climatic effects on growth

It is clear that the climatic seasons have a profound effect on the growth, feeding behaviour and physical condition of Ngezi crocodiles. Hatchlings emerge in January and, although they grow throughout their first year, growth is greatly reduced during the cool-dry season of March until October. Larger juveniles not only stopped growing during this period, but also lost condition and some declined in length. Similar seasonal shrinkage is reported in the American alligator *Alligator mississippiensis* Daudin (Chabreck & Joanen 1979).

There is some disagreement in the literature as to which environmental factors are most important to crocodiles living in seasonally varying environments. Webb *et al.* (1978) concluded that rainfall rather than temperature had the most profound effect on the biology of the estuarine crocodile, although the rainy and hot seasons were complementary in their study area, as they are at Ngezi. Buffrénil (1980) suggested that the Siamese crocodile *Crocodylus siamensis* Schneider has an endogenous growth rhythm, based essentially on the alternation of wet and dry seasons in south-east Asia, while the American alligator certainly responds to seasonal temperature variations (Chabreck & Joanen 1979). From the data presented here, it would appear that temperature is the most important factor to the Nile crocodile. Growth is exactly synchronous with the plateau of water temperature, beginning after the start of the rains and ending before the rainy season is over.

Nile crocodiles attempt to maintain preferred body temperatures, which vary between size-classes, by specific behaviours in response to the thermal environment (Loveridge 1984). Although large crocodiles are better able to maintain body temperatures than juveniles, it has been found that American alligators of all sizes rely heavily on water to help them maintain body temperature during cool periods and at night (Spotila, Soule & Gates 1972). At night, Ngezi juveniles retreat to the water and T_b conforms to T_w. As T_w may be 30 °C in the hot season, but 15 °C in the cool season (Fig. 1), juveniles in the water in the cool season are well below their preferred temperatures of 29·7–33·4 °C Loveridge 1984).

It has been known for many years that temperature affects ectotherm digestion (e.g. Riddle 1909). At its preferred body temperature of 30 °C, the spectacled caiman *Caiman crocodilus* L. takes 4 days to digest a meal of 5% of its body weight. Above and below this optimum temperature both digestive efficiency and the level of spontaneous feeding decrease. At 15 °C, digestion time is increased by 325% and large animals refuse to eat Diefenbach 1975a,b). Coulson & Hernandez (1983) reported that the ideal temperature for maximal appetite and growth in the American alligator may be as high as 32 °C and they note that: 'At temperatures below 25 °C, appetite is reduced greatly and below 20 °C it is gone entirely. Renal impairment is seen at any temperature below 18 °C ...'. Low cool season temperatures at Ngezi are presumed to affect crocodiles in the same way, depressing appetite and making digestion slower, leading to the cessation of growth and loss of condition. The growth of hatchlings at Ngezi, together with observations on

captive-reared Nile crocodiles (J. M. Hutton, unpublished) suggests that hatchlings are more tolerant of low temperatures than larger juveniles.

The Nile crocodile is known to bask during the day, which usually raises T_b above T_w (Cott 1961; Cloudsley-Thompson 1964; Modha 1968; Loveridge 1984). Ngezi crocodiles of all sizes were seen basking in all months (Fig. 6) and in the cool season the body temperatures of basking juveniles quickly rose well above water temperatures. Lang's (1979) suggestion that tropical crocodiles are thermoconformers, avoiding rapid heating during the day, is clearly too general.

Growth curves

The variation in individual growth is not as extreme in free-living crocodiles as it is in captivity where it responds dramatically to temperature, population density and food—both quality and quantity (Coulson & Hernandez 1973; Joanen & McNease 1974; Blake & Loveridge 1975; Whitaker & Whitaker 1977). Nevertheless, the variation of growth within a theoretical cohort (Fig. 3) shows that, 3 years after hatching, it is impossible to separate Ngezi crocodiles into accurate age-classes without a detailed knowledge of growth and the individuals concerned. Cott (1961) was also unable to separate Nile crocodiles into age-classes after their third year. Webb, Buckworth & Manolis (1983) noted the same problem in the Australian freshwater crocodile *Crocodylus johnstoni* Krefft and the estuarine crocodile, and it can be inferred from McIlhenny (1934) for the American alligator.

