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Thermoregulation in captive broad-snouted caiman (*Caiman latirostris*)

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Abstract

Background: Crocodylians are ectothermic animals. For this reason, the environmental temperature has substantial effects on their physiology and behavior. The thermoregulatory behavior of these animals involves the selective use of different types of environments. This behavior enables them to reach the temperature level for their metabolic activities. This study aimed to determine the influence of sex, body size, and reproductive stage on the body temperature (T_b) of adult broad-snouted caiman (*Caiman latirostris*) in captivity. Thermal sensors were surgically implanted in the peritoneal cavity of 16 adult females and 4 adult males and programmed to register T_b hourly during 6 months.

Results: The diel T_b pattern of the broad-snouted caiman reflected the variation among the microenvironmental temperatures used by the species (water surface, pool bottom, and ground). The sex of the animals had influence on their T_b , but body size did not. Reproductive females had higher T_b than non-reproductive females during October to early November. It is possible that this difference is a result of the ovulation period of the species. Sick animals appeared to show behavioral fever.

Conclusions: The results of the present study suggest that several factors can affect the T_b of adult broad-snouted caiman in captivity. Future studies should focus on the possible effect of thermoregulatory behavior on individuals' growth rate and reproductive performance.

Keywords: Crocodylians; Body temperature; Ovulation; Social behavior; Behavioral fever; Reproduction

Background

Crocodylians are ectothermic animals. For this reason, environmental temperature has substantial effects on their physiology and behavior (Pough et al. 2003). In crocodylians, the main source of heat is solar radiation, but heat conduction from the substrate may also play a fundamental role in behavior (Sajdak and Molina 1992). Body temperature (T_b) depends on three basic components: behavioral (physical movement to increase or decrease exposure to thermal environmental energy), physiological (organic variations, for example, changes in blood flow), and genetic (medium- and long-term changes, for example, changes in hormone level) (Silva 2000).

The thermoregulatory behavior of these animals involves different uses of the available environments (Asa et al. 1998; Fincatti and Verdade 2002; Fish and Cosgrove 1987; Seebacher et al. 1999; Verdade et al. 2006). This behavior enables them to reach a T_b for their metabolic activities (Seebacher and Franklin 2005; Smith et al. 1978). In this context, the aquatic environment is extremely important (Brandt and Mazzotti 1990). Caimans (*Caiman* spp.) are able to maintain their T_b up to 4°C above water temperature with only their backs out of the water (Diefenbach 1975a; Fincatti and Verdade 2002). The presence of osteoderms (dense bony plates derived from the skin) in the crocodylians facilitates this process because small holes filled with arterioles can absorb heat and carry it to other parts of the body (Seidel 1979).

T_b can influence diverse ecophysiological aspects of crocodylians (Lang 1987), including growth rate. Food consumption and growth rate were higher in American alligators (*Alligator mississippiensis*) maintained at 32°C than in animals kept at 28°C (Staton et al. 1992). Broad-

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Table 1 Composition of experimental groups

Enclosure	M/F	Individuals
ARN1	1:4	USP 123 (F)
		USP 124 (M)
		USP 126 (F)
		USP 127 (F)
		USP 128 (F)
ARN2	1:4	USP 113 (F)
		USP 114 (M)
		USP 116 (F)
		USP 117 (F)
		USP 121 (F)
ARN3	1:4	USP 115 (F)
		USP 118 (F)
		USP 119 (F)
		USP 120 (M)
		USP 122 (F)
ARN4	1:4	USP 125 (M)
		USP 129 (F)
		USP 130 (F)
		USP 131 (F)
		USP 132 (F)

F, females; M, males.

snouted caiman (*Caiman latirostris*) hatchlings when maintained at 34°C showed relatively high values of growth rate and weight gain (Vianna 1995). Pantanal caiman (*Caiman crocodilus yacare*) hatchlings kept at 32°C showed higher growth rates than individuals maintained at 28°C (Miranda et al. 1999).

