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A growth model for *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) from the Rio Negro predicts growth of individuals from the Xingu River, Brazil

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Abstract

A growth model for *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) from the Rio Negro predicts growth of individuals from the Xingu River, Brazil. Patterns of growth of crocodilians vary geographically within the same species, so models developed in one area may not predict size-age relationships in others. We used recapture data for three females and six males of *Paleosuchus trigonatus* from the Belo Monte hydroelectric dam area on the Xingu River to validate a growth model developed on a tributary of the Rio Negro. Individuals were recaptured between two and 10 years after marking (2012–2022). The data indicate that the monomolecular (von Bertalanffy by length) model is adequate to model growth of intermediate size animals. Recapture of one female after eight years indicates that the Rio Negro model can be used to model growth with accuracy for individuals from the Xingu River.

Keywords: Brazilian Amazonia, Growth, Hydroelectric dam, Schneider's dwarf caiman.

Resumo

Um modelo de crescimento de *Paleosuchus trigonatus* (Crocodylia: Alligatoridae) do Rio Negro prevê o crescimento de indivíduos do rio Xingu, Brasil. Os padrões de crescimento dos crocodilianos variam geograficamente dentro da mesma espécie, de modo que os modelos desenvolvidos em uma área não preveem relações tamanho-idade em outras. Usamos dados de recaptura de três fêmeas e seis machos de *Paleosuchus trigonatus* da área da hidrelétrica de Belo Monte no rio Xingu para validar um modelo de crescimento desenvolvido em um afluente do rio Negro. Os jacarés foram recapturados entre dois e dez anos após a marcação (2012–2022). Os dados indicam que o modelo monomolecular (von Bertalanffy por comprimento) é adequado para modelar

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o crescimento de animais de tamanho intermediário, e a recaptura de uma fêmea após oito anos indica que o modelo Rio Negro pode ser usado para modelar o crescimento com razoável precisão para indivíduos do Rio Xingu.

Palavras-chave: Amazônia brasileira, Crescimento, Jacaré-coroa, Usina hidrelétrica.

Introduction

Paleosuchus trigonatus (Schneider, 1801) is a small species of crocodilian that reaches a maximum total length of about 2.3 m (Medem 1981, Campos *et al.* 2020), and is mainly encountered in Amazonian rainforest streams (Figure 1). Magnusson and Lima (1991) recorded a slower growth rate for *P. trigonatus* in Reserva Adolpho Ducke, a terra-firme area in central Amazonia, than those of other species of crocodilians. That study was based mainly on the growth of very large and very small individuals, and the authors had to assume a monomolecular model for the growth curve. One long-term recapture of an individual indicated that the equations reported in the original study can be used to predict the growth of individuals with accuracy (Magnusson *et al.* 1997). That individual was recaptured in the same study site in which the equations were developed, and it is not known whether they can be used in other areas with different ecological conditions.

Size-age relationships of crocodilians have generally been based on the relationship between growth rate and length of individuals (e.g. Magnusson and Sanaiotti 1995, Dalrymple 1996, Saalfeld *et al.* 2008, Campos *et al.* 2013) using sigmoidal growth models (Andrews 1982). Crocodilian mark-recapture studies often lack data on adults (Abercrombie 1992), but the study by Magnusson and Lima (1991) lacked information on intermediate-sized animals, which are necessary to determine the form of the growth curve.

Validation of growth models requires recapture of known-age animals after long periods, which has been done for some economically important species, such as *Alligator mississippiensis* Daudin, 1801 (Rootes *et al.* 1991, Wilkinson and Rhodes 1997, Wilkinson *et al.* 2016), and authors have reported differences in growth rates due to both environmental conditions and density-dependent processes (Abercrombie 1989, Da Silveira *et al.* 2013).

