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GROWTH RATES OF *PALEOSUCHUS PALPEBROSUS* AT THE SOUTHERN LIMIT OF ITS RANGE

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Abstract: We estimated growth rates of Dwarf Caiman (*Paleosuchus palpebrosus*) with capture–recapture data from 40 individuals collected over 6 yr in streams surrounding the Brazilian Pantanal, near the southern limit of the species' distribution. Repeated recaptures of eight animals indicate that within-individual variation is much greater than between-individual variation, possibly reflecting climatic influences. Growth rates of juveniles increased linearly until individuals were about 28 cm snout–vent length (SVL), and then growth rates decreased gradually after attaining that size. The rate of decrease, however, differed between males and females. Data for 30 juveniles with known age were used to validate the growth curve based on the growth rate-on-size analysis. The length of the smallest female recorded nesting (SVL = 60 cm) allowed us to estimate the age at first reproduction to be about 8 yr for females. Our data do not support our initial hypothesis that *P. palpebrosus* would have slow growth rates and relatively old age at first reproduction, as has been suggested for *Paleosuchus trigonatus*.

Key words: Age; Body size; Brazil; Dwarf Caiman; Sexual maturity

Growth rates of crocodilians vary within and between species, and estimated times to maturity are not closely related to the maximum size of the species (Webb et al., 1978; Wilkinson and Rhodes, 1997). *Paleosuchus trigonatus* has an estimated age at maturity that is similar to that of larger species, such as *Alligator mississippiensis* (Magnusson et al., 1997). Although *P. trigonatus* lives in tropical climates, opportunities to thermoregulate are limited in tropical rain forests, and this species probably has mean body temperature lower than other studied species of crocodilians (Magnusson, 1989). This limitation could explain its low growth rate compared with that of other small crocodilians (e.g., *Caiman crocodilus*; Magnusson and Sanaiotti, 1995). *Paleosuchus palpebrosus* also probably has lower body temperatures than other crocodilians and occurs at higher altitudes than other sympatric crocodilians (Medem, 1981). Despite having an extensive range and occurring in many South American countries, *P. palpebrosus* is one of the least studied crocodilians, and most conclusions about its biology are speculative (Magnusson, 1989).

Paleosuchus palpebrosus occurs in small hillside streams that drain into the Pantanal wetlands (Campos et al., 2010). These small streams generally have fast-flowing water with mean temperatures around 20°C. No other crocodilians are resident in these streams, although *Caiman crocodilus yacare* occurs in a variety of habitats at lower elevations (Campos et al., 2005). Based on the small size of *P. palpebrosus*, what is known of the similarly sized *P. trigonatus*, and the fact that the former species occurs in habitats apparently unsuitable for other crocodilians, it might be assumed that growth rates of *P. palpebrosus* are slow compared with those of other crocodilians. However, there is currently no published information on the growth of *P. palpebrosus* in the wild.

Data on growth are used to estimate mean growth trajectories, effects of environmental factors on growth rates, age at maturity, causes of sexual dimorphism, and many other aspects of a species' biology. Growth rates can be estimated from sizes of known-age animals, mark–recapture measurements, growth annuli, or demographic structure, and there are correspondingly many methods to estimate size–age relationships (Andrews, 1982). The most appropriate analysis depends on the data available and the questions being addressed. Individuals might show marked differences in

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growth trajectories (Webb et al., 1983; Magnusson and Sanaiotti, 1995; Eaton and Link, 2011), and mean growth rates might provide uncertain estimates of growth for most individuals.

Most studies of crocodilian growth have used mark–recapture data to estimate the growth rates of different-sized individuals (Abercrombie, 1992). The relationship between size and age can be constructed by integration of the growth rate on size relationship, but this process is prone to mathematical error if the time interval between captures is long, and measurement error if the time interval is short (Andrews, 1982). Therefore, most researchers use nonlinear estimates of the integrated form of the size–age relationship to describe growth (Andrews, 1982; Brisbin et al., 1987). The integrated form of the size–age relationship is known for only a relatively small number of sigmoidal curves, however, such as those in the Richards family (Brisbin, 1990). The relationships between size and growth rate for several species of crocodilians do not fit these models, especially if data on small individuals are included (Magnusson and Sanaiotti, 1995). Furthermore, models of the growth rate-on-size relationship are needed if the objective is to determine the effects of environmental variables on growth rate.

