

Growth Rate of *Crocodylus porosus* (Reptilia: Crocodylia) from Arnhem Land, Northern Australia*

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Abstract

In *C. porosus* < 80 cm SVL (snout-vent length), growth rate decreases as body size increases; males grow faster than females, and both sexes grow faster in the wet season than in the dry season. If the exponential growth curve for specimens < 80 cm SVL is extrapolated, it underestimates the maximum size of *C. porosus*. A second growth curve for specimens > 80 cm SVL has been derived separately, and the two curves intersect in the vicinity of 70 cm SVL. The size at which *C. porosus* cease growing seems quite variable and some data indicate a range of 3.9-6.0 m total length for males. The two-curve growth model is thought to reflect an energetic advantage in feeding on large rather than small prey.

Introduction

The relationship between size and age is a fundamental aspect of an animal's natural history which is usually quantified by capture-recapture of marked individuals. Among the reptiles, growth of squamates and chelonians has been well studied (see Fukada 1961; Wilbur 1975; Andrews 1976), and is typically exponential (von Bertalanffy 1960), but there is a paucity of data on crocodiles. Growth curves for a number of species have been formulated from the growth of captive specimens (Cott 1961; Dowling and Brazaitis 1966; Graham 1968); however, studies with *Alligator mississippiensis* have shown that growth rate in captivity can be doubled by optimizing temperatures throughout the year (Joanen and McNease 1976).

Graham (1968) attempted to age wild *Crocodylus niloticus* by using growth zones in the dentary bone and the weight of the eye lens as morphological indicators of age; however, his results were variable and neither the validity nor the reliability of his methods was established. Only with *A. mississippiensis* has a size-age curve based on absolute growth of wild animals been constructed (McIlhenney 1934; Chabreck 1965; Nichols *et al.* 1976).

The present study reports on the growth of free-living *Crocodylus porosus* as revealed by the recapture of marked individuals. The study area was the Liverpool River system on the north coast of Arnhem Land, northern Australia, in which there is an estimated (June 1977) 300-400 *C. porosus* (80% juveniles). As elsewhere in Australia, the adults are wary, few in number and difficult to catch, so consequently our study deals mainly with juveniles.

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The Study Area

The Liverpool River system is composed of the Tomkinson and Liverpool Rivers, and a number of small creeks (maps in Webb *et al.* 1977; Webb and Messel 1978a). The sections of the river system under tidal influence meander across flood plains and have muddy banks typically lined with either mangrove forest or floodplain grasses and sedges. The river water is discoloured with suspended sediment and there are two tidal cycles per day; tidal range is about 3 m.

Annual average rainfall at the mouth of the Liverpool River (Maningrida Settlement; 134°15'E., 12°2'S.) is 1141 mm; 83% falls between December and March and 95% between November and April, which gives distinct wet and dry seasons.

During the dry season a salt wedge moves upstream from the sea, and by November brackish water (>5‰) may be at the limit of tidal influence (about 60 km upstream). During the wet season, extensive flooding can occur and zero salinity has been measured in the mouth of the Liverpool River at this time.

Maximum air temperatures measured at 0900 and 1500 h ranged from monthly means of 32.7°C in November to 30.0°C in July, and minimum air temperatures from 25.0°C in December to 16.3°C in July (means for 15–17 years from the Australian Bureau of Meteorology). Water temperatures typically range between 21 and 31°C, depending on the time of year.

In the Liverpool River system, *C. porosus* nest between November and April (in the wet season), with nests upstream of 30 km made on the riverside and those downstream restricted to freshwater swamps, usually back from the river's edge. Eggs hatch between February and June, but there is a high egg mortality due to flooding; approximately 90% of nests studied by Webb *et al.* (1977) had all or most embryos killed by inundation with flood waters.

In nests upstream of 30 km hatchling crèches are sometimes formed and maintained for up to 2½ months. One-year-olds are mostly found in the same general areas as hatchlings, but there is a shift away from these areas by older age groups, in particular a downstream movement by males (Webb and Messel 1978a). The present study of growth represents a further contribution to a series of papers which examine the life history of *C. porosus* (see references).

Methods

Juvenile crocodiles were mostly caught with a handnet, a harpoon or a set of 'Pilstrom' tongs (Rogers, Arkansas), which have been described in detail elsewhere (Webb and Messel 1977a). In the present study, snout-vent length (SVL) and head length (HL) were used as standard measures of body size. A complete list of measurements taken from each animal, and the equations for converting one measurement to another, are in Webb and Messel (1978b). SVL was measured from the tip of the snout to the anterior extremity of the cloaca (to the nearest centimetre), and HL was measured with calipers from the tip of the snout to the median hind edge of the cranial platform, i.e. the supra-occipital bone (to the nearest millimetre).

Animals were sexed by direct observation of the spread cloaca, a method which experienced observers can use to sex 2-month-old crocodiles. Where different sexes were assigned to a crocodile when caught as a hatchling and when recaptured at an older stage, the later sex determination was accepted.

Each crocodile was consecutively numbered by branding a sequence of tail scute whorls, and released at the site of capture, usually within 24 h of capture. Most catching and recatching was in the dry season, between May and November.

