



Growth Rates of Black Caiman *Melanosuchus niger* and Spectacled Caiman *Caiman crocodilus*, and the Recruitment of Breeders in Hunted Caiman Populations

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ABSTRACT

Hunted populations of black caiman Melanosuchus niger are unable to persist, but many hunted populations of spectacled caiman Caiman crocodilus appear to be maintaining their numbers. Previous authors explained these observations by noting that black and spectacled caiman differ in the length of time that individuals are highly vulnerable to hunting before they reach sexual maturity. This time period is believed to be long for black caiman, making recruitment of breeders difficult, but short for spectacled caiman, making recruitment of breeders relatively easy. Data on the growth rates of 16 black caiman and two spectacled caiman in an oxbow lake in Peru support this explanation. Furthermore, these data provide preliminary evidence that black caiman populations are even more vulnerable to extinction from hunting than previously thought.

INTRODUCTION

Commercial hunting in the Amazon basin has threatened the survival of the black caiman *Melanosuchus niger* and the spectacled caiman *Caiman crocodilus* (Groombridge & Wright, 1982; Plotkin *et al.*, 1983) but to unequal degrees (Magnusson, 1982; Rebêlo & Magnusson, 1983). The black caiman

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has been exterminated from most of its original range and is in danger of extinction, whereas the spectacled caiman remains common in many areas.

In part, this difference in the effect of hunting can be explained by the black caiman's longer history of exploitation. Commercial hide-hunting of caiman began in the 1930s (Plotkin *et al.*, 1983), and for several decades the black caiman was the preferred species. Hunters and tanners favor the black caiman because it is larger and has fewer bony plates in its skin than the spectacled caiman (Groombridge & Wright, 1982; Magnusson, 1982). The black caiman was also slaughtered by ranchers who viewed it as a threat to their cattle, and hunted by local residents as a source of meat and oil (Plotkin *et al.*, 1983).

As the black caiman became rare, however, commercial hide hunters increased their harvest of spectacled caiman (Magnusson, 1982; Rebêlo & Magnusson, 1983). Indeed, since the early 1970s the spectacled caiman has been hunted with an intensity similar to that suffered by the black caiman. Nevertheless, the spectacled caiman appears to be maintaining its numbers more effectively than the black caiman (Groombridge & Wright, 1982; Magnusson, 1982; Rebêlo & Magnusson, 1983). This observation suggests that biological, in addition to historical, factors may underlie the difference in the effect of hunting on the black and spectacled caiman (Magnusson, 1982).

Rebêlo & Magnusson (1983) argue that the most important of these biological factors is the ability of hunted caiman populations to recruit new breeders and provide evidence that hunted spectacled caiman do so much more easily than hunted black caiman. Rebêlo & Magnusson (1983) begin with an examination of skins confiscated from poachers from which they conclude that hunters preferentially harvest larger caiman. Specifically, hunters seek black caiman longer than 100 cm in total length and spectacled caiman longer than 110 cm. For both species these lengths fall below maturity levels: black caiman mature at 200 cm (Brazaitis, 1973); spectacled caiman mature at 130 cm (Staton & Dixon, 1977). Thus, Rebêlo & Magnusson (1983) note that every caiman passes through a period during which it is large enough to be a member of the most intensively hunted group but still too small to reproduce. As the length of this period for the members of a species increases, the probability that individuals of that species will breed before being killed decreases.

Calculations of the duration of the period between the entry of a caiman into the most intensively hunted group and its achievement of sexual maturity require knowledge of the caiman's growth rate. Using Magnusson's unpublished data for the spectacled caiman, Rebêlo & Magnusson (1983) estimated that members of this species grow 20–30 cm per year. Thus, after reaching 110 cm and entering the group most vulnerable to

hunting, spectacled caiman must grow another 20 cm to reach maturity, which they can do in 8–12 months. No data were available to Rebêlo & Magnusson (1983) on the growth rates of black caiman in the wild. Using data from a single captive individual (Dowling & Brazaitis, 1966) and analogies to the American alligator *Alligator mississippiensis* and the Nile crocodile *Crocodilus niloticus*, Rebêlo & Magnusson (1983) estimated that black caiman grow 30–35 cm per year. These figures imply that after entering the most intensively hunted group at 100 cm, black caiman require approximately three years of growth to reach sexual maturity. That black caiman are highly vulnerable but immature for at least two years longer than spectacled caiman suggests that it is much more difficult for hunted populations of black caiman to recruit new breeders (Rebêlo & Magnusson, 1983).