In this study, we use mark–recapture data collected over 6 yr to describe patterns in growth rate and estimate age at first reproduction of *P. palpebrosus* in hillside streams that drain into the Brazilian Pantanal. We also evaluate the effects of seasonal variation in weather conditions and individual differences on deviations from the mean growth trajectory.

Materials and Methods

Our study was conducted between October 2005 and November 2011, in streams in the Estação Ecológica Serra das Araras (EESA; 15°37′S, 57°12′W; datum = WGS84), in the Taquari River (18°22′S, 54°36′W; datum = WGS84), in Serra da Bodoquena (20°66′S, 56°75′W), and in the Serra do Urucum (19°08′S, 57°34′W), all of which are areas surrounding the Pantanal. The streams have rocky substrates, and the water is fast flowing, similar to the streams described by Campos et al. (1995), especially during the rainy period when water levels increase quickly because of runoff from the headwaters. The dry season extends from August to October, and the rainy season usually starts in November (Soriano, 2000). Caimans were captured and recaptured by hand or with nooses, along the major streams and their tributaries in nocturnal surveys on foot in January–May and September–October each year. All caimans were individually marked with numbered plastic tags attached to the raised single tail scutes, aluminum numbered tags attached to the interdigital membrane of the left hind leg, and/or by removing the tips of single and double tail scutes in unique combinations. The snout–vent length (SVL; ± 0.1 cm) was measured, using a measuring tape, from the tip of the snout to the end of the cloacal scales, with the caiman lying on it back. The sex of caimans was recognized from the presence of penis or clitoris. We could not confidently determine the sex of juveniles under 30 cm SVL, and they were recorded as indeterminate.

The growth rate was estimated as the difference in SVL between captures divided by the interval between recaptures. We used the geometric mean SVL to illustrate the relationship between growth rate and size. The age of juveniles <30 cm SVL was estimated as the interval between the month of capture and April, the month in which individuals hatch at our study site (Campos et al., 2012). The relationship between age and size was estimated by integrating the straight-line segments using the von Bertalanffy by-length model (Andrews, 1982). Parameters describing the two straight-line segments and their intersection were estimated using breakpoint regression in the SYSTAT program (Wilkinson, 1990). Temperature (± 1°C) and rainfall (± 1 mm) data were obtained from the Corumbá Meteorological Station (18.9967°S, 57.6375°W).

Original data have been deposited in repository of Programa de Pesquisa em Biodiversidade (www.ppbio.inpa.gov.br).

Results

In 6 yr, we captured 143 Dwarf Caimans (87 in streams of the EESA, 29 in Pedras

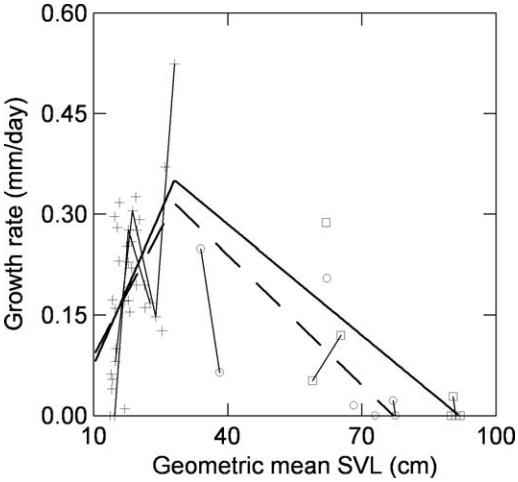

FIG. 1.—Relationship between growth rate and geometric-mean snout–vent length (between capture and recapture) of (+) juveniles of indeterminate sex, (○) female and (□) male *Paleosuchus palpebrosus* in streams around the Pantanal, Brazil.