In 1973 and 1974, 508 *C. porosus* were marked and released in the Liverpool River system, and by the end of the 1975 dry season 198 had been recaptured once and 24 twice; an additional five animals marked in 1975 were recaptured in the 1975-76 wet season, and a further three animals, one subadult and two adults, were recaptured in November 1976 and May 1977 respectively. Of the total of 254 capture-recapture records, nine were from animals in which sex was not positively determined (all were hatchlings recaptured within the first year). There were thus 245 records from animals of known sex.

Results

Variables Influencing Growth Rate

In Fig. 1, growth rate, expressed as millimetres of SVL per day, is plotted against mean snout-vent length (MSVL) between captures, i.e. $[(l_2 - l_1)/2] + l_1$, where l_1 and l_2 refer to lengths at capture and recapture respectively. Calculating growth in this manner assumes that in the period between captures deviations between the real growth curve and an assumed linear growth are negligible, an assumption which has been tested (see p. 388).

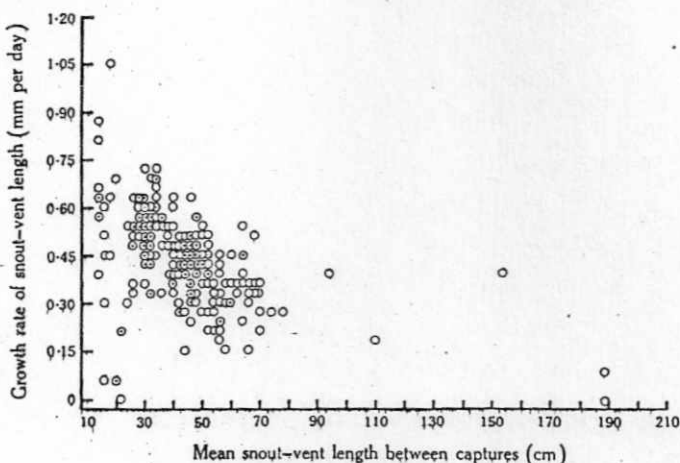


Fig. 1. Growth rates (in terms of snout-vent length) of all *C. porosus* which were recaptured. ○ Single records. ◻ Multiple records.

Multiple regression analysis was used to derive the relationship between growth rate and SVL and to quantify the influence of some variables on growth rate. Preliminary analyses were carried out to delimit important sources of variation and to test whether or not the sample could be considered homogeneous; possible sources of variation examined were:

Mean SVL.

Sex.

Season. Assuming 1 January was day number 1, days 1-120 and 334-365 were considered wet season and days 121-333 dry season: the variable was the percentage of dry season days in the year.

Time. Defined as the actual number of days in the sampled growing period: of the 245 growth records, 4.1% had sampled growing periods between 1 and 99

days; 4.5%, 100-199; 4.5%, 200-299; 73.1%, 300-399; 0.8%, 400-499; 0.4%, 500-599; 6.1%, 600-699; 5.3%, 700-799; 0.8%, 800-899 and 0.4%, 1100-1199 days. Testing this variable partly tests the validity of assuming linear growth in determining each growth rate, because if an appreciable error was so incurred, growth rates would decrease with an increase in the time between captures.

Distance upstream. Defined as the recapture location in kilometres from the mouth of the Liverpool River. Implicit in this variable is salinity, inasmuch as animals further upstream were in fresh water for longer periods of the year than those downstream. Salinity itself changes with tide and season, and measurements at any one time are of limited use in describing the salinity regime of an area.

Abnormalities. Animals with jaw abnormalities were sometimes stunted, which may reflect an inability to catch sufficient food (Webb and Messel 1977b).

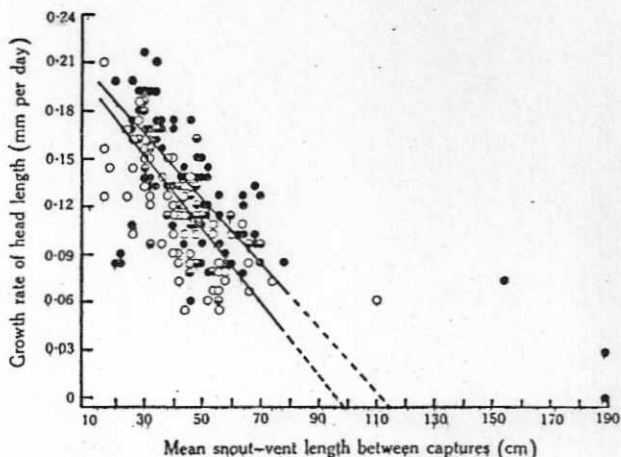


Fig. 2. Growth rates (in terms of head length) of *C. porosus*, used for the analysis of factors influencing growth (excluding the four values from specimens above 80 cm SVL). ● Males. ○ Females. ◐ Both sexes. Lines are regressions for males (upper) and females (lower) on the assumption that seasonal factors are constant (see text). Broken line indicates theoretical maximum size if growth of specimens over 80 cm SVL were to follow the exponential defined by specimens less than 80 cm SVL.

Short-term recaptures. This is distinct from the 'time' variable and refers to the few animals recaptured within 50, 100 and 200 days of release. In these animals the measurement error could be large relative to actual growth, and handling could temporarily influence feeding following release.