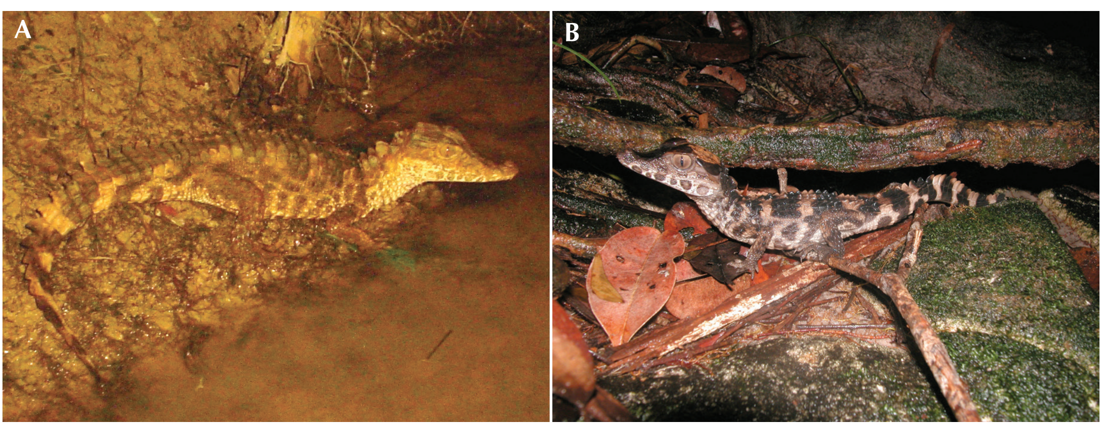

Figure 1. (**A**) Individual of *Paleosuchus trigonatus* in the Jaciparaná River, a tributary of the Madeira River, Rondônia state, northern Brazil. Photo: Zilca Campos. (**B**) Hatchling of *P. trigonatus* in the igarapé, Negro River, Amazonas state, northern Brazil. Photo: William E. Magnusson.

The study by Magnusson and Lima (1991) was undertaken in black-water streams that drain to the Rio Negro, in the Reserva Adolpho Ducke. The area was relatively undisturbed and the streams were under closed-canopy rainforest. In contrast, the Xingu River (Figure 2) has clear water and the Belo Monte dam has resulted in many areas of closed-canopy rainforest being replaced by open-water habitats (Campos *et al.* 2021). In this study, we used long-term mark-recapture data for *P. trigonatus* from the area around the Belo Monte Dam to determine whether growth of individuals in this area can be modeled by equations derived near the Rio Negro, 900 km distant. Size-age relationships of crocodilians show large differences among individuals (Eaton and Link 2011), locations, and species (Da Silveira *et al.* 2013). Whether estimated values can be considered to have sufficient precision depends on the question and whether age is being estimated from size or size is being estimated from age (Magnusson 2012). Deviations from models are presented so that researchers can draw their own conclusions.

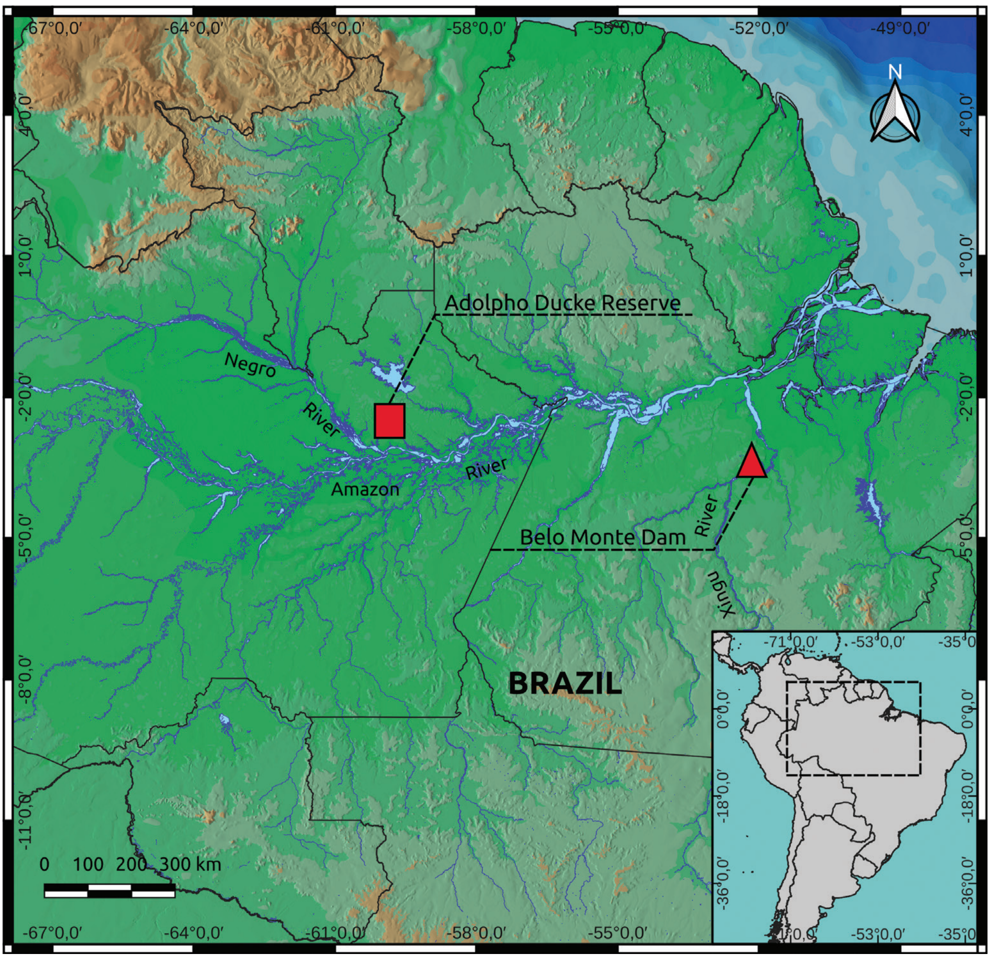

Figure 2. Two study areas in the Amazon region of Brazil: Reserva Adolpho Ducke in the Negro River (red square), and Belo Monte Dam in the Xingu River (red triangle).

