



Thermal relations of dwarf caiman, *Paleosuchus palpebrosus*, in a hillside stream: Evidence for an unusual thermal niche among crocodylians

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ABSTRACT

Body temperatures of 13 *Paleosuchus palpebrosus*, 7 males and 6 females, were monitored by radio-telemetry during cold periods (dry season) and warm periods (wet and dry seasons) in a stream draining into the Brazilian Pantanal. The mass of the caimans varied from 2.5 to 20.0 kg, and snout–vent length from 47.5 to 95.0 cm. Mean monthly body temperature was 21.6 °C, and varied from 20.1 to 25.6 °C throughout the year. Body temperature was correlated with air and water temperature but did not differ between males and females. Unlike all other crocodylians investigated in detail to date, the caimans did not show evidence of attempts to obtain higher body temperatures when ambient temperatures were low, and had low and generally constant temperatures in relation to the surrounding air and water throughout the year. The caimans remained in burrows during cold periods in the dry season, which may explain why they did not seek higher temperatures. Tolerance of relatively low and constant body temperatures may be a key adaptation of species of *Paleosuchus*, allowing them to occupy environments inhospitable to other crocodylians.

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1. Introduction

Most crocodylians thermoregulate actively during cold periods by shuttling between land and water, and between places exposed to the sun and in the shade (Seebacher and Grigg, 1997; Campos and Magnusson, 2011). Some species, such as the Mugger crocodile, *Crocodylus palustris*, also use burrows as refuges during cold and dry periods (Ross et al., 1989). Body temperatures of crocodylians are generally > 30 °C during the active season, even in species that live in temperate areas. For instance, the mean body temperature of the Alligator, *Alligator mississippiensis*, is about 32 °C, varying between 29.9 and 35.6 °C during the active season (Johnson et al., 1978; Seebacher et al., 2003), and the Pantanal caiman, *Caiman crocodylus yacare*, has a mean body temperature of about 30 °C, but some individuals reach 37 °C in the warm season in the Brazilian Pantanal (Campos et al., 2005).

Secretive species, such as species of *Osteolaemus* and *Paleosuchus*, rarely show basking behavior in the wild, and little is known of their body temperatures. Schneider's dwarf caiman, *Paleosuchus trigonatus*, is restricted to tropical areas, but Cuvier's dwarf caiman, *Paleosuchus palpebrosus*, also occurs in subtropical areas, sometimes

at moderate altitudes where temperatures may be low in winter (Magnusson, 1989), and it occurs in a variety of habitats, including rivers, flooded forest, savanna streams and hillside streams (Campos et al., 2010). Medem (1967, 1981) considered *P. palpebrosus* to be resistant to low temperatures encountered at moderate altitudes in Colombia and that individuals do not bask to raise their temperatures, but he did not provide data to support his findings.

In this study, we report on the body temperatures of *P. palpebrosus* in a hillside stream draining into the Pantanal that is subject to seasonal extremes in temperature due to cold fronts originating in southern regions, and test the hypotheses that the species generally has low body temperatures in relation to available air and water temperatures, and does not thermoregulate to achieve higher body temperatures.

2. Materials and methods

2.1. Study area

The study was undertaken in Pedras Stream, in the Urucum Range, around the Pantanal, Corumbá, MS (19°08'S, 57°34'W). The stream has a rocky bottom and fast running water, similar to the streams described by Campos et al. (1995). The climate is markedly seasonal, with rain concentrated at the end of summer (October–April) and a cold dry autumn and winter

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(May–September). September temperatures fluctuate widely due to cold fronts from the south (Soriano, 2000). Data-loggers (Stow-Away temp Onset[®]), placed in the shade on the bank and at 50 cm depth in the streams were used to record air and water temperatures, respectively. The data loggers registered temperatures at intervals of 1 h throughout the period that caimans were monitored.