*Deletion of *C. porosus* over 80 cm MSVL.* From Fig. 1 it is obvious that a linear regression through the data up to 80 cm MSVL would hardly describe the growth rates of the larger animals.

Mean SVL, sex and season all accounted for significant proportions of the variation; time and distance upstream did not. There was a significant rise in explainable variation by deleting animals over 80 cm MSVL, animals with abnormalities, and animals with up to 50 days between captures. Because of the more precise measurement of HL, a further increase was obtained by expressing growth in terms of HL rather than SVL; the relationship between HL (h) and SVL (l) is essentially linear [$h = 0.89 + 0.282 l \pm 0.37$ cm; $n = 1332$; $r^2 = 0.997$; range, 12-210 cm SVL; for reverse prediction:

$l = -3.03 + 3.534 h \pm 1.32$ cm; range, 4–59 cm HL; obtained from data in Webb and Messel (1978b)].

As the season variable referred to wet and dry seasons which are not necessarily the 'cold' and 'hot' parts of the year, a further variable 'temperature', defined as the mean temperature over the growing period, was derived. Each day of the year was assigned a mean 0900-h air temperature for the month in which it fell, as follows:

	°C		°C		°C		°C
Jan.	28.0	Apr.	27.0	July	21.4	Oct.	28.0
Feb.	27.2	May	25.1	Aug.	23.2	Nov.	29.1
Mar.	27.2	June	22.9	Sept.	25.6	Dec.	28.9

The variable used was the overall daily average for the sampled growing period. Ideally, water temperature would have been used but data were not available, and air temperatures were sufficient to separate the cold from the hot parts of the year.

For the final analysis there were 229 growth records (Fig. 2) and the complete model to which they were fitted was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 (X_1 X_4) + \beta_6 (X_2 X_4) + \beta_7 (X_3 X_4) + \beta_8 (X_1 X_2) + \beta_9 (X_1 X_3) + \beta_{10} (X_2 X_3) + \beta_{11} (X_4 X_1 X_2) + \beta_{12} (X_4 X_1 X_3) + \beta_{13} (X_4 X_1 X_2 X_3),$$

where Y is growth rate of HL in millimetres $\times 10^{-2}$ per day; X_1 the mean SVL in centimetres, for the range 15–80 cm; X_2 the temperature in °C for the range 25–29°C; X_3 the season as percentage dry season for the range 35–90%; X_4 sex, with females 0 and males 1; β_0 – β_{13} the sequential order of calculated coefficients.

This model accounted for 57.6% of the variation in growth rate and indicated that several of the variables accounted for insignificant proportions of the variability. Logarithmic transformations of dependent and independent variables indicated that no transformations were required and, after several further intermediate models, a final one was obtained:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_3 + \beta_3 X_2 + \beta_4 (X_1 X_2) + \beta_5 X_4 + \beta_6 (X_1 X_4) + \beta_7 (X_3 X_4),$$

where Y and X_1 – X_4 are as above and the β subscripts are the new variable sequence. The β coefficients were: β_0 , 48.141; β_1 , -0.927; β_2 , -0.062; β_3 , -0.864; β_4 , 0.027; β_5 , 10.869; β_6 , 0.024 and β_7 , -0.0174. The model accounted for 55.4% of the variation in growth rate and the percentages of variance accounted for by each variable were: X_1 , 37.3%; X_3 , 6.9%; X_2 , 0.1%; $(X_1 X_2)$, 1.1%; X_4 , 5.6%; $(X_1 X_4)$, 1.1% and $(X_3 X_4)$, 3.3%; these percentages indicate the relative importance of each variable when fitted in the order shown.

The particular order of variables in the above model is one of several which would fit the data equally well. This one was chosen specifically so that differences in growth rate exclusively attributable to sex [X_4 , $(X_1 X_4)$, $(X_3 X_4)$] could be examined after any dependence on sex implicit in size, season and temperature had been eliminated. The percentage variances above indicate that sex *per se* remains a major variable, and thus the problem can be considered a two-group one based on sex. Given that sex is coded 0 and 1, the model can be reduced to

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_3 + \beta_3 X_2 + \beta_4 (X_1 X_2),$$

with the following coefficients and their standard deviations:

	Females	Males
β_0	48.141 ± 18.90	59.011 ± 18.23
β_1	-0.927 ± 0.45	-0.903 ± 0.45
β_2	-0.062 ± 0.03	-0.236 ± 0.03
β_3	-0.864 ± 0.66	-0.864 ± 0.66
β_4	0.027 ± 0.02	0.027 ± 0.02

The β_0 coefficients above indicate that if all other variables were equal to zero, males grow faster than females. The β_1 coefficients indicate that if all other variables were zero, growth rate decreases as size increases, the decrease being greater in females than in males. Similarly, the β_2 coefficients indicate that growth rate decreases as the percentage dry season increases, and the effect is more pronounced in males than in females.

The influence of temperature is more clearly expressed as $(\beta_3 + \beta_4 X_1) X_2$, and equals zero when MSVL \approx 32 cm. Below 32 cm MSVL, growth rate slows down as temperature increases, and above 32 cm MSVL growth rate increases as temperature increases. The temperature-size interaction, though accounting for a significant portion of the variance, did not reach statistical significance within the 80-cm MSVL upper limit of the data, thus it is possible that it is a statistical artefact. However, it could also be indicating important differences between small and large *C. porosus* and thus have considerable ecological significance; further investigation is required to determine whether the influence of temperature on growth is important in *C. porosus*.