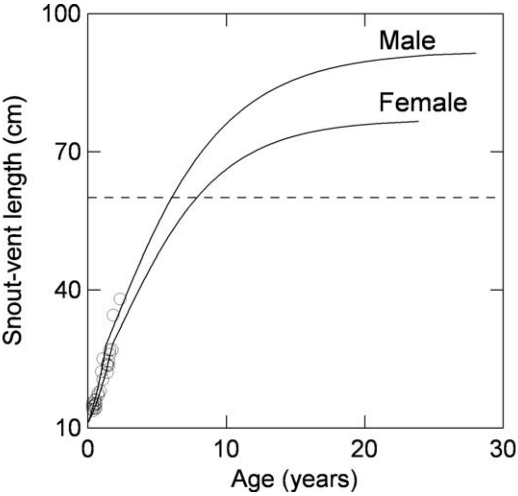

FIG. 2.—Estimated relationship between snout–vent length and age of male and female *Paleosuchus palpebrosus*. Circles represent known-age individuals and the dashed line represents the estimated size at first reproduction by females.

stream in the Serra do Urucum, 14 in Salobra stream in the Serra da Bodoquena, and 13 in the Taquari River), of which 40 were recaptured. The interval between captures varied from 50 to 1659 d. Seven individuals were recaptured twice, and one individual was recaptured three times.

The relationship between growth rate and size did not conform to any of the Richards curves, and the general form was of two straight-line segments (Fig. 1). Break-point regression, using data for unsexed individuals for both males and females, estimated the intersection of the two curves as 28.1 cm SVL for both sexes. The age-on-size relationship (Fig. 2) was estimated by integrating the relationships for the two segments of the curve, using the parameters estimated by the break-point regression. The relationship between age (yr) and SVL (cm) for males was given by the following equation:

$$\begin{aligned}\text{Age} = \{&1/-0.00152\times\log[(-5.08465-11)/\\&(-5.08465-\text{SVL})]/360\}\\&+\{1/0.00055\\&\times\log[(91.92545-28.1)/\\&(91.92545-\text{L})]/360\}\times(\text{SVL}>28.1)\end{aligned}$$

The equivalent relationship for females was given by the following equation:

$$\begin{aligned}\text{Age} = \{&1/-0.001256\times\log[(-2.91481-11)/\\&(-2.91481-\text{SVL})]/360\}\\&+\{1/0.000646\\&\times\log[(77.06656-28.1)/\\&(77.06656-\text{L})]/360\}\times(\text{SVL}>28.1)\end{aligned}$$

The last term (SVL $>$ 28.1 cm) in the equations is a conditional statement. When SVL $>$ 28.1 cm, the expression is given the value 1, and the portion of the equation following the plus sign is included in estimating the age. When SVL $\leq$ 28.1 cm, the expression is given the value 0, and that same portion of the equation does not affect the result.

Data from the recaptured subjects indicate that individuals generally have parallel growth rate-on-size trajectories (Fig. 1). However, seasonal growth makes individual growth rates fluctuate about the two straight-line segments. This fluctuation is most obvious for individuals in the first year of life, which had an N-shaped relationship, with a low initial growth rate, accelerating to an intermediate level, followed by a sharp decline during the dry season

(August–October), and then a sharp rise to attain maximum growth rate at about 28 cm SVL. A multiple regression analysis indicated that deviations from mean growth rate (DG) estimated by the growth rate-on-size relationships was affected by climatic conditions, but the high correlation ($r = 0.81$) between mean temperature (TEMP, °C) and mean rainfall (RAIN, mm) did not permit evaluation of their independent effects. Both rainfall ($DG = -0.14 + 0.0014 \times RAIN$, $r^2 = 0.34$, $P = 0.006$) and mean temperature ($DG = -0.60 + 0.023 \times TEMP$, $r^2 = 0.32$, $P = 0.006$) were related to deviations in growth rate.

Assuming a hatching date in April, the ages of 30 juveniles could be estimated with confidence. Data for those individuals indicate that the growth rate-on-age curve is a reasonable estimate for most animals, at least up to about 40 cm SVL (Fig. 2).