2.2. Radio telemetry

Dwarf caimans (7 male and 6 female) were captured on foot during the day and night using lassos attached to poles and their mouths were strapped shut with duct tape. Snout–vent length (SVL—centimeter measured to the posterior margin of the cloaca) was measured with a tape graduated in millimeter, and body mass was read from a spring balance (Pesola[®] model Macro Line 50 kg, USA) graduated in 0.5 kg. A radio transmitter (Sirtrack[®] model sensitive temperature implant, New Zealand) was surgically implanted in the abdominal cavity of each caiman under sterile conditions in the Empresa Brasileira de Pesquisa Agropecuária (Embrapa) Pantanal Wildlife Laboratory by 2 veterinarians, Leonardo Hasenclever and Walfrido Tomás, following the techniques described by Campos et al. (2005), and following ethical practices recommended by Embrapa. The radio transmitters measured approximately $3 \times 2 \times 2 \text{ cm}^3$, had a 47 cm external antenna and weighed 50 g. Transmitters were encapsulated in resin in the factory, had frequencies in the 164–166 MHz range, and a battery life of up to 8 months. Radios were calibrated against a thermometer accurately to 0.5 °C before implantation. Radio signals were detectable by a receiver (Telonics[®] TR4, USA) at distances up to 500 m, even when caimans were in burrows. A Sirtemp encoder[®] was used to decode the temperature from the radio signal. Caimans were released the same day at the site of capture and observed until they moved into the water.

In 2007, we monitored the temperature of 2 females from August to September and 4 males between April and December. In 2008, we monitored 3 females and 1 male between February and December, and in 2009 we monitored 1 male and 1 female that had been previously monitored in 2007. 1 male and 1 female were monitored in 2010 between March and June. Temperatures were recorded at hourly intervals throughout each day that caimans were monitored.

Monitoring covered periods in the day and night and cold and warm seasons. Because of the dense vegetation, it was not possible to determine whether the monitored animals were in the sun or shade when out of burrows, but some individuals were seen during the day exposed on rocks and logs.

The effect of size, mean water temperature, and sex on mean body temperature and mean amplitude of body temperature of the dwarf caimans was evaluated by analysis of covariance (ANCOVA) with sex (male and female) as a categorical variable. As the analysis was based on means, each animal contributed only one record for each variable.

3. Results

3.1. Seasonal variation in body temperature

The females monitored had SVLs between 47.5 and 76.5 cm and the males had SVLs between 59.0 and 95.0 cm (Table 1). Based on 7793 temperatures recorded at hourly intervals over several months for each caiman, and 3 consecutive days and nights for one of the caimans, the mean body temperature of the

Table 1

Snout–vent length (SVL) and body temperature (BT) of *Paleosuchus palpebrosus* in the streams draining into the Pantanal, Brazil. N=number of records of the one still seven months.

Radio	Sex	SVL (cm)	Mass (kg)	Year	Mean BT \pm SD (°C)	Min (°C)	Max (°C)	N
164,360	M	73.0	10.0	2007	24.0 \pm 2.50	18.6	30.2	291
164,660	M	95.0	20.0	2007	25.5 \pm 1.00	23.8	28.8	207
164,620	M	92.0	17.5	2007	22.3 \pm 1.91	18.1	25.7	179
164,550	M	92.0	18.0	2007	20.4 \pm 2.89	13.7	26.5	1548
164,600	M	59.0	5.0	2008	25.1 \pm 2.06	25.1	25.5	608
164,920	M	62.5	6.0	2009	23.7 \pm 2.56	17.8	28.5	283
164,300	M	90.5	15.0	2010	22.6 \pm 2.70	15.3	27.9	1021
164,420	F	75.0	9.0	2007	20.8 \pm 3.84	15.1	31.1	99
164,740	F	76.5	12.0	2007/ 2009	22.6 \pm 2.71	13.5	29.8	1541
164,940	F	47.5	2.5	2007	22.7 \pm 1.93	18.7	27.7	376
164,880	F	70.0	9.0	2008	22.8 \pm 2.27	14.6	29.9	1219
164,260	F	65.0	6.0	2008	25.4 \pm 1.10	15.6	29.1	356
164,962	F	73.0	10.0	2010	23.6 \pm 1.37	21.3	26.5	65