When the sampled growing period is one year, temperature (X_2) and season (X_3) in the above equations become constants (26.12°C and 58.63% respectively), and thus the male and female growth rate equations can be reduced to:

$$Y = 21.938 - 0.222 m \text{ for females and}$$

$$Y = 22.606 - 0.198 m \text{ for males,}$$

where m is MSVL in centimetres; the pooled error (SD) calculated by comparing predicted with real values is $\approx 1.622 \times 10^{-2} h$ per day, where h is HL in millimetres. If the above equations are extrapolated to where growth rate equals zero (obtained by setting $Y = 0$), the maximum-sized male and female would be 114 and 99 cm SVL respectively, which is clearly an underestimate. Thus, the growth relationship for animals below 80 cm SVL does not account for the growth of larger specimens.

Growth Curve for *C. porosus* up to 80 cm SVL

To calculate the growth curve from the 229 values used above, MSVL (m) in the latter two equations was converted to HL (h) by the formulae given previously, and all units were converted to centimetres. Thus

$$Y = (22.6107 - 0.785 h)/1000 \text{ for females, and} \quad (1)$$

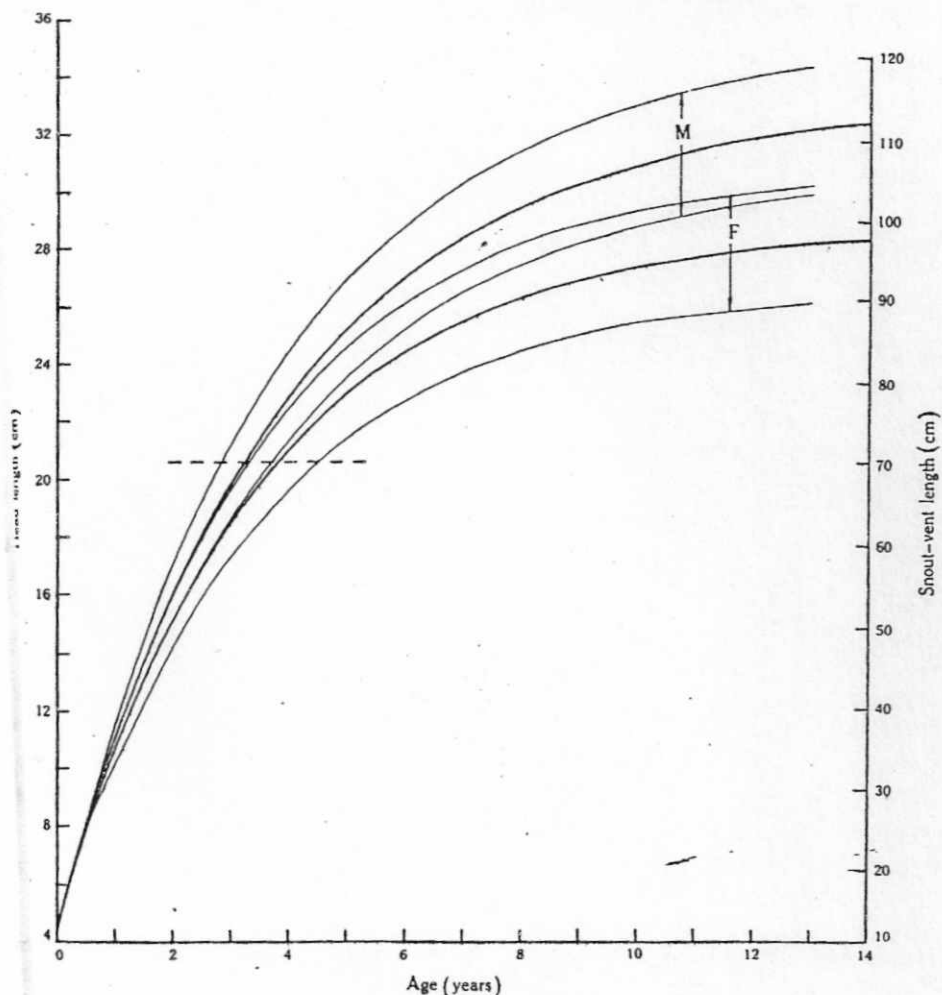
$$Y = (23.206 - 0.700 h)/1000 \text{ for males,} \quad (2)$$

where Y is growth of HL in centimetres per day rather than millimetres per day, and the SD of Y becomes 1.622×10^{-3} .

Solving the linear differential equation [since $Y = dS(t)/dt$], it can be shown that

$$S(t) = (S_m - S_0)[1 - \exp(-t/\tau)], \quad (3)$$

where $S(t)$ is S , HL in centimetres at time t in days; S_m is the theoretical maximum HL attained in centimetres, S_0 is the initial size HL in centimetres; τ is the time constant, the inverse of the slope of the growth rate-size relationship. For females, $\tau = 1/(0.785 \times 10^{-3}) = 1274$; for males, $1/(0.700 \times 10^{-3}) = 1429$.