Materials and Methods

We applied the growth equation derived by Magnusson and Lima (1991) for male [growth rate in cm per day (GR) = 0.02812 - 0.00035 * snout–vent length (SVL) in cm] and female (GR = 0.03946 - 0.00058*SVL) *P. trigonatus* captured around the reservoir of the Belo Monte Hydroelectric dam (Table 1) to determine how well they could predict growth of individuals from this area. In Magnusson and Lima (1991; Fig. 1), GR was erroneously given as mm per day. In the Xingu River, between 2012 and 2022, we captured and marked 300 individuals of *P. trigonatus* (hatchlings, juveniles, and adults) with numbered plastic tags, aluminum tags, and combination of tail-scute clips. Snout–vent length was measured with a graduated tape (limit of reading 1 mm) and sex identified by inspection of the cloaca at recapture.

Growth rates were estimated as the differences in SVL between captures divided by the intervals between captures. The growth-rate-on-size relationship uses mean sizes of individuals during the growth interval, and we used arithmetic means, as in Magnusson and Lima (1991). Observed data for animals from the Xingu for the size-age relationship were calculated by estimating the age at first capture based on size at first capture from the sex-specific equations given by Magnusson and Lima (1991). We then added this to the interval between captures to estimate age at recapture. Ages (A) were estimated from the equation $A = -1/r*\ln[(S_m-S_o)/(S_m-S)]$ given by Webb *et al.* (1983), where r is the slope of the growth-rate-on-size relationship, S_m = mean asymptotic SVL (68 cm for females and 80 cm for males), S_o = SVL at hatching (12 cm for both sexes), and S = present SVL. Obviously, the expected values from the equation cannot be used to validate the equation, so the usefulness of the data depends on the relative duration of the observed interval to the total age estimate. Only one female was captured at such a small size (14 cm, estimated age 2 months) that the interval

Table 1. The snout–vent length before (SVL_1 cm), after (SVL_2 cm) and mean (SVL_mean) of *Paleosuchus trigonatus* recaptured in the UHE Belo Monte region. DAYS is the interval between capture and recapture. INIT_AGE_EST is the age at first capture estimated from the relationship based on animals captured near the Rio Negro (see methods). TIME is the period between capture and recapture.

SVL_1 (cm)	SVL_2 (cm)	RATE_CM_DAY	DAYS	DATE_1	DATE_2	SEX	INIT_AGE_EST (years)	TIME (years)	SVL_MEAN (cm)
45.7	76.0	0.0120	2597	07 Feb 2014	29 Mar 2021	Male	3.23	7.12	60.85
14.0	61.0	0.0160	2920	14 Feb 2014	16 Feb 2022	Female	0.17	8.00	37.50
54.0	67.0	0.0051	2562	03 Sep 2012	10 Sep 2019	Male	4.54	7.02	60.50
41.0	45.0	0.0090	447	18 Jul 2014	05 Oct 2015	Male	2.63	1.22	43.00
44.5	55.8	0.0250	457	18 Jul 2013	20 Oct 2014	Female	4.10	1.25	50.15
39.0	54.0	0.0154	970	19 Jun 2012	13 Apr 2014	Male	2.39	2.66	46.50
45.7	79.0	0.0111	2997	07 Feb 2014	24 Apr 2022	Male	3.23	8.21	62.35
71.5	81.0	0.0031	3024	10 Jul 2013	24 Oct 21	Female	9.37	8.28	76.25
71.5	89.0	0.0052	3376	23/1/2013	24/4/2022	Male	9.82	9.25	80.25

between first and last captures (8 years) can be considered a known age. For this reason, the validation points on the size-age graph are proportional to the ratio of the known interval to the total estimated age. Larger symbols carry more independent information.

Results

Six male and three female *P. trigonatus* were recaptured after periods of between 447 and 3376 days. The data for intermediate-sized animals were consistent with the linear, decreasing, monomolecular model for both males and females, though one female recaptured after 457 days had a growth rate double that predicted by the model (Figure 3).

In general, the estimated ages were well predicted by the model (Figure 4), though the model tended to underestimate ages of larger males and females. The only known-age (to within a few months) female had an estimated age (9.8 years) close to her known age (about 8.1 years).