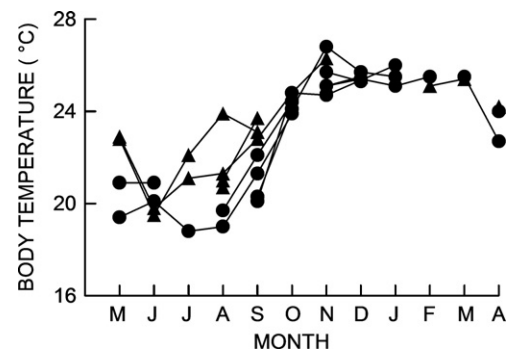


Fig. 1. Mean monthly temperature of *Paleosuchus palpebrosus* in a stream draining into the Brazilian Pantanal. Males are represented by circular symbols and females by triangular symbols. Lines connect data for the same individual.

13 caimans was 23.1 °C ($S=2.33$), with a range of 13.7–31.1 °C. Analysis of covariance indicated a significant effect of season ($P=0.000$; Fig. 1) on body temperatures, and some evidence for differences among individuals ($P=0.077$). Mean air temperature was 25.3 °C ($S=3.39$; range 17.8–31.4 °C) and mean water temperature was 21.9 °C ($S=2.72$; range 18.0–26.1 °C).

3.2. Daily variation in body temperature

Although seven individuals were seen exposed to the sun in months between July and September (it is not known if they had transmitters), we have no evidence that the animals basked to increase their temperatures. There was generally little daily variation in body temperature of caimans. Most individuals had temperatures only slightly above water temperature, and frequently less than air temperature, in the cool season (Fig. 2). This probably reflects the relatively stable thermal conditions in burrows. However, in September, when a cold front passed through the area, the temperature of 1 male (SVL=92.0 cm; mass=18 kg) changed by 6 °C within a few hours (Fig. 3).

During the warm season, body temperatures were often less than both air and water temperatures, indicating that caimans were seeking cool refuges even though they could have achieved higher body temperatures by thigmothermy without having to bask (Fig. 4).