The logistic growth curve derived for Ngezi females is poor because the growth rate to size relationship is the result of an extremely variable relationship amongst individuals less than 200 mm SVL, coupled with a paucity of data for larger animals. Variation in the juvenile growth rate–size relationship is due to alteration of growth rates with time as much as distinct individual differences. Large animals were growing in intermittent spurts and as recapture intervals were relatively short, data on the mean daily growth rates of these animals are inadequate. The construction of a growth curve by this method was more successful in a study of the Australian freshwater crocodile because the frequency of recapture was high and growth data from over 2 or 3 years were available for a large proportion of the population (Webb, Buckworth & Manolis 1983).

In crocodiles up to 45 years old, skeletochronology estimates age with an error of less than 15% (Hutton 1986) and growth curves derived from the estimation of individual age in this way are more accurate than any from the measurement of growth over relatively short periods. The difference between the growth of Ngezi crocodiles and that of Beadle is probably due to their thermal environments (Table 1). In Zimbabwe, wild female crocodiles generally attain sexual maturity at sizes over 2600 mm TL (Hutton 1984). It is notable that the rapid early growth of Beadle allowed her to reach this size in 22 years while Ngezi females take 10 years longer. The observation that the growth rate of male declines more slowly than that of females is in accordance with growth in other crocodilians (Webb *et al.*, 1978; Chabreck & Joanen 1979). The age/size relationship indicates that the growth of crocodiles larger than 2200 mm TL should be in the order of 30 mm year^{-1}, but very little was actually recorded during the study period, which provides additional evidence that these animals grow in irregular spurts.

corresponding with the tooth-line) and later relative broadening of the head are interpreted as adaptations towards the efficient capture of prey of different sizes. Further, it has been suggested that marked broadening of the head at a size of 800 mm SVL allows the estuarine crocodile to secure larger prey and, as a result, achieve a relative gain in energy and growth (Webb et al. 1978).

At Ngezi, allometric growth was most pronounced in hatchlings in which the head rapidly lengthened relative to its width, with the post-orbital portion of the head growing slowly. Although this allometry was reversed at 200 mm SVL, the pre-orbital portion of the head continued to grow at a proportionally faster rate than both the length and width of the post-orbital part until a size of 600 mm SVL was attained. The growth rate of the post-orbital portion of the head then increased proportional to the pre-orbital part and also to the trunk, while the rate of growth of the pre-orbital section slowed relative to the trunk. The part of the head behind the eyes is the region of attachment of the jaw musculature which also increases at 600 mm SVL as the head becomes more massive. As insects become less important than fish and birds in the diet of crocodiles of this size (Fig. 8), allometric changes of body form of the Nile crocodile, as in other species, are associated with changes in feeding. At 600 mm SVL, juvenile crocodiles disperse from the Ngezi River into the lake (Hutton 1984) and therefore experience a change (unmeasured) in the relative availability of prey. This may explain the sharpness of the dietary transition which was considerably more abrupt than that found in the same species by Cott (1961) (although Cott's study was not of a single population) and in the estuarine crocodile by Taylor (1979). It does not account for the transition, which actually represents an increase in prey target size (Webb, Manolis & Buckworth 1982).

ACKNOWLEDGMENTS

REFERENCES

Blake, D. K. & Loveridge, J. P. (1975). The role of commercial crocodile farming in crocodile conservation. Biological Conservation, 8, 261–272.

Buffrénil, V. de. (1980). Mise en évidence de l'incidence des conditions de milieau sur la croissance de Crocodylus siamensis (Schneider, 1801) et valeur des marques de croissance squelettiques pour l'évaluation de l'âge individuel. Archives de zoologie expérimentale et général, 121, 63–76.

Chabreck, R. H. & Joanen, T. (1979). Growth rates of American alligators in Louisiana. Herpetologica, 35, 51–57.

Cloudsley-Thompson, J. L. (1964). Diurnal rhythm of activity in the Nile crocodile. Animal Behaviour, 12, 98–100.

Cott, H. B. (1961). Scientific results of an enquiry into the ecology and economic status of the Nile crocodile (Crocodylus niloticus) in Uganda and Northern Rhodesia. Transactions of the Zoological Society of London, 29, 211–356.