Discussion

Relationships between size and growth rate, and hence size and age, for crocodilians show large scatter (Da Silveira *et al.* 2013). If the variation is temporal within individuals, models of means will generally predict size-age relationships reasonably well (Magnusson 2012). If individuals differ systematically in size-specific growth rates, models of means will be very imprecise for individuals (Eaton and Link 2011), and the form of the growth model could vary among areas.

We lack repeated recaptures for intermediate-size *P. trigonatus* from any area, except for one individual from near the Rio Negro (Magnuson and Lima 1991). Long-term recaptures of intermediate-sized *P. trigonatus* are rare, because juveniles usually disperse long distances (Magnusson and Lima 1991). The data indicate that the monomolecular (linear, decreasing)

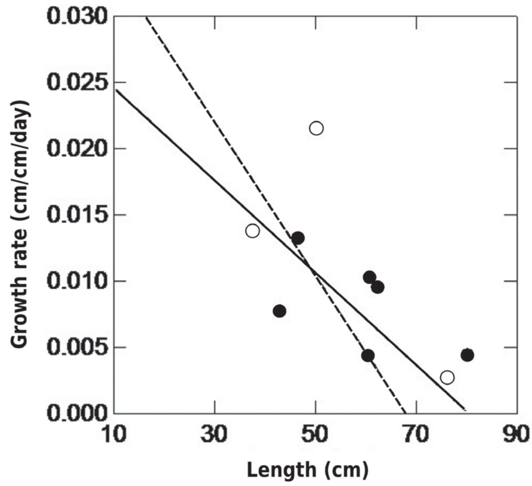

Figure 3. Growth rates of male (filled circles) and female (open circles) *Paleosuchus trigonatus* from the region of the Belo Monte Dam on the Xingu River. The lines are the relationships (males solid line, females dashed line) predicted for animals from the region of the Rio Negro.

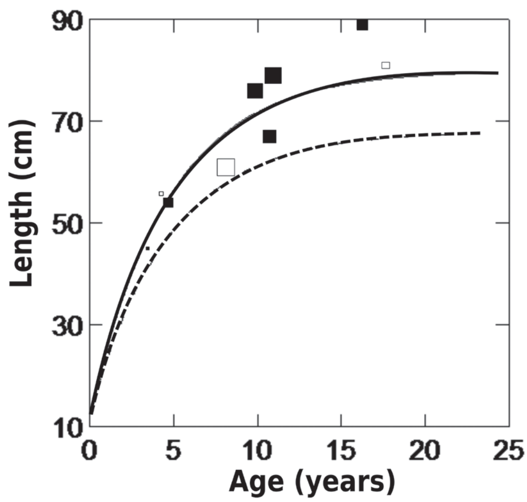

Figure 4. Estimated relationships between age and length for male (solid squares) and female (open squares) *Paleosuchus trigonatus* from the region around the Belo Monte Dam on the Xingu River. Sizes of symbols are proportional to the estimated age based on the interval between captures. The lines are the relationships (males solid line, females dashed line) predicted for animals from the region of the Negro River.

model of growth rate on size derived for individuals from closed-canopy forest near the Rio Negro can be applied to individuals from the Xingu River, and that estimates for individuals based on the reconstituted size-age relationship are at least as precise as those published for other Amazonian species (Da Silveira *et al.* 2013).

The great cost of mark-recapture studies of crocodilians carried out over their life spans (many decades) means that it is unlikely that results from longitudinal studies of individuals will be available for most species of crocodilians in the near future, especially for species such as *P. trigonatus* that are neither endangered nor have commercial value. The models for the Rio Negro tended to underestimate lengths of females and large males at a given age for individuals from the Xingu River. The growth-rate on size relationships indicate that the estimated growth rates are reasonable, but there is reason to believe that the asymptotic sizes differ between the two areas. Fifteen females and seven males captured near the Xingu River had snout-vent lengths larger than the mean for the Rio Negro study, and larger individuals have been reported from other areas (Medem 1981). Estimates based on size-age relationships will always be imprecise for large individuals, but better estimates of asymptotic size in each area may reduce bias, and these are probably easier to obtain in the medium term than multiple recaptures of medium- and large-size individuals.

Because it is unlikely that data for large numbers of animals will be available from any individual study, it is important that researchers make their data available so that the accumulated information is accessible. Also, studies with repeated captures of individuals will allow evaluation of whether individual growth rates tend to be parallel to the mean growth curve or oscillate around it. Without more data, speculation about possible differences among sites is still unwarranted, but the limited data from several areas do support the contention that, despite being of small size, the species takes several decades to reach maturity (Magnusson and Lima 1991), similar to the pattern seen in larger crocodilians.

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