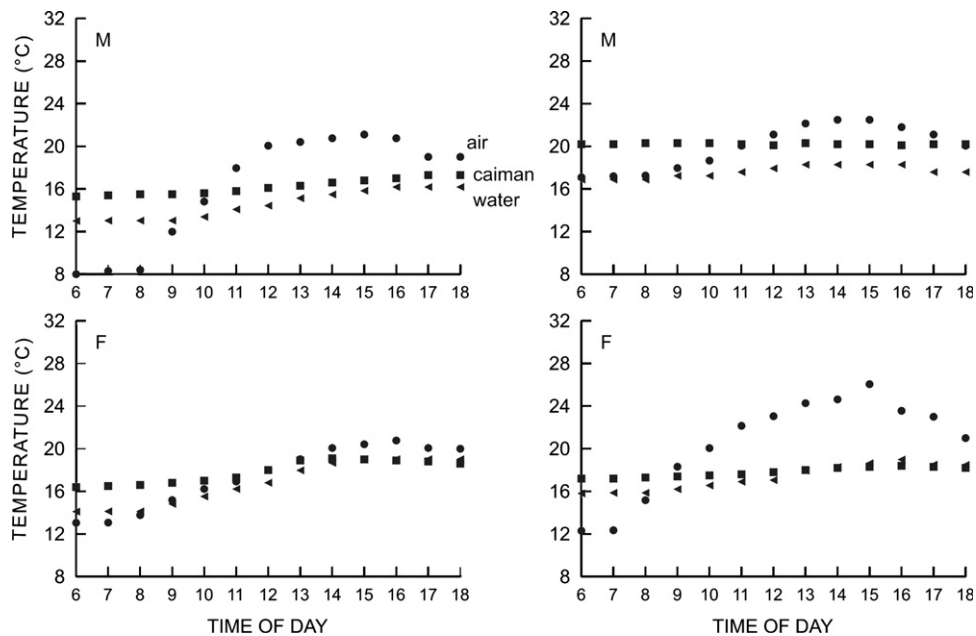


Fig. 2. Relationships between mean hourly body temperature of 4 caimans (squares), air temperature (circles) and water temperature (triangles) during daylight hours on 4 different days in the cool season (May–September). Letters indicate sex (M=male, F=female).

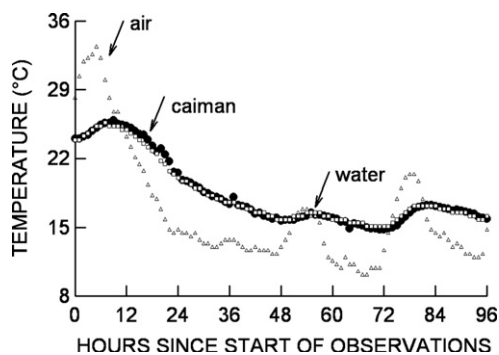


Fig. 3. Body temperature (closed circles) of a male *P. palpebrosus*, water temperature (open squares) and air temperature in the shade (open triangles) during the passage of a cold front between 7 and 11 May 2007, in a hillside stream draining into the Pantanal. The x axis represents time from the start of observations (08:00, 07 May 2007).

3.3. Effects of size and sex on temperature

Analysis of covariance indicated that mean monthly body temperature (Fig. 5a) was affected by mean ambient (water) temperature ($P=0.000$), but not by sex ($P=0.967$) or body mass ($P=0.510$). Mean daily amplitude of temperature (Fig. 5b) was not affected by sex ($P=0.836$), body mass ($P=0.495$) or mean daily temperature ($P=0.302$).

4. Discussion

The mean monthly body temperature of *P. palpebrosus* in the stream we studied varied little (20.1–25.6 °C) throughout the year and was generally close to water temperature in the stream. The Pantanal caiman, *C. crocodilus yacare*, also has body temperatures that approximate water temperature in the warm season, but body temperatures of Pantanal caimans are often considerably

higher than water temperatures in the cold season, even though they rarely exceed air temperature (Campos et al., 2005).

Body temperatures of *P. palpebrosus* in the Pedras Stream were often higher than water temperatures and much less variable than air temperatures, possibly reflecting their use of terrestrial burrows. Use of burrows should be equally effective for small and large caimans and, unlike Pantanal Caiman, we detected no relationship between caiman size and amplitude of daily fluctuations in body temperature of *P. palpebrosus*.

Crocodylians occur in cold climates, but they are generally inactive during the coldest months of the year, and attain relatively warm body temperatures when active by shuttling between air and water or by basking (Lang, 1987; Downs et al., 2008). Most species do not occur in environments that have temperatures that are constantly below about 25 °C. However, *P. trigonatus* occurs in tropical rainforest streams that have water temperatures ~25 °C, and where opportunities to bask are limited (Magnusson, 1989; Magnusson and Lima, 1991). *P. palpebrosus* occurs at higher altitudes than other sympatric crocodylians, where water temperatures are generally cool and constant. Medem (1967) hypothesized that it can do this because individuals are tolerant of low body temperatures rather than being able to main high body temperatures by thermoregulation, and our data support this hypothesis.