Discussion

Even though the asymptotic size of the species has historically been underestimated (Campos et al., 2010), *P. palpebrosus* is a relatively small species of crocodilian. It often occupies habitats that appear to be unsuitable for other crocodilians (Magnusson, 1989), and its only congener has relatively low growth rate in at least one locality (Magnusson and Lima, 1991). Therefore, we expected it to have an unusual growth rate-on-size relationship. Its growth rate accelerates linearly with size for about 16 mo, however, and then abruptly changes to a linear decline until it reaches zero, a pattern similar to that for *C. crocodilus* in Amazonia (although *C. crocodilus* reaches its peak growth rate at a smaller size; Magnusson and Sanaiotti, 1995).

It is not clear why this pattern of change in growth rate occurs, and the sharp change from a positive to a negative relationship does not correspond to the slow curvature predicted by exponential models (Van Devender, 1978). The relationship is not related to the mortality of individuals with low initial growth rates because the relationship is evident in growth curves of individuals that had multiple recaptures. The initial increase may reflect the influence of experience as the hatchlings learn to catch their prey more effectively, with the peak occurring when the individuals reach their behavioral potential and feeding is limited by external factors, such as prey availability. In contrast, older hatchlings might devote less time to feeding as they disperse away from hatchling groups and the attendant adult. Without further study, the suggested mechanisms remain speculative, but the pattern is strong and must be taken into account when estimating size–age relationships for small individuals.

Most studies of crocodilian growth have concluded that growth can be predicted by the von Bertalanffy model because of the decreasing linear relationship between size and growth rate. The von Bertalanffy model applies to size measured as mass, however, and the linear relationship of growth on length corresponds to the monomolecular model (Brisbin, 1990). Regardless of the nature of the relationship, the linear decrease may only apply to larger animals. Several species show an initial positive relationship of growth rate-on-length (Magnusson and Sanaiotti, 1995; this study), and data for other species indicate low initial growth rates (Magnusson and Lima, 1991; Moulton et al., 1999).

Individual variation in growth rates might make models based on mean growth rates inaccurate (Webb et al., 1983; Magnusson and Sanaiotti, 1995; Eaton and Link, 2011). Repeated recaptures of three animals indicate that within-individual variation is much greater than between-individual variation, however, possibly reflecting climatic influences.

Crocodilians are ectotherms and growth rates might be reduced by low environmental temperatures. Chabreck and Joanen (1979) assumed that *A. mississippiensis* grows during only 8 mo of each year because of low winter temperatures; but temperature has generally not been included in crocodilian growth models. *Paleosuchus palpebrosus* has low mean body temperature (20°C) in streams around the Pantanal in winter (Campos and Magnusson, 2013). Temperature and/or rainfall affects relative growth rates of *P. palpebrosus* in our study area but entered only as noise in our analyses of the size–age relationship. We also did not have a sufficient number of subjects with repeated recaptures to justify a hierarchical model with parameters for individual animals (Eaton and Link, 2011).

Nonetheless, data for known-age individuals indicated that our estimated size-on-age curve was reasonably accurate, at least for smaller individuals, for which individual differences in growth and seasonal effects are likely to be most pronounced.

The smallest recorded size of reproduction for female *P. palpebrosus* is 60 cm SVL (Campos et al., 2012), a size that our analysis indicates a female would attain at 8 yr of age. This might be an underestimate, however, because individuals have different growth rates and asymptotic sizes. It is not clear whether small reproductive females are slow growers that have essentially stopped growing or are young animals that will continue to grow after reproducing. Data for *A. mississippiensis* indicate that growth might be determinate (Woodward et al., 2011) and that females grow little after they start to reproduce (Chabreck and Joanen, 1979). Only long-term data on larger individuals will allow an evaluation of age at first reproduction in *P. palpebrosus*.

Analyses similar to those used in our study indicate that other small crocodilians reproduce at similar or slightly younger ages. The data reported here do not support our initial hypothesis that *P. palpebrosus* would have slow growth rates and relatively old age at first reproduction, as has been suggested for *P. trigonatus*.

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LITERATURE CITED

Abercrombie, C.L. 1992. Fitting curves to crocodilians age-size data: Some hesitant recommendations. Pp. 5–21 in Crocodiles. Proceedings 11th Working Meeting Crocodile Specialist Group/SSC/IUCN. The World Conservation Union, Gland, Switzerland.

Andrews, R.M. 1982. Patterns of growth in reptiles. Pp. 273–320 in C. Gans and F.H. Pough (Eds.), Biology of the Reptilia, Volume 12. Academic Press, USA.