3. Growth curve of *C. porosus* less than 80 cm SVL. The broken line represents the region in which growth in the field increases relative to that predicted from the curve. Heavy lines, means; thin lines, approximate prediction errors (see text).

The initial size, S_0 , varies between nests; the mean from five nests was 4.6 cm HL. Variation in these means could be accounted for by ± 2 weeks growth, the error matching size was considered negligible, and S_0 treated as a constant.

As mentioned previously, when growth rate Y equals zero in the growth rate-size relationship, HL equals S_m , the theoretical maximum size, or asymptote of the growth curve describing growth of *C. porosus* less than 80 cm SVL. The error on Y can be used to obtain an error approximation on $S_m(E_{s,m})$; for females $S_m = 28.82 \pm 2.07$ cm HL, and for males $S_m = 33.17 \pm 2.32$ cm HL.

To obtain an error approximation for the equations predicting either S or t , it has been assumed that the error on S_m , (E_{sm}) adequately accounts for the interrelated error on τ , thus the equation for predicting S becomes:

$$S = (S_m - S_o)[1 - \exp(-t/\tau)] + S_o \pm E_{sm}[1 - \exp(-t/\tau)], \quad (4)$$

where symbols are as above and E_{sm} is the error on S_m .

The growth curves for males and females are in Fig. 3, and the equations for predicting HL (S) of *C. porosus* less than 80 cm SVL whose ages (t) are known become:

$$S = 24.2[1 - \exp(-t/1274)] + 4.6 \pm 2.1[1 - \exp(-t/1274)] \text{ for females, and} \quad (5)$$

$$S = 28.6[1 - \exp(-t/1429)] + 4.6 \pm 2.3[1 - \exp(-t/1429)] \text{ for males.} \quad (6)$$

Where S is known and t required, the equation is:

$$t = \tau \ln[(S_m - S_o)/(S_m - S)] \pm \tau [(S - S_o)/(S_m - S_o)(S_m - S)] \cdot E_{sm}. \quad (7)$$

Formulae for converting other body measurements to HL are in Webb and Messel (1978b).

Growth Curve for *C. porosus* over 80 cm SVL

From the relationships of growth rate to size (Figs 1 and 2) it was clear that the growth rates of all *C. porosus* could not be modelled by a single straight line, which was the reason why only *C. porosus* < 80 cm SVL were examined in the previous sections. In this section, an attempt is made to construct theoretical growth curves for large *C. porosus*, i.e. in the range where there are virtually no data.

Separate straight lines which describe the approximate growth rate-size relationship in the larger animals could be included in Fig. 2, again yielding an exponential growth curve in the larger *C. porosus*, though defined by a separate curve to that of the specimens below 80 cm SVL. These straight lines would cut the X axis at the maximum size (S_m), and intersect the regression line describing growth of specimens < 80 cm SVL somewhere between 60 and 80 cm SVL (17.8 and 23.5 cm HL respectively); 70 cm SVL (20.6 cm HL) has been chosen as the estimate of the point of intersection for both males and females.

Hunters are generally of the opinion that the typical maximum size (S_m) of *C. porosus* males varies in different river systems and regions, but is usually between 4.2 and 5.0 m total length [TL is approximately twice SVL (Webb and Messel 1978b)], though some specimens exceed 6.0 m TL (Webb and Messel 1978b). In the present study, one large male (A) (3.9 m TL; 53.0 cm HL) showed no measurable growth in 3.3 y—it had presumably reached its maximum size—whereas another male (B) of the same SVL grew 2.5 cm HL (9 cm SVL) in 2.3 y and had clearly not reached its maximum size. Four HL values were chosen to estimate a range of male S_m values: 53, 65, 75 and 85 cm (approximately 187, 230, 266 and 302 cm SVL respectively).

Less information is available on the maximum size of female *C. porosus*, though hunters usually place the range between 3.2 and 3.7 m total length. A 4-m specimen was reported from Papua New Guinea (John Lever, personal communication), so the range of female S_m estimates chosen was 45, 51 and 56 cm HL (156, 179 and 199 cm SVL respectively).

Given that at 20.6 cm HL (70 cm SVL) growth rate for males is 8.79×10^{-3} cm day⁻¹ (equation 2 and Fig. 2) and at 53 cm HL (the first of the four S_m estimates for males)

growth rate equals zero, the slope of the growth rate to size relationship can be calculated as $(8.79 \times 10^{-3}) / (53 - 20.6) = 2.71 \times 10^{-4}$ cm HL daily per centimetre of HL, from which τ can be obtained (3686 days; $\tau = 1/\text{slope}$). If the estimated size at intersection had been 50 cm SVL (15 cm HL) rather than 70 cm SVL, the τ value