There are more sympatric crocodylians (generally 3–4) throughout the distribution of the genus *Paleosuchus* than in most other regions of the world (generally 1–2). Magnusson (1989) hypothesized that the niche of *P. trigonatus* differs from that of other crocodylians because temperatures in its main habitat are moderate, relatively invariant, and opportunities to bask are limited, but provided no data on body temperatures. It is likely that the thermal niche of *Paleosuchus* is also different from that of other crocodylians, and that both species of this genus are able to occupy environments in which opportunities to thermoregulate are too limited for other crocodylians. West African *Osteolaemus* is morphologically similar, occupies similar habitats to those of *Paleosuchus* (Magnusson, 1985), and 3–4 broadly sympatric species of crocodylians occur within the range of *Osteolaemus*. It is

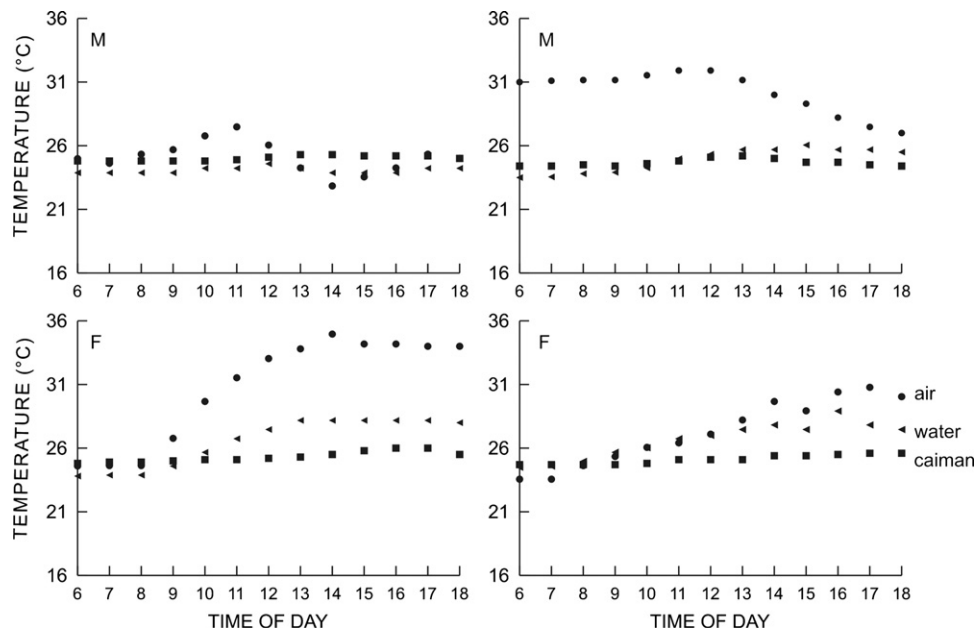


Fig. 4. Relationships between mean hourly body temperatures of 4 caimans (squares), air temperature (circles) and water temperature (triangles) during daylight hours on 4 different days in the warm season (October–April). Letters indicate sex (M=male, F=female).

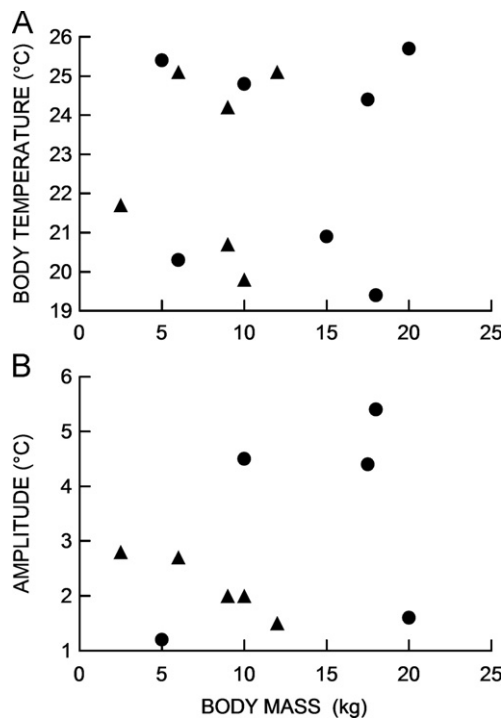


Fig. 5. Mean body temperature (a) and mean daily amplitude of temperature (b) of male (circles) and female (triangles) *P. palpebrosus* in relation to body mass. Each symbol represents a different animal.

likely that members of that genus are also tolerant of low and relatively constant body temperatures.

