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Original Article

Temperature variation in nests of *Paleosuchus palpebrosus* (Crocodylia: Alligatoridae) near the southern edge of the species´ range, Brazil

Variação da temperatura nos ninhos de *Paleosuchus palpebrosus* (Crocodylia: Alligatoridae) próximo ao limite sul da área de distribuição da espécie, Brasil

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Abstract

We monitored the temperature of seven *Paleosuchus palpebrosus* nests found on the banks of streams surrounding the Brazilian Pantanal, near the southern limit of the species´ distribution, between 2008 and 2013. The mean temperature of the nests between 45 and 68 days incubation, the presumed period of sex determination, varied between 26.1 and 31.5º C. Nest temperatures were 2 to 5°C higher than air temperatures, presumably due to metabolic heat of decay of material within the nests, but air temperature explained 10–50% of the variance in egg-chamber temperatures. The estimated incubation periods for nests from which eggs hatched were 80, 84, 86, 90 and 104 days with a mean of 89 (SD =9.23) days, though these are probably slight overestimates because eggs may have hatched in the period between inspections. For these nests, there was no significant relationship between mean temperature and incubation period ($r^2 = 0.23$, $p = 0.411$).

Keywords: nest temperature, Cuvier´s dwarf caiman, incubation period, clutch size.

Resumo

Nós monitoramos a temperatura de sete ninhos de *Paleosuchus palpebrosus* encontrados nas margens de riachos ao redor do Pantanal, próximo ao limite sul da distribuição da espécie, entre 2008 e 2013. A temperatura média dos ninhos entre 45 e 68 dias de incubação, período presumido de determinação do sexo, variou entre 26,1 e 31,5º C. As temperaturas dos ninhos foram 2 a 5°C mais altas que as temperaturas do ar, presumivelmente devido ao calor metabólico de decomposição do material dentro dos ninhos, mas a temperatura do ar explicou 10-50% da variação na temperatura da câmara de ovo. Os períodos de incubação estimados para os ninhos dos quais os ovos eclodiram foram de 80, 84, 86, 90 e 104 dias com uma média de 89 (DP = 9,23) dias, embora sejam provavelmente pequenas superestimavas porque os ovos podem ter eclodido no período entre as inspeções. Para esses ninhos, não houve relação significativa entre temperatura média e período de incubação ($r^2 = 0{,}23$, $p = 0{,}411$).

Palavras-chave: temperatura do ninho, jacaré anão de Cuvier, período de incubação, tamanho da desova.

1. Introduction

Temperatures in crocodilian nests are affected by insolation, rainfall and the metabolism of embryos (Magnusson, 1979) and this determines the sex of the embryos (González et al., 2019). For the alligatorids *Alligator mississippiensis* (Daudin, 1801), *Caiman yacare* (Campos, 1993; Lang and Andrews, 1994) and *Caiman latirostris* (Daudin 1801) (Piña et al., 2003; Piña et al., 2007; Marcó et al., 2017; González et al., 2019), the maximum proportion of males is produced at or above 32.5°C, with generally higher proportions of females at lower temperatures (29º C). The proportion of males in nests of *Paleosuchus trigonatus* (Schneider 1801) in central Amazonia peaks at about 32°C, but higher temperatures have not been recorded for this species. Like those of other crocodilians (Lang and Andrews, 1994; Piña et al., 2007; Charruau, 2012; Marcó et al., 2017; González et al., 2019), *P. trigonatus* nests in central Amazonia produce few or no males at temperatures lower than 31°C (Magnusson et al., 1990).

Within species, individuals at higher latitudes generally have lower pivotal temperatures to produce males (González et al., 2019). *Paleosuchus palpebrosus* (Cuvier 1807) occurs at much higher latitudes than *P. trigonatus*, and the species occurs at higher elevations than other

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caimans (Medem, 1981). *P. palpebrosus* from a small stream on the periphery of the Brazilian Pantanal has an unusual thermal niche and individuals maintain body temperatures that are lower than those reported for most crocodilians (Campos and Magnusson, 2013), but data on nest temperatures have been reported for only one nest of this species (Medem, 1971).

The incubation period of *P. palpebrosus* in Colombia has been estimated at over 100 days (Medem, 1971), similar to that of *P. trigonatus* in central Amazonia (Magnusson, 1989), but these studies included few nests in each locality.