In this paper I present data on the growth of 16 black and two spectacled caiman in an oxbow lake in southeastern Peru. My data support Rebêlo & Magnusson's (1983) conclusions and suggest that black caiman take even longer than three years to grow from 100 to 200 cm. Thus populations of black caiman may be even less resistant to extinction from hunting than Rebêlo & Magnusson (1983) predict.

METHODS

Study site

My study site was Cocha Cashu, an oxbow lake located at 11°51' S, 71°19' W in the Manu National Park of Peru. The lake has a surface area of approximately 20 ha, 4000 m of shoreline, and a maximum depth of 2.5 m.

Cocha Cashu is unusual, at least by present standards, in that it contains substantial populations of both black and spectacled caiman. Based on direct nocturnal counts (Herron, 1985), I estimate that during the first year of my study the lake contained 115 black and 105 spectacled caiman. Both populations included several adults and females of both species nested in the forest near the lake (Herron *et al.*, 1990).

The region surrounding Cocha Cashu was placed under protection in 1970 and became the Manu National Park in 1973 (Terborgh, 1983). Although some caiman hunting and selective tree cutting occurred prior to 1970 (local residents, pers. comm.), the lakes and forests along the Manu River are essentially pristine. In addition to the black and spectacled caiman, Cocha Cashu supports giant otters *Pteronura brasiliensis* and large populations of fish and turtles. Detailed information about the area surrounding Cocha Cashu can be found in Terborgh (1983).

Captures and capture techniques

During June through September 1983 I caught, measured, marked and released 63 black and 35 spectacled caiman. During June through August 1984 I caught, measured, marked and released 36 black and 13 spectacled caiman. The 1984 captures included 16 black and two spectacled caiman first marked in 1983.

I caught most of the small individuals and some of the large individuals by spotlighting and noosing, as described by Chabrek (1965) and Jones (1966). I caught the rest of the small animals with baited cage traps (Herron, 1985) and the rest of the large individuals with floating set-snares (Herron, 1985) similar in design to that described by Murphy & Fendley (1973).

Marking techniques

I marked each caiman captured with two independent systems. First, I cut off certain of the cartilaginous ridges (scutes) on the dorsal side of the tail according to a numbered code (see Whitaker, 1978; Bustard & Choudhury, 1981). Second, I placed one or two numbered tags in tail scutes. Individuals under 125 cm total length received a metal tag (1005-3, #3 Fish and Small Animal Tag, National Band and Tag Co., Newport, KY) placed in the first unpaired tail scute. Individuals over 125 cm total length received a cattle ear tag (302, Perma-lok Cattle Tag, National Band and Tag Co.) placed in the first unpaired scute and a hog ear tag (C1635, Rototag, Nasco Farms, Fort Atkinson, WI) placed in the second or third unpaired scute.

Measurements and measurement error

Using a flexible tape, I measured to the nearest 0.5 cm the total length (TL) and snout-vent length (SVL, tip of snout to anterior edge of cloaca) of each animal I captured. The growth increment for each animal is the difference between the SVL at the 1984 capture and the SVL at the 1983 capture.

The magnitude of error in my measurements of growth increment can be estimated from data on eight caiman that I captured twice within 10 days. Assuming that these animals did not grow at all between captures, their 'growth increments' are entirely the result of measurement error. A regression of the absolute values of these 'growth increments' on mean SVL reveals that the measurement error (ME) is positively correlated with SVL:

$$ME = 0.021 * SVL - 0.609 \quad (r^2 = 0.951; p < 0.01)$$

For most of the 18 caiman for which I measured growth increments over long periods of time (Table 1), the measurement error, as estimated by this

regression equation, is small compared to the growth increment. One exception is the largest black caiman: its measurement error is nearly as large as the growth increment. Although I have reported the data for this animal in Table 1 and in Fig. 1, I have excluded them from all statistical analyses. However, leaving them in the analyses would not change any of my qualitative conclusions.

Conversion of SVL to TL

Rebêlo & Magnusson (1983) used measurements of TL throughout their analysis. In this paper, however, I report my measurements of growth as increments in SVL. I do so because this is the standard procedure for most studies of reptiles and because the majority of the animals for which I have growth data were missing the tips of their tails. A regression of log(TL) on log(SVL) for 44 black caiman with complete tails yields the allometric equation

$$\log(TL) = 0.965 * \log(SVL) + 0.377$$

or

$$TL = 2.382 * SVL^{0.965} \quad (r^2 = 0.998; p < 0.01)$$

Likewise, a regression of log(TL) on log(SVL) for 35 spectacled caiman with complete tails yields the equation

$$\log(TL) = 0.944 * \log(SVL) + 0.388$$

or

$$TL = 2.443 * SVL^{0.944} \quad (r^2 = 0.996; p < 0.01)$$

For comparisons of my data to Rebêlo & Magnusson's, I use these equations to convert my measurements of SVL into equivalent TLs.