Coulson, T. D., Coulson, R. A. & Hernandez, T. (1973). Some observations on the growth of captive alligators. Zoologica (New York), 58, 47–52.

Coulson, R. A. & Hernandez, T. (1983). Alligator Metabolism. Studies on Chemical Reactions In Vivo. Pergamon Press, England.

Diefenbach, C. O. Da C. (1975a). Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia). I. Rate of gastric digestion and motility as a function of temperature. *Comparative Biochemistry and Physiology*, **51A**, 259–265.

Diefenbach, C. O. Da C. (1975b). Gastric function in *Caiman crocodilus* (Crocodylia: Reptilia). II. Effects of temperature on pH and proteolysis. *Comparative Biochemistry and Physiology*, **51A**, 267–274.

Dodson, P. (1975). Functional and ecological significance of relative growth in *Alligator*. *Journal of Zoology (London)*, **6**, 265–270.

Graham, A. (1968). *The Lake Rudolf crocodile* (Crocodylus niloticus *Laurenti*) *population*. Report to Kenya Game Department (Mimeo).

Hutton, J. M. (1984). *Population ecology of the Nile crocodile* Crocodylus niloticus *Laurenti, 1768, at Ngezi, Zimbabwe*. Unpublished D. Phil Thesis, University of Zimbabwe.

Hutton, J. M. (1986). Age determination of living Nile crocodiles from the cortical stratification of bone. *Copeia*, 1986(2), 332–341.

Joanen, T. & McNease, L. (1974). *Propagation of immature American alligators in controlled environmental chambers*. Proceedings of the southern Zoo Workshop, Monroe, Louisiana, 1974, pp. 1–8.

Lang, J. W. (1979). Crocodilian thermal behaviours: alligators vs crocodiles. *American Naturalist*, **19**, 975.

Loveridge, J. P. (1984). *Thermoregulation of the Nile Crocodile* Crocodylus niloticus. *The Structure, Development and Evolution of Reptiles* (Ed. by M. W. J. Ferguson), pp. 443–467. Symposia of the Zoological Society of London, No. 52. Academic Press, London.

McIlhenny, E. A. (1934). Notes on the incubation and growth of alligators. *Copeia*, 1934, 80–88.

Modha, M. L. (1968). Basking behaviour of the Nile crocodile on Central Island, Lake Rudolf. *East African Wildlife Journal*, **6**, 81–88.

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Riddle, O. (1909). The rate of digestion in cold-blooded vertebrates. The influence of season and temperature. *American Journal of Physiology*, **24**, 447–458.

Spotilia, J. R., Soule, O. H. & Gates, D. M. (1972). The biophysical ecology of the alligator. Heat energy budgets and climate spaces. *Ecology*, **53**, 1094–1102.

Taylor, J. A. (1979). The foods and feeding habits of sub-adult *Crocodylus porosus* Schneider in Northern Australia. *Australian Wildlife Research*, **6**, 347–359.

Taylor, J. A., Webb, G. J. W. & Magnusson, W. E. (1978). Methods of obtaining stomach contents from live crocodilians. *Journal of Herpetology*, **12**, 415–417.

Webb, G. J. W., Buckworth, R. & Manolis, S. C. (1983). *Crocodylus johnstoni* in the McKinlay River Area, N.T. III. Growth, movement and the population age structure. *Australian Wildlife Research*, **10**, 383–401.

Webb, G. J. W., Manolis, S. C. & Buckworth, R. (1982). *Crocodylus johnstoni* in the McKinlay River Area, N.T. I. Variation in the diet and a new method of assessing the relative importance of prey. *Australian Journal of Zoology*, **30**, 877–899.

Webb, G. J. W. & Messel, H. (1978). Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, Northern Australia. *Australian Journal of Zoology*, **26**, 1–27.

Webb, G. J. W., Messel, H., Crawford, J. & Yerbury, M. J. (1978). Growth rate of *Crocodylus porusus* (Reptilia: Crocodilia) from Arnhem Land, Northern Australia. *Australian Wildlife Research*, **5**, 385–399.

Whitaker, R. & Whitaker, Z. (1977). Growth rates of *Crocodylus palustris*. *Journal of the Bombay Natural History Society*, **75**, 231–232.