We studied the nest temperatures and incubation periods of *P. palpebrosus* between 2008 and 2013 in the streams bordering the Brazilian Pantanal, at latitudes from 15º37`S to 19º13`W, which is close to the southern limit of the species´ range. In this region, the species nests during the rainy season between December and February (Campos et al., 2015), which is characterized by sporadic rainfall events and wide fluctuations in temperature.

2. Materials and Methods

Nests were located by walking along riparian forests that follow small streams in the Estação Ecológica Serra das Araras – EESA (15º37`S and 57º12`W Datum WGS 84) and the Serra do Urucum (19º13`S and 57º 23`W Datum WGS 84), near on the southern edge of the species range, Brazil. The streams have stony bottoms and clear fast-running water (Campos et al., 1995).

Temperatures in the egg cavities of seven nests, one in the EESA and six in the Serra do Urucum (2010= 3 nests, 2011= 1 nest, 2012= 1 nest, 2013 = 1 nest), were registered with data loggers (ONSET model Optic StowAway temp) programed to record temperatures at hourly intervals. Air temperature in the shade was recorded hourly with the same model of data logger in one nest in the EESA and three nests in the Serra do Urucum.

Daily rainfall in the area was obtained from the website of the Instituto Nacional de Meteorologia –INMET (https://portal.inmet.gov.br/) for Estação Corumbá, MS. One egg was collected from each nest on the day it was located and the age of the embryo estimated from the development table for *P. trigonatus* given in Ruesta (1982). Nests were inspected at about 10-day intervals to determine the date of hatching for those nests in which not all eggs were taken by predators.

We used basic statistics (Mean, standard deviation-SD) to obtain the average temperatures of each nest and the average air temperatures. Linear regression was used to verify the significance of the relationship between the average nest temperature and mean air temperature.

3. Results

The number of eggs per nest varied from 8 to 14, and embryos were estimated to be 0 to 50 days old when first found (Table 1). The estimated incubation periods for nests from which eggs hatched were 80, 84, 86, 90 and 104 days with a mean of 89 (SD =9.23) days, though these are probably slight overestimates because eggs may have hatched in the period between inspections. For these nests, there was no significant relationship between mean temperature and incubation period (r^2 = 0.23, p = 0.411). We therefore assumed, based on data from *A. mississippiensis* (Lang and Andrews, 1994), that the temperature-sensitive period for sex determination was approximately between days 48 and 68 of incubation, which corresponds to the third quarter of development for an incubation period of 89 days.

Temperatures in Nest 1 varied from 25.9°C to 28.6°C over 70 days, with a mean of 27.1°C and standard deviation (SD) of 0.73ºC. The mean temperature during the presumed period of sex determination was 26.1°C (SD = 0.88°C). Air temperature (mean = 24.4°C; S = 0.73°C) was consistently about 2.7°C below nest temperature, though nest and air temperatures tended to vary synchronously (Figure 1). Air temperature (AT) explained about 26% of the variance in egg-chamber temperatures (ET) for this nest (ET = 15,660 + 0.468*AT; N = 70; r^2 = 0.26; P < 0.001).

Temperatures in Nest 2 varied from 25.9°C to 31.3°C over 66 days, with a mean of 28.4°C (SD = 1.39 °C). The mean temperature during the presumed period of sex determination was 27.7°C (SD =1.51°C). Air temperature (mean = 26.4°C; SD = 1.51°C) was consistently about 2°C

Table 1. Egg-cavity temperatures (°C), clutch size and estimated incubation period (days) for seven nests of the *Paleosuchus palpebrosus* found in forest of streams in higher areas surrounding the Pantanal between 2008 to 2013. Nests without estimated incubation period were attacked by predators and no young hatched from these nests.

Nest	Locality	Mean temperature (°C)	Mean temperature critical period (°C)	Estimated embryo age (days)	Number of eggs	Incubation period (days)
1	Serra das Araras	27.1 ± 0.73	26.1 ± 0.88	20	14	90
2	Serra do Urucum	28.4 ± 1.39	27.7 ± 1.51	20	8	86
3	Serra do Urucum	32.0 ± 0.94	31.5 ± 0.71	10	9	-
4	Serra do Urucum	28.8 ± 0.93	28.6 ± 0.92	0	10	-
5	Serra do Urucum	28.6 ± 1.12	28.3 ± 1.10	20	8	80
6	Serra do Urucum	30.1 ± 1.03	30.3 ± 0.70	50	11	106
7	Serra do Urucum	27.4 ± 1.35	28.3 ± 1.24	40	13	84