Normalization of growth increments

I measured growth increments of caiman over durations ranging from 281 to 415 days (Table 1). For Fig. 1 and for analysis, I normalized the growth increments to one year between captures. I note here, however, that this is not necessarily the most appropriate treatment. Webb *et al.* (1983) found that Johnston's crocodiles *Crocodylus johnstoni* grow only during the wet season, apparently because food is scarce during the dry season. Because Webb *et al.* (1983) captured animals during successive dry seasons, every animal had the same effective growing time between measurements and the data did not have to be normalized.

I lacked sufficient data to test for a seasonal dependence of growth rate in

caiman at my study site. However, potential prey species appeared to remain abundant during the dry season, and the seasonal temperature variation at Cocha Cashu is small, with the highest and lowest mean monthly air temperatures differing by less than 3.5°C (Terborgh, 1983). Based on these considerations, I assumed that the growth of caiman was uniform throughout the year and therefore normalized my data.

RESULTS

Table 1 contains the capture dates and SVLs for the 16 black and two spectacled caiman captured in 1983 and 1984. The last two columns include the times between captures and the absolute growth increments. In Fig. 1 the growth increments are normalized to 1 year between captures and plotted as a function of initial (1983) SVL. Excluding the data on the largest animal, which may be unreliable (see section on Measurements and measurement error above), the normalized growth increments of the black caiman ranged

TABLE 1
Data on Black and Spectacled Caiman Captured in both 1983 and 1984

1983 Capture date	1984 Capture date	1983 SVL (cm)	1984 SVL (cm)	Time between captures (days)	Growth increment (cm)
<i>Melanosuchus niger</i>					
9/17	8/23	25.0	34.5	341	9.5
8/3	7/30	26.0	34.5	362	8.5
6/29	8/4	28.0	39.0	402	11.0
6/29	8/5	29.5	37.5	403	8.0
6/29	7/27	30.0	36.0	394	6.0
6/19	8/3	31.5	39.5	411	8.0
7/1	7/29	31.5	37.5	394	6.0
9/21	8/4	34.0	41.5	318	7.5
6/29	8/7	34.0	44.5	405	10.5
7/9	8/16	44.0	55.0	404	11.0
6/22	8/1	47.5	54.0	406	6.5
9/12	6/27	88.0	97.5	289	9.5
9/19	6/26	91.0	97.0	281	6.0
9/7	6/26	93.0	101.0	293	8.0
9/22	7/6	116.0	124.5	288	8.5
8/26	6/21	134.0	137.0	300	3.0
<i>Caiman crocodilus</i>					
6/29	8/17	29.5	42.5	415	13.0
6/22	8/6	34.5	45.0	411	10.5

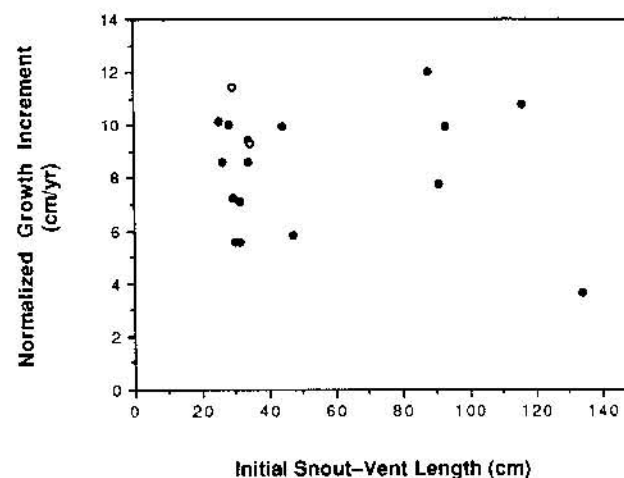


Fig. 1. Normalized one-year growth increments for black caiman (solid dots; $n = 16$) and spectacled caiman (open dots; $n = 2$) plotted as a function of initial snout-vent length.

from 5.6 to 12.0 cm/year with an average of 8.6 cm/year. The normalized growth increments of the two spectacled caiman were 11.4 and 9.3 cm/year.

Many authors fit their data on growth rates to theoretical models of animal growth (see Andrews, 1982, for a review). Herpetologists use two growth models: Bertalanffy and logistic. The former predicts that the growth rate in length will be a decreasing linear function of length, the latter that the growth rate in length will increase as the animal grows to either 50% or 63% of the maximum length (depending on whether growth is modeled as logistic by length or logistic by weight), after which it will decrease.