Brisbin, I.L. 1990. Growth curves analyses and their applications to the conservation and captive management of crocodilians. Pp. 116–145 in Crocodiles. Proceedings of the 9th Working Meeting of Crocodile Specialist Group SSC/IUCN, Gland, Switzerland.

Brisbin, I.L., C.T. Collins, G.C. White, and D.A. McCallum. 1987. A new paradigm for the analysis and interpretation of growth data: The shape of things to come. Auk 104:552–554.

Campos, Z., and W.E. Magnusson. 2013. Thermal relations of the dwarf caiman, *Paleosuchus palpebrosus*, in a hillside stream: evidence for an unusual thermal niche among crocodilians. Journal of Thermal Biology 38:20–23.

Campos, Z., M. Coutinho, and C. Abercrombie. 1995. Size structure and sex ratio of dwarf caiman in the Serra Amolar, Pantanal, Brazil. Herpetological Journal 5:321–322.

Campos, Z., M. Coutinho, and W.E. Magnusson. 2005. Field body temperatures of caimans in the Pantanal, Brazil. Herpetological Journal 15:97–106.

Campos, Z., T. Sanaiotti, and W.E. Magnusson. 2010. Maximum size of dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807) in the Amazon and habitats surroundings the Pantanal, Brazil. Amphibia-Reptilia 31:439–442.

Campos, Z., T. Sanaiotti, F. Muniz, I. Farias, and W.E. Magnusson. 2012. Parental care in the dwarf caiman, *Paleosuchus palpebrosus* Cuvier, 1807 (Reptilia: Crocodilia: Alligatoridae). Journal of Natural History 46:2979–2984.

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

Eaton, M.J., and W.A. Link. 2011. Estimating age from recapture data: Integrating incremental growth measures with ancillary data to infer age-at-length. Ecological Applications 21:247–297.

Magnusson, W.E. 1989. *Paleosuchus*. Pp. 101–109 in P. Hall and R. Bryant (Eds.), Crocodiles: Their Ecology, Management, and Conservation. IUCN, Switzerland.

Magnusson, W.E., and A.P. Lima. 1991. The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. Journal of Herpetology 25:41–48.

Magnusson, W.E., and T.M. Sanaiotti. 1995. Growth of *Caiman crocodilus crocodilus* in central Amazônia, Brazil. Copeia 1995:498–501.

Magnusson, W.E., A.P. Lima, V.L. Costa, A.C. Lima, and M.C. Araújo. 1997. Growth during middle age in a Schneider's dwarf caiman, *Paleosuchus trigonatus*. Herpetological Review 28:183.

Medem, F. 1981. Los Crocodylia de Sur America Volume 1. Los Crocodylia de Colombia. Colciencias, Bogota. Ed. Carrera 7ª Ltda., Colombia.

Moulton, T.P., W.E. Magnusson, and M.T.Q. Melo. 1999. Growth of *Caiman latirostris* inhabiting a coastal environment in Brazil. Journal of Herpetology 33:479–484.

Soriano, B.M.A. 2000. Climatologia. Pp. 69–81 in J.S.V. Silva (Ed.), Zoneamento ambiental da borda oeste do Pantanal: Maciço do urucum e adjacências. Embrapa Comunicação e Transferência de Tecnologia, Brazil.

Van Devender, R.W. 1978. Growth ecology of a tropical lizard, *Basiliscus basiliscus*. Ecology 59:1031–1038.

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

Webb, G.J.W., S.C. Manolis, and R. Buckworth. 1983. *Crocodylus johnstoni* in the McKinlay River area, N.T, III. Growth, movement and the population age structure. Wildlife Research 10:383–401.
Wilkinson, L. 1990. SYSTAT. The System for Statistics. SYSTAT Inc., USA.
Wilkinson, P.M., and W.E. Rhodes. 1997. Growth rates of American alligators in coastal South Carolina. Journal of Wildlife Management 61:397–402.
Woodward, H.N., J.R. Horner, and J.O. Farlow. 2011. Osteological evidence for determinate growth in the American alligator. Journal of Herpetology 45:339–342.

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