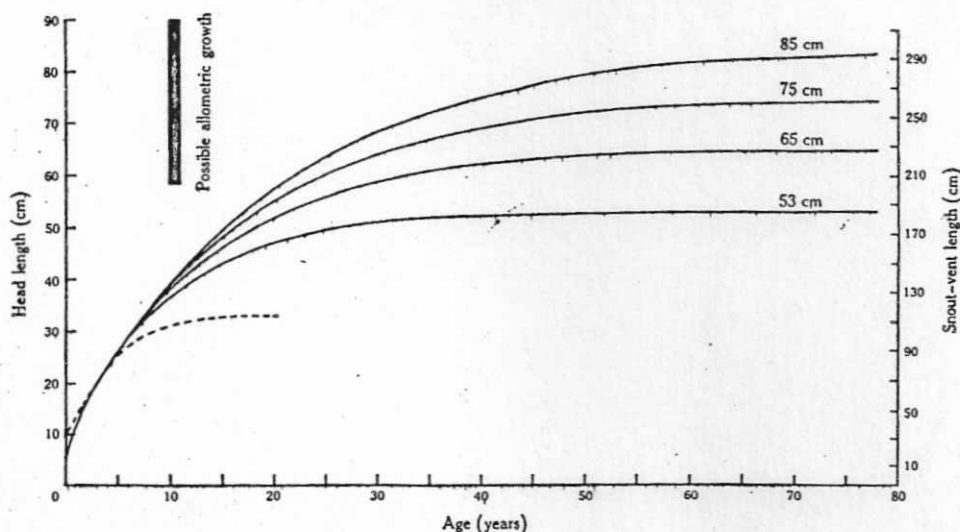


Fig. 4. Growth curves of male *C. porosus*, with theoretical maximum head lengths of 53, 65, 75 and 85 cm. The broken line indicates the hypothetical continuation of the growth of specimens below 80 cm SVL (right) and the hypothetical initiation of the curves of specimens above 80 cm SVL (left; only the 65-cm HL maximum size figured). See text for explanation of allometric growth.

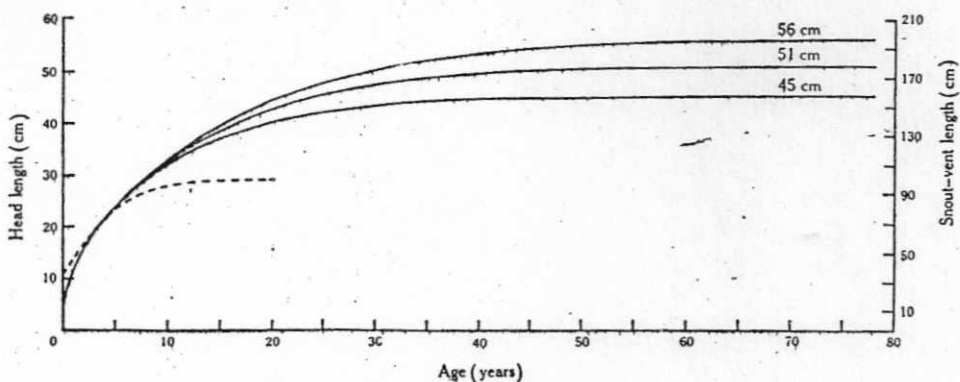


Fig. 5. Growth curves of female *C. porosus*, with theoretical maximum head lengths of 45, 51 and 56 cm. The broken line indicates the hypothetical continuation of the growth of specimens below 80 cm SVL (right) and the hypothetical initiation of the curves of specimens above 80 cm SVL (left; only the 51-cm HL maximum size figured).

would have been 3507 days, which is not appreciably different. If the SD of growth rate ($\pm 1.62 \times 10^{-3}$) was applied to the growth rate at 20.6 cm HL (i.e. to 8.79×10^{-3} cm day⁻¹ HL), τ would range between 3112 (+SD) and 4519 (-SD).

With $\tau = 3686$ days, $S_m = 53$ cm HL and the age (t) from equation 7 of a 20.6-cm

HL(S) male *C. porosus* being 1171 days, equation 3 describing the growth curve can be solved for S_0 , the theoretical size at zero time of the second growth curve; in this case it equals 8.5 cm HL.

This method has been used to derive the coefficients for the male and female S_m values chosen above; the resulting theoretical growth curves are given in Figs 4 and 5; the coefficients are in Table 1.

An actual growth record of a large *C. porosus* can be used to calculate the slope of the growth rate-size relationship (and hence τ), from which S_m and the age (t) can be estimated for that particular animal. For example, consider specimen B with a 57.1-cm HL which grew 2.5 cm HL in 2.3 years or 2.98×10^{-3} cm HL per day. The slope of the straight line expressing the growth rate-size relationship is $(8.79 - 2.98) \times 10^{-3} / (57.1 - 20.6) = 1.592 \times 10^{-4}$ cm HL daily per centimetre HL, and thus $\tau = 1 / 1.592 \times 10^{-4} = 6282$ days. Using the derived value of the slope, we may extrapolate the straight line above to the axis, yielding the value for zero growth rate, $S_m = 57.1 + (2.98 \times 10^{-3} / 1.592 \times 10^{-4}) = 75.8$ cm. S_0 was calculated as before, and the specimen's age (t) determined from the equations with the new coefficients; it equalled 21.8 y. If the growth rate at the intersection was ± 1 SD (1.622×10^{-3} cm HL per day), the age estimate (t) ranged between 20.0 and 24.1 y.