Although I have too few data to attempt to fit them to any of these models, a visual inspection of the black caiman results allows some qualitative conclusions to be drawn. My data on black caiman do not appear to fit the Bertalanffy model because the growth rate in length does not decrease with size. Indeed, a regression of the normalized growth increment on initial SVL demonstrates no relationship between growth increment and size ($r^2 = 0.226$; ns). This is in contrast to the findings of Webb *et al.* (1978) on saltwater crocodiles *Crocodylus porosus*, Chabreck & Joanan (1979) on American alligators, and Webb *et al.* (1983) on Johnston's crocodiles, all of whom showed that the rate of growth in a linear dimension decreases with increasing size.

Whether my data might fit a logistic model is unclear because they cover only a relatively small portion of the total size range of black caiman, spanning SVLs of 26.0–134.0 cm, whereas the total size range of black caiman runs from 14 cm (Herron *et al.*, 1990) to 250 cm or more (Brazaitis,

1973; Medem, 1981). I also lack data for black caiman with SVLs between 47.5 and 88.0 cm. For the discussion below I assumed that the rate of growth of black caiman between 47.5 and 88.0 cm was similar to that of individuals on either side of this range.

DISCUSSION

The black caiman in my sample grew considerably more slowly than Rebêlo & Magnusson's (1983) estimate of 30–35 cm/year. When my measurements of black caiman SVLs are converted into equivalent TLs (see Conversion of SVL to TL above) they yield normalized growth increments in TL ranging from 11.3 to 23.6 cm/year with an average of 17.2 cm/year (as above, I excluded the largest individual). Combined with Rebêlo & Magnusson's data on confiscated hides, these figures imply that black caiman are highly vulnerable to hunting, while still immature, for an average of 6 years with a range of 4–9 years. Even the minimum duration predicted from my data exceeded the typical duration (3 years) predicted by Rebêlo & Magnusson (1983). Thus my data support Rebêlo & Magnusson's conclusion that hunted populations of black caiman have extreme difficulty recruiting breeders.

A note of caution is in order. My data on the growth rates of black caiman represent a small sample collected over a single year from only one population and these may not for two reasons be typical of the species in general. First, there are regional and temporal variations in such factors as temperature, rainfall, productivity, and food availability, and the conditions in Cocha Cashu during 1983–84 may not have been representative of those usually experienced by black caiman. Second, black caiman are locally common in Cocha Cashu and as abundant as spectacled caiman. Although this ecological setting may have prevailed until recently, it is at present unusual for black caiman over most of their range (Groombridge & Wright, 1982; Magnusson, 1982; Plotkin *et al.*, 1983; Rebêlo & Magnusson, 1983). Locally rare black caiman may grow more rapidly than locally common animals because of reduced intraspecific competition. On the other hand, locally rare black caiman may grow more slowly because of increased interspecific competition with spectacled caiman. The latter appear to do well in habitats disturbed by man (Magnusson, 1985) and may expand their habitat use when black caiman are removed (Medem, 1971; Magnusson, 1982). Whether locally rare black caiman grow faster or slower than locally common individuals depends, in part, on the precise ecological relationship between black and spectacled caiman. This relationship needs further study

black caiman living under a variety of ecological conditions and covering long periods of time. However, to my knowledge my data are the best that are currently available.

The two spectacled caiman in my sample had normalized growth increments equivalent to increases in TL of 21.6 and 17.5 cm/year. These animals may not be appropriate for comparison because (at equivalent TLs of 59.6 and 69.1 cm in 1983) they were much smaller than 110 cm TL, the size at which spectacled caiman become highly vulnerable to hunting (Rebêlo & Magnusson, 1983). However, unless the growth rates of larger spectacled caiman in Cocha Cashu are considerably slower than those of the two individuals I sampled, my data are consistent with Rebêlo & Magnusson's conclusion that hunted spectacled caiman populations recruit breeders more easily than hunted black caiman populations.

CONCLUSIONS

Rebêlo & Magnusson (1983) offered a partial explanation for the observation that the spectacled caiman has remained relatively abundant under hunting pressure while the black caiman is in danger of extinction. Because of differences in (1) the sizes at which black and spectacled caiman become highly vulnerable to hunting, (2) the sizes at which the species mature, and (3) the rates at which they grow, hunted populations of black caiman have much greater difficulty recruiting breeders. The data presented here support this argument by showing that a sample of free-living black caiman grew even more slowly than the estimated rate used by Rebêlo & Magnusson (1983) in their analysis.

Clearly, if the black caiman is to recover from its endangered status, remaining populations will have to be strictly protected. Any measures that reduce the length of time that black caiman are highly vulnerable to hunting before maturity, or that otherwise assist the recruitment of breeders, should be helpful. One possibility is the captive rearing of juvenile caiman for release at maturity.

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