Environmental temperature can also affect food consumption in broad-snouted caiman (Larriera et al. 1990;

Verdade 1992a, b). Seasonal variations in temperature can act directly to change the food consumption in American alligators (Coulson and Hernandez 1983). Furthermore, in crocodylians, the rate of food digestion in the gastrointestinal tract depends on T_b (Diefenbach 1975a, b; Vianna et al. 1995).

Social behavior in crocodylians can directly influence thermoregulatory behavior. Social dominance can be related to habitat use and to the resources available in the habitat (Alcock 1993; Krebs 1985; Krebs and Davis 1991). Sajdak and Molina (1992) report that the presence of dominant animals in one location may make other individuals occupy locations that are less adequate from a thermoregulatory standpoint perspective. A variety of evidence shows that territorial behavior in crocodylians is expressed on the margins of a water body and not necessarily in its interior (Lang 1987, 1989; Verdade 1992b; Verdade et al. 2006). The margins are the area where animals primarily sunbathe (Ayarzaguen 1983; Molina and Sajdak 1993) and spend time during the day (Verdade et al. 2006).

The present study aimed to determine the pattern of T_b variation in adult broad-snouted caiman in captivity and its relationship with sex, body size, and reproductive status. Such information is important for the management of individuals in breeding farms, as well as for the understanding of reproduction in wild individuals.

Methods

Data were collected in the captive colony of the broad-snouted caiman at the Laboratório de Ecologia Animal of the Universidade de São Paulo (Brazil) between August 2000 and January 2001. The facilities consisted of four 9 × 10 m modules, each containing a 4 × 6 m pool (1 m deep) and five 2 × 2 m nesting areas. The

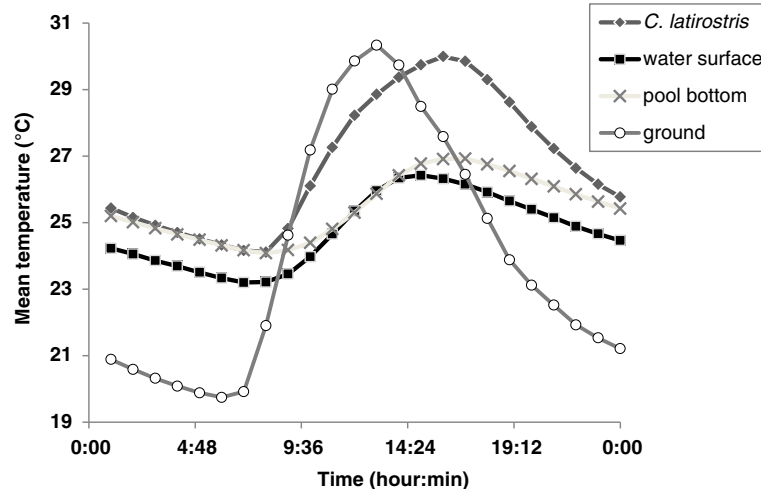


Figure 1 Mean temperature variation of broad-snouted caiman and different microhabitats of the animals' facilities.

Table 2 Statistical values of the relationship between body temperature and body size in captive adult broad-snouted caiman