Table 1. Coefficients for growth curves in Figs 4 and 5

Formulae and explanation in text. S_m , maximum head length; S_0 , initial head length; τ , time constant

Males				Females			
svL (cm)	S_m (cm)	S_0 (cm)	τ (days)	svL (cm)	S_m (cm)	S_0 (cm)	τ (days)
<80	33.2	4.6	1429	<80	28.8	4.6	1274
>80	53.0	8.5	3686	>80	45.0	9.9	3789
>80	65.0	9.0	5051	>80	51.0	10.3	4721
>80	75.0	9.3	6189	>80	56.0	10.5	5497
>80	85.0	9.4	7327	—	—	—	—

To derive the theoretical growth curves for *C. porosus* over 80 cm svL, a linear relationship between HL and svL was assumed. However, in one large *C. porosus* examined, there was a pronounced negative allometry of HL relative to svL (Webb and Messel 1978b); this would invalidate the use of the curves with this specimen. Such 'short-headedness' is rare among *C. porosus* under 210 cm svL, though in larger specimens it could be more common. If predictions are to be made from a large animal, the proportions of that animal should be checked with those in Webb and Messel (1978b) to determine whether or not there has been allometric growth of HL. If so, the theoretical linearly related HL can be calculated for the animal and the age predicted from this. In Fig. 4 the region where allometric growth of head length could influence predictions is indicated by the vertical bar.

An example of the type of error incurred can be taken from specimen B; it appeared to have a relatively short HL, and when the measured HL's at capture and recapture were compared with the HL's estimated from its other head measurements (formulae in Webb and Messel 1978b), HL was a mean of 2.2 cm shorter than predicted at capture and 2.8 cm shorter at recapture. If the recorded growth (which is also perhaps a slight underestimate) is assigned to a corrected mean HL of 59.6 cm ($57.1 + 2.5$ cm), the mean age estimate given previously (21.8 y) increased to 23.1 y.

Discussion

Extrapolation of the exponential curve fitted to the growth data for *C. porosus* of less than 80 cm SVL predicted 114 and 99 cm as the maximum size of males and females respectively, which was clearly an underestimate for both sexes. Separate curves were then derived for *C. porosus* of more than 80 cm SVL and these additional curves provided a more realistic fit to all data. The necessity for the additional curves indicates that the growth pattern established between *C. porosus* of <80 cm SVL and their food source resulted in a predictable decline in growth rate (Fig. 2) with increased body size, and was altered by a net increase in energy gain, which reduced the rate at which growth rate was declining; such a change could be expected to be at least related to food and feeding habitats, or both, as postulated for the stunted *C. niloticus* in Lake Rudolf (Graham 1968).

Juvenile *C. porosus* in tidal rivers feed mainly on small crustaceans and insects of the water's edge (Allen 1974; Taylor 1977; personal observations), though they are adept at exploiting sporadic abundances of suitable-sized prey, for example small fish (Taylor 1977). The growth curve for animals of up to 80 cm SVL reflects such a diet, and the maximum sizes extrapolated from these curves are presumably the size at which it is no longer energetically worth while to feed on such small prey.

The diet of large *C. porosus*, although not well studied, consists of larger crabs, fish, other reptiles (including juvenile *C. porosus*), birds and mammals (Allen 1974; Taylor 1977; personal observations; information from hunters); Taylor (1977) found the remains of such prey becoming more common in *C. porosus* around 70 cm SVL. An obvious explanation of the two-curve growth model is that crocodiles gain in energy from feeding on such prey. The region of intersection of the two curves is the range of sizes at which such a gain becomes significant, the actual point of intersection being of more theoretical than practical significance.

A relative gain of energy could be achieved not only by securing larger prey, but also by developing less energetically wasteful feeding behaviour, and in this light, a positive allometry of head width to both head length and snout-vent length develops in *C. porosus* around 80 cm SVL (Kramer and Medem 1955; Webb and Messel 1978b); this has been interpreted as an adaptation towards more efficient capture of large prey (Dodson 1975; Webb and Messel 1978b).

There is thus evidence from a number of sources which points towards 70-80 cm SVL (1.4-1.6 m total length; 3.8-5.2 years old for females and 3.2-4.2 years old for males) as being a size at which *C. porosus* undergoes some basic behavioural changes in life style, the quantification of which would seem a fruitful area for future research.

The changes characterizing *C. porosus* appear to have their counterparts in other crocodylian species. In *A. mississippiensis* a steady increase in prey size accompanies increased body size (see summary by Dodson 1975), the head shows allometric growth (Mook 1921; Dodson 1975), and the growth curve (Nichols *et al.* 1976) is clearly more accurately modelled by two rather than one exponential curve. Similarly, *C. niloticus* prey size increases with body size (Corbet 1960; Cott 1961; Graham 1968), and the growth curve of a single wild specimen (Cott 1961) showed a marked increase in growth rate between 1.6 and 2.0 m total length (4-6 years of age). In *Crocodylus acutus* and *Caiman crocodilus*, the head shows a well defined allometry (Mook 1921); however, detailed studies of diet and growth are lacking.

The frequency of scarring in *C. porosus* rises sharply and significantly in the group of 70–80 cm SVL (Webb and Messel 1977b). Although this presumably indicates increased intraspecific interaction with possibly some cannibalism, but more likely social behaviour (Cott 1961), as the proximate factor, it could in part reflect the same change in life style as above.