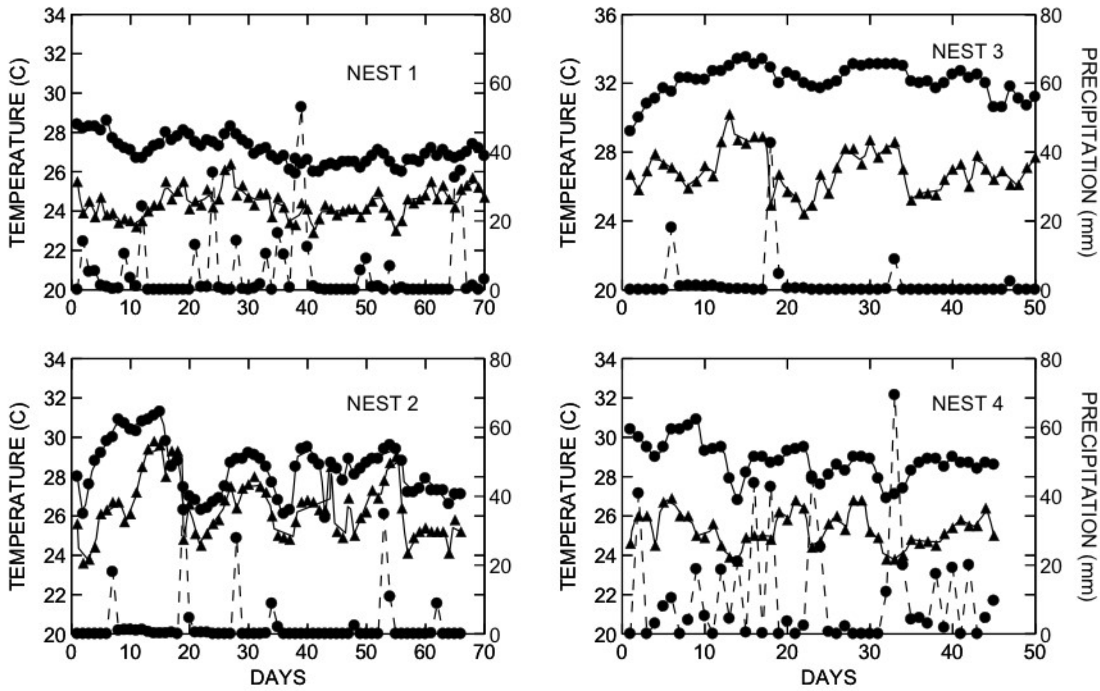

Figure 1. Egg-chamber temperature (upper filled circles), air temperature in the shade near the nest (triangle), and rainfall (lower filled circles). Nest 1 was from the ESSA in 2008; Nest 2 from the Serra do Urucum in 2010; Nest 3 from the Serra do Urucum in 2010; and Nest 4 from the Serra do Urucum in 2011.

below nest temperature, though nest and air temperatures tended to vary synchronously (Figure 1). Air temperature (AT) explained about 50% of the variance in egg-chamber temperatures (ET) for this nest (ET = 11,256 + 0.650*AT; N = 66; r^2 = 0.49; P < 0.001).

Temperatures in Nest 3 varied from 29.2°C to 33.5°C over 57 days, with a mean of 32°C (SD =0.94 °C). The mean temperature during the presumed period of sex determination was 31.5°C (SD =0.713 °C). Air temperature (mean = 27°C; SD = 1.25°C) was consistently about 5°C below nest temperature, though nest and air temperatures tended to vary synchronously (Figure 1). Air temperature (AT) explained about 10% of the variance in egg-chamber temperatures (ET) for this nest (ET = 25,423 + 0.244*AT; N = 45; r^2 = 0.105 P = 0.014).

Temperatures in Nest 4 varied from 26°C to 30.9°C over 66 days, with a mean of 28.8°C (SD = 0.930 °C). The mean temperature during the presumed period of sex determination was 28.6°C (SD = 0.92 °C). Air temperature (mean = 26.4°C; SD = 1.51°C) was consistently about 2.4°C below nest temperature, though nest and air temperatures tended to vary synchronously (Figure 1). Air temperature (AT) explained about 33% of the variance in egg-chamber temperatures (ET) for this nest (ET = 13,584 + 0.603*AT; N =45; r^2 = 0.33; P < 0.001).

The sporadic peaks in rainfall were not associated with reductions in nest temperatures (Figure 1), so the relationship between air temperatures and egg temperatures may have been due to clouds impeding insulation or due to conductance from the air.