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References

- Campos, Z., Coutinho, M., Abercrombie, C., 1995. Size structure and sex ratio of dwarf caiman in the Serra Amolar, Pantanal. *Braz. Herpetol. J.* 5, 321–322.
- Campos, Z., Coutinho, M., Magnusson, W.E., 2005. Field body temperatures of caimans in the Pantanal. *Braz. Herpetol. J.* 15, 97–106.
- Campos, Z., Sanaiotti, T., Magnusson, W.E., 2010. Maximum size of dwarf caiman, *Paleosuchus palpebrosus* (Cuvier, 1807) in the Amazon and habitats surrounding the Pantanal. *Braz. Amphib. Reptiles* 31, 439–442.
- Campos, Z., Magnusson, W.E., 2011. Emergence behaviour of yacare caimans (*Caiman crocodilus yacare*) in the Brazilian Pantanal. *Herpetol. J.* 21, 91–94.
- Downs, C.T., Greaver, C., Taylor, R., 2008. Body temperatures and basking behaviour of Nile crocodile (*Crocodilus niloticus*) during winter. *J. Therm. Biol.* 33 (3), 185–192.
- Johnson, C.R., Voigt, W.G., Smith, E.N., 1978. Thermoregulation in crocodylians—III thermal preferences, voluntary maxima, and heating and cooling rates in the American alligator, *Alligator mississippiensis*. *Zool. J. Linn. Soc.* 62, 179–188.
- Lang, J.W., 1987. Crocodylian behaviour: implications for management. In: Webb, G.J., Manolis, S.C., Whitehead, P.J. (Eds.), *Wildlife Management: Crocodiles and Alligators*. Surrey Beatty and Sons Pty Limited., Chipping Norton, Australia, pp. 301–317.
- Magnusson, W.E., 1985. Habitat selection, parasites and injuries in Amazonian crocodylians. *Amazoniana* 9, 193–204.
- Magnusson, W.E., 1989. *Paleosuchus*, crocodiles: their ecology, management, and conservation, A Special Publication of the IUCN/SSC Crocodile Specialist Group. IUCN, Gland, Switzerland, pp. 168–175.
- Magnusson, W.E., Lima, A.P., 1991. The ecology of a cryptic predator, *Paleosuchus trigonatus*, in a tropical rainforest. *J. Herpetol.* 25, 41–48.
- Medem, F., 1967. El genero *Paleosuchus* en Amazonia. *Atas Simpósio Biota Amazonica* 3, 141–162. (Limnologia).
- Medem, F., 1981. In: Colciencias (Ed.), *Los Crocodylia de Sur America*. Los Crocodylia de Colombia, vol. 1. Carrera 7a Ltda, Bogota.
- Ross, C.A., Garnett, S., Pyrzakowshi, T., 1989. *Crocodiles and Alligators, An Illustrated Encyclopedic Survey by International Experts*. Meerhust Press, London.
- Seebacher, F., Grigg, G.C., 1997. Patterns of body temperature in wild freshwater crocodiles, *Crocodylus johnstoni*: thermoregulation versus thermoconformity, seasonal acclimatization, and effect of social interactions. *Copeia* 3, 549–557.
- Seebacher, F., Elsey, R.M., Trosclair III, P.L., 2003. Body temperature null distributions in reptiles with nonzero heat capacity: seasonal thermoregulation in the American alligator (*Alligator mississippiensis*). *Physiol. Biochem. Zool.* 76 (3), 348–359.
- Soriano, B.M.A., 2000. Climatologia, in: Silva, J.S.V. (Ed.), *Zoneamento ambiental da borda oeste do Pantanal: maciço do Urucum e adjacências*, Embrapa Comunicação e Transferência de Tecnologia, Brasília, pp. 69–81.