	Mean temperature		Minimum temperature		Maximum temperature	
	SVL	Body mass	SVL	Body mass	SVL	Body mass
Aug. 10 to 20, 2000	$p = 0.325; S = 1.1; r^2 = 6.5\%$	$p = 0.232; S = 1.1; r^2 = 9.4\%$	$p = 0.427; S = 1.2; r^2 = 4.3\%$	$p = 0.427; S = 1.2; r^2 = 4.3\%$	$p = 0.271; S = 1; r^2 = 8\%$	$p = 0.271; S = 1; r^2 = 8\%$
Aug. 21 to 31, 2000	$p = 0.247; S = 0.7; r^2 = 8.8\%$	$p = 0.460; S = 0.7; r^2 = 3.7\%$	$p = 0.193; S = 1.1; r^2 = 11\%$	$p = 0.193; S = 1.1; r^2 = 11\%$	$p = 0.544; S = 0.7; r^2 = 2.5\%$	$p = 0.544; S = 0.7; r^2 = 2.5\%$
Sept. 1 to 10, 2000	$p = 0.789; S = 0.8; r^2 = 0.5\%$	$p = 0.995; S = 0.8; r^2 = 0\%$	$p = 0.299; S = 0.2; r^2 = 7.2\%$	$p = 0.299; S = 0.2; r^2 = 7.2\%$	$p = 0.140; S = 0.6; r^2 = 13.9\%$	$p = 0.140; S = 0.6; r^2 = 13\%$
Sept. 11 to 20, 2000	$p = 0.373; S = 0.6; r^2 = 5.3\%$	$p = 0.325; S = 1.1; r^2 = 6.5\%$	$p = 0.536; S = 0.4; r^2 = 2.6\%$	$p = 0.536; S = 0.4; r^2 = 2.6\%$	$p = 0.714; S = 0.7; r^2 = 0.9\%$	$p = 0.714; S = 0.7; r^2 = 0.9\%$
Sept. 21 to 30, 2000	$p = 0.264; S = 0.6; r^2 = 8.2\%$	$p = 0.247; S = 0.7; r^2 = 8.8\%$	$p = 0.858; S = 0.4; r^2 = 0.2\%$	$p = 0.858; S = 0.4; r^2 = 0.2\%$	$p = 0.580; S = 0.9; r^2 = 2.1\%$	$p = 0.580; S = 0.9; r^2 = 2.1\%$
Oct. 1 to 10, 2000	$p = 0.539; S = 0.6; r^2 = 2.6\%$	$p = 0.789; S = 0.8; r^2 = 0.5\%$	$p = 0.363; S = 0.5; r^2 = 5.5\%$	$p = 0.544; S = 0.5; r^2 = 5.5\%$	$p = 0.473; S = 0.9; r^2 = 3.5\%$	$p = 0.473; S = 0.9; r^2 = 3.5\%$
Oct. 11 to 20, 2000	$p = 0.278; S = 0.6; r^2 = 7.8\%$	$p = 0.373; S = 0.6; r^2 = 5.3\%$	$p = 0.903; S = 0.8; r^2 = 0.1\%$	$p = 0.903; S = 0.8; r^2 = 0.1\%$	$p = 0.911; S = 1; r^2 = 0.1\%$	$p = 0.911; S = 1; r^2 = 0.1\%$
Oct. 21 to 31, 2000	$p = 0.195; S = 0.7; r^2 = 10.9\%$	$p = 0.264; S = 0.6; r^2 = 8.2\%$	$p = 0.316; S = 0.7; r^2 = 6.7\%$	$p = 0.316; S = 0.7; r^2 = 6.7\%$	$p = 0.059; S = 0.8; r^2 = 21.8\%$	$p = 0.059; S = 0.8; r^2 = 21\%$