Temperatures in the nests for which we do not have air temperatures showed similar patterns of fluctuation (Figure 2). The mean nest temperatures between 45 and 68 days incubation for these nests were 28.3° C (SD=1.12; Nest 5), 30.3°C (SD=0.70; Nest 6) and 28.3°C (SD=1.24; Nest 7).

Mean temperatures above 30°C in the presumed critical period for sex determination were only attained in two of the seven nests.

4. Discussion

The number of eggs per nest (max. = 14) in this study was much less than the number reported for Colombia and Suriname (max. = 22), and for a previous study in the same area (max. = 21) (Campos et al., 2015). As clutch size is generally related to female size in crocodilians (Campos et al., 2008), including *P. palpebrosus* (Campos et al., 2015), it is possible that the nests were made by small, presumably young, females, though we cannot discount the possibility that some eggs had been taken by predators and the females repaired the nests. Incubation period depends on nest temperature (Webb et al., 1983; Piña et al., 2003; Charruau et al., 2017), but the incubation periods we recorded were similar to or less than those

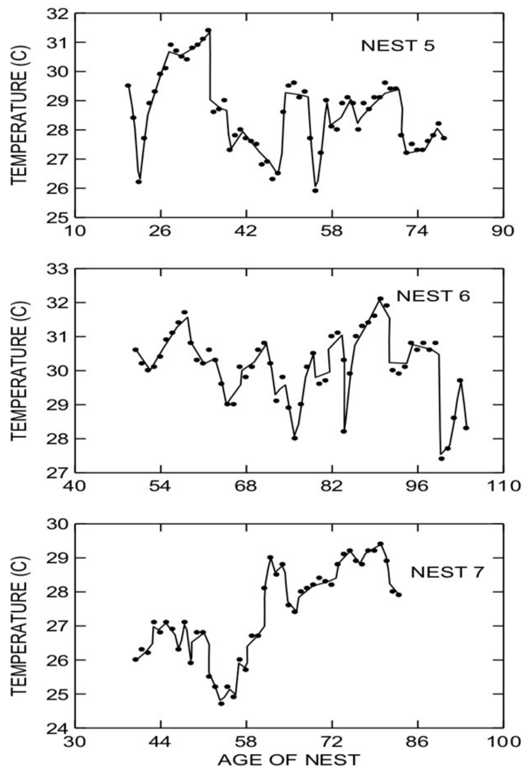

Figure 2. Egg-chamber temperatures for three nests in the Serra do Urucum, in 2010, 2012, and 2013.

reported for *P. palpebrosus* from Colombia (Medem, 1971), and for *P. trigonatus* in the Amazon (Magnusson, 1989).

Paleosuchus palpebrosus individuals in the streams around the Pantanal tend to have body temperatures lower than those of other crocodilians (Campos and Magnusson, 2013), suggesting that conditions for thermoregulation may be limiting. Nevertheless, the nest temperatures we recorded are similar to those that have been reported for *P. palpebrosus* in Colombia (Medem, 1981), *P. trigonatus* in the Amazon (Magnusson et al., 1985) and the ecologically similar crocodylid, *Osteolaemus* sp. nov. cf. *tetraspis*, in Africa (Amoah et al., 2021). In captive situations, *P. palpebrosus* eggs are incubated at a temperature between 28°C to 32°C for an incubation period of 96 to 130 days (Medem, 1971, 1972; Rugeles, 2001).

Nest temperatures in this study were 2 to 5°C higher than air temperatures, presumably due to metabolic heat of decay of material within the nests, but air temperature explained 10–50% of the variance in egg-chamber temperatures. Temperatures in nests of *P. trigonatus* in central Amazonia were significantly related to rainfall, but not air temperature (Magnusson et al., 1990). Amoah et al. (2021) also found only a weak relationship between nest and air temperatures in *Osteolaemus* sp. Nov. cf. *tetraspis*, so air temperature may have less effect on crocodilian nests in tropical climates, where it varies less. Rainfall was sporadic during our study and rainfall events did not result in detectable fluctuations in nest temperatures.

Temperature-dependent sex determination could make crocodilians sensitive to climate change, but the estimated ages of crocodilian species (Riff et al., 2010) indicates that all have survived the strong temperature fluctuations of the Quaternary. That temperatures of *P. palpebrosus* nests near the southern edge of the species distribution, where adults tend to have low body temperatures, are similar to those of tropical crocodilians indicates that climate change is unlikely to be critical for the species in most of its range.

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