The analysis of factors influencing the growth rate of *C. porosus* (pp. 389–90) demonstrated a significant decrease in growth rate associated with more dry season in the growing period. This seasonal effect is particularly interesting because distinct wet and dry seasons characterize many areas in which crocodiles live (see, for example, Cott 1961; Staton and Dixon 1977), and a similar seasonal effect was shown in the lizard *Anolis aeneus* (Stamps 1977). With *C. porosus*, a crocodile in a tidal river, it was not surprising to find that the wet season was associated with increased growth relative to that in the dry season. The wet season is associated with an abundance of animal and plant life, and high water levels allow crocodiles to exploit new feeding areas and at least to remain for long periods on the edge of or amongst the vegetation, in which insects and crustaceans are abundant. The greater mobility of juvenile males (Webb and Messel 1978a) could allow them to utilize new feeding areas better and give them the slightly greater seasonal effect that was found (see β_2 coefficients on p. 390). Stamps (1977) interpreted the seasonal changes in *Anolis aeneus* growth rates as an indication of food availability.

In other species of crocodylians, the seasonal effect could be reversed. For example, in the Venezuelan llanos (Staton and Dixon 1975; Lang, personal communication) water levels fall during the dry season, leaving many isolated ponds with extremely high densities of both *Caiman crocodilus crocodilus* and a major food source, catfish, *Hoplosternum* sp. In these situations, growth may be enhanced during the dry season, because food is more abundant, even though in some of these ponds food may become scarce towards the end of this season (Staton and Dixon 1975).

The interaction between temperature and growth in the present study was complicated, inasmuch as the size-temperature interaction was not significant within the 80-cm-SVL limit of the data, yet it accounted for a significant proportion of the variation within this limit. The tendency of the interaction was for crocodiles of less than 32 cm SVL to have high growth rates when temperatures were low and low growth rates when temperatures were high, with the situation reversed in large crocodiles.

'Temperature', as used above, refers to a mean air temperature derived in order to separate 'warm' from 'cold' periods of the year; its absolute value is meaningless and it is here used only for assessing the effect of gross seasonal temperature changes on growth.

From an absolute point of view, water temperature is probably far more important than air temperature in determining *C. porosus*' activity and growth. During the cooler months of the year (June, July), water temperatures are in the range 20–24°C and *C. porosus* often spend the day exposed in the sun on mudbanks, presumably trying to raise body temperatures to acceptable or preferred levels (32–33°C; Johnson

If it can be assumed that ambient temperatures during the cooler parts of the year are indeed suboptimal for *C. porosus* feeding, digestion, growth, or some combination of these, the interactive effect indicates that small crocodiles are better able to feed and grow during the cooler periods than are large crocodiles. This finding is consistent with McNease and Joanen's (1975) observations that juvenile *A. mississippiensis* 'were consistently more active over a wider range of environmental conditions than were adult alligators'; also, Pooley and Gans's (1976) observations that juvenile *C. niloticus* were 'not as sensitive to lowered body temperature' and continued to eat when adults would not. Whether or not the above results indicate that juveniles can operate over a wider range of temperatures than can adults, or alternatively that within a given climate space (Spotila *et al.* 1972) they can utilize their small body size and attain preferred temperature levels for longer periods, becomes an interesting problem for future study.

That the warmer period of the year was associated with a marked rise in the growth rates of large *C. porosus* is not surprising, but the fall in growth rate of small crocodiles cannot be readily explained; this result is thought to be more than likely a statistical artefact, and further data are required before its significance can be meaningfully discussed.

In northern Australia, *C. porosus* males and females probably mature over a range of body sizes, as do *C. niloticus* in Lake Rudolf (Graham 1968); however, with *C. porosus* there are few data on this range. The little we have is presented because it allows gross estimates of the sizes at maturity, and, by use of the growth curves, approximations of ages at maturity. However, the estimates can only be considered as broad guidelines. The testes of two males of 150 cm SVL (and a number of smaller specimens) were thin strips of tissue, clearly not the well developed ovoid structures of two larger specimens (186 and 207 cm SVL). An estimate of 160 cm SVL has been made as the male size at maturity. The tracks of crocodiles attending nests indicate mature females of between 2 and 3 m TL (1.0–1.5 m SVL) (Webb *et al.* 1977), and one individual found with six hatchlings in an isolated upstream billabong had an SVL of 100 cm. An estimate of 110 cm SVL has been chosen as the mean size at which females mature. The age of a male of 160 cm SVL would be about 16 y (by the 64-cm-HL asymptote curve; Table 1), and that of a female of 110 cm SVL, 10 y (50-cm-HL curve; Table 1).

In Lake Rudolf, maturity estimates for males and females were 25–30 and 15–18 y respectively; however, these animals were considered stunted (Graham 1968). Estimates for normal *C. niloticus* were 10 y for males and 12–15 y for females (Cott 1961; Graham 1968). Equivalent estimates for *A. mississippiensis* were 9 y for females and 7 for males (Nichols *et al.* 1976), and for *Caiman crocodilus crocodilus*, 3–4 y for females (Staton and Dixon 1977). Unfortunately, until more reliable data for *C. porosus* are available, detailed comparisons are of questionable merit.

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