Nov. 1 to 10, 2000	$p = 0.192; S = 0.9; r^2 = 11.1\%$	$p = 0.539; S = 0.6; r^2 = 2.6\%$	$p = 0.225; S = 0.9; r^2 = 9.6\%$	$p = 0.225; S = 0.9; r^2 = 9.6\%$	$p = 0.295; S = 1.1; r^2 = 7.3\%$	$p = 0.295; S = 1.1; r^2 = 7.3\%$
Nov. 11 to 20, 2000	$p = 0.211; S = 1; r^2 = 10.2\%$	$p = 0.278; S = 0.6; r^2 = 7.8\%$	$p = 0.858; S = 1.1; r^2 = 0.2\%$	$p = 0.858; S = 1.1; r^2 = 0.2\%$	$p = 0.230; S = 1.2; r^2 = 9.5\%$	$p = 0.230; S = 1.2; r^2 = 9.5\%$
Nov. 21 to 30, 2000	$p = 0.225; S = 1; r^2 = 9.7\%$	$p = 0.195; S = 0.7; r^2 = 10.9\%$	$p = 0.625; S = 1.1; r^2 = 1.6\%$	$p = 0.625; S = 1.1; r^2 = 1.6\%$	$p = 0.265; S = 1.4; r^2 = 8.2\%$	$p = 0.265; S = 1.4; r^2 = 8.2\%$
Dec. 1 to 10, 2000	$p = 0.245; S = 1.1; r^2 = 8.9\%$	$p = 0.192; S = 0.9; r^2 = 11.1\%$	$p = 0.284; S = 1.2; r^2 = 7.6\%$	$p = 0.284; S = 1.2; r^2 = 7.6\%$	$p = 0.333; S = 1.4; r^2 = 6.2\%$	$p = 0.333; S = 1.4; r^2 = 6.2\%$
Dec. 11 to 20, 2000	$p = 0.251; S = 1.2; r^2 = 8.7\%$	$p = 0.211; S = 1; r^2 = 10.2\%$	$p = 0.437; S = 1.2; r^2 = 4.1\%$	$p = 0.437; S = 1.2; r^2 = 4.1\%$	$p = 0.471; S = 1.2; r^2 = 3.5\%$	$p = 0.471; S = 1.2; r^2 = 3.5\%$
Dec. 21 to 31, 2000	$p = 0.258; S = 1.3; r^2 = 8.5\%$	$p = 0.225; S = 1; r^2 = 9.7\%$	$p = 0.631; S = 1.5; r^2 = 1.6\%$	$p = 0.631; S = 1.5; r^2 = 1.6\%$	$p = 0.999; S = 1.9; r^2 = 0\%$	$p = 0.999; S = 1.9; r^2 = 0\%$
Jan. 1 to 10, 2001	$p = 0.239; S = 1.4; r^2 = 9.1\%$	$p = 0.245; S = 1.1; r^2 = 8.9\%$	$p = 0.441; S = 1.8; r^2 = 4\%$	$p = 0.441; S = 1.8; r^2 = 4\%$	$p = 0.817; S = 1.6; r^2 = 0.4\%$	$p = 0.817; S = 1.6; r^2 = 0.4\%$
Jan. 11 to 20, 2001	$p = 0.263; S = 1.5; r^2 = 8.3\%$	$p = 0.251; S = 1.2; r^2 = 8.7\%$	$p = 0.241; S = 1.7; r^2 = 9\%$	$p = 0.241; S = 1.7; r^2 = 9\%$	$p = 0.719; S = 1.4; r^2 = 0.9\%$	$p = 0.719; S = 1.4; r^2 = 0.9\%$
Jan. 21 to 31, 2001	$p = 0.266; S = 1.8; r^2 = 8.2\%$	$p = 0.258; S = 1.3; r^2 = 8.5\%$	$p = 0.300; S = 2.1; r^2 = 7.1\%$	$p = 0.300; S = 2.1; r^2 = 7.1\%$	$p = 0.332; S = 2; r^2 = 6.3\%$	$p = 0.332; S = 2; r^2 = 6.3\%$

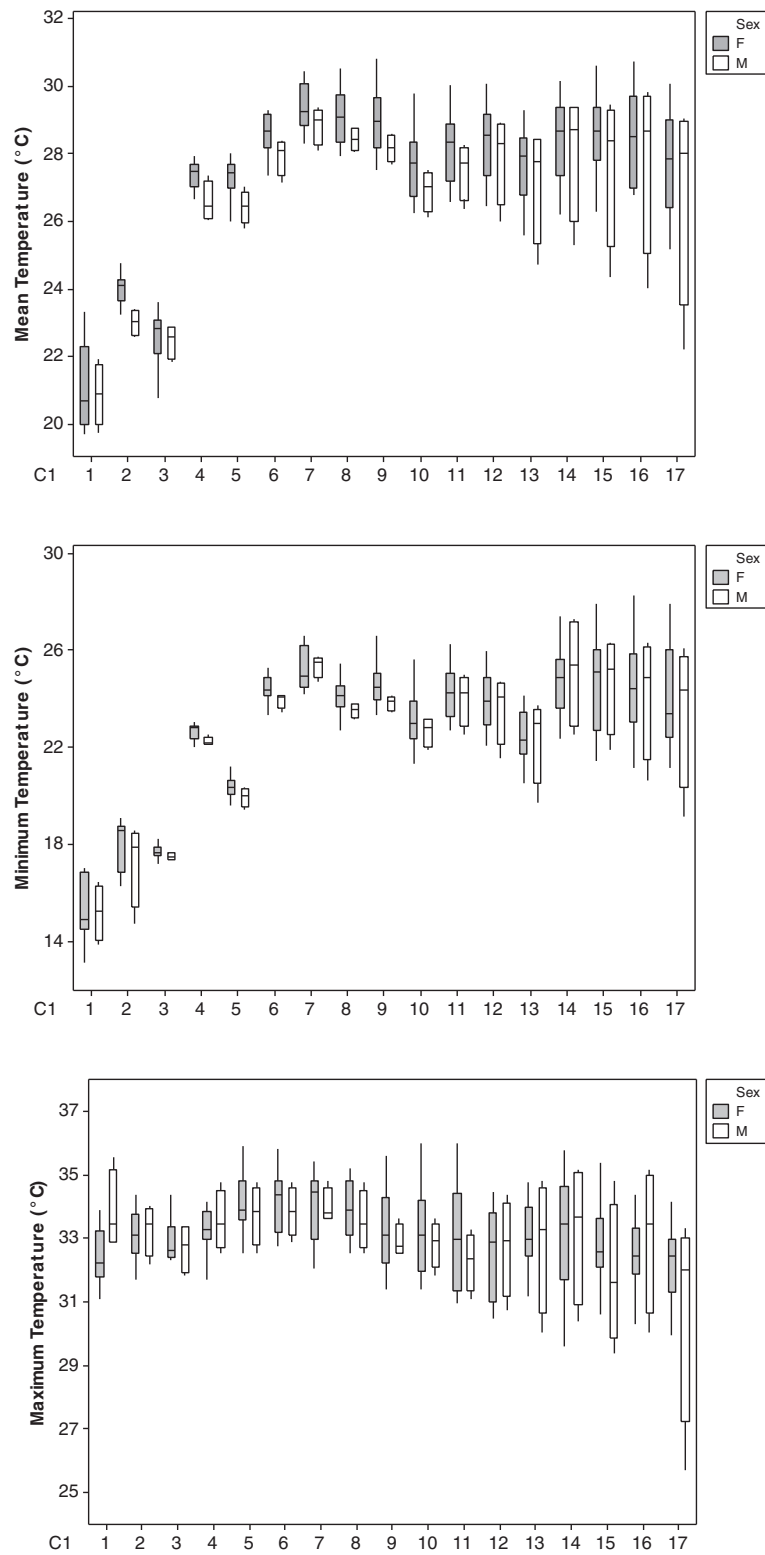


Figure 2 Pattern of body temperature variation between sexes in captive adult broad-snouted caiman. 1 - Aug. 10 to 20, 2000; 2 - Aug. 21 to 31, 2000; 3 - Sept. 1 to 10, 2000; 4 - Sept. 11 to 20, 2000; 5 - Sept. 21 to 30, 2000; 6 - Oct. 1 to 10, 2000; 7 - Oct. 11 to 20, 2000; 8 - Oct. 21 to 31, 2000; 9 - Nov. 1 to 10, 2000; 10 - Nov. 11 to 20, 2000; 11 - Nov. 21 to 30, 2000; 12 - Dec. 1 to 10, 2000; 13 - Dec. 11 to 20, 2000; 14 - Dec. 21 to 31, 2000; 15 - Jan. 1 to 10, 2001; 16 - Jan. 11 to 20, 2001; 17 - Jan. 21 to 31, 2001.

designs of the nesting areas for crocodilians were initially proposed by Bustard (1975) and adapted by Verdade et al. (1993) for the broad-snouted caiman.

The experimental groups were composed of the founding individuals of the captive colony at the Laboratório de Ecologia Animal, registered in the Regional Studbook for this species in Brazil (Verdade and Kassouf-Perina 1993) and totaling 20 animals (16 females and 4 males; see Table 1). The animals were measured, weighed, marked with interdigital tags, and sexed by visual inspection of the gonads with the help of a human nasal speculum (Allstead and Lang 1995). The animals' diet was maintained at a constant level during the entire experimental period. The diet consisted of a mixture of ground chicken, pork, and fish in equal proportions. The diet was supplied weekly at a level of 7% of the live mass of the animals (Sarkis-Gonçalves 2000). Nesting females were identified by their parental behavior, namely the construction and protection of the nest (Bustard 1980; Hunt 1987; Widholzer et al. 1986).

Thermal sensors HOBO TBI32-20+50 (Onset Computer Corporation, Bourne, MA, USA) were implanted in the animals. The sensors were covered with non-toxic plastic. They measured 3 cm in basal diameter and 1.5 cm in height. They were programmed to record the T_b each hour (precision $\pm 0.1^\circ\text{C}$) for a period of 180 days. After that period, infiltration could occur, resulting in error in data collection. The thermal sensor was inserted in the body coelomic cavity below the peritoneum as described by Troiano (1991), between the jejunum and ileum, which are of equal size on both the left and right

sides of the peritoneal cavity, as described by Merwe and Kotze (1993) for *Crocodylus niloticus*. Local anesthesia was applied with lidocaine (Eurofarma Laboratórios Ltda, São Paulo, Brazil) (diethylaminoaceto- α -2,6-xylylide) at a concentration of 2 g/100 ml per regional block. The skin suture was performed with a black nylon monofilament (size 0) accompanied by the use of a topical antibiotic with a chloramphenicol base to prevent bacterial growth. After surgery, the animals were maintained for 24 h in a dry and cold location. Thermal sensors were also placed in three environments in the crocodilians' facilities: the water surface (4), pool bottom (4), and ground (4). This study was carried out in compliance with the guidelines of the Brazilian Association of Wildlife Veterinary Medicine (ABRAVAS). The methods herein used were previously approved by the Ethics Commission of the University of São Paulo at Piracicaba.

The individuals' mean, maximum, and minimal daily temperatures, at 10-day intervals from August 10 to January 31, 2001, were treated as independent variables and compared among the animals. Sex, size, body mass, reproductive status, and health condition were treated as dependent variables. Student's t test was used to verify possible differences in T_b (mean, maximum, and minimum temperatures) between the sexes and health condition (healthy and sick). Linear regression was applied to verify the relationship between T_b (mean, maximum, and minimum temperatures) and snout-vent length (SVL) and body mass. Analysis of variance (ANOVA) was used to analyze differences in T_b between females (n, non-reproductive female; sf, female laying fertile eggs;

Table 3 Statistical values of comparison of body temperature between sexes in captive adult broad-snouted caiman

	Mean temperature	Minimum temperature	Maximum temperature
1 - Aug. 10 to 20, 2000	$t_{1,16} = 0.4; p = 0.681$	$t_{1,16} = 0.4; p = 0.704$	$t_{1,16} = -2; p = 0.129$
2 - Aug. 21 to 31, 2000	$t_{1,16} = 3.3; p = 0.009$	$t_{1,16} = 0.7; p = 0.527$	$t_{1,16} = -0.4; p = 0.673$
3 - Sept. 1 to 10, 2000	$t_{1,16} = 0.6; p = 0.800$	$t_{1,16} = 1.8; p = 0.092$	$t_{1,16} = 0.5; p = 0.624$
4 - Sept. 11 to 20, 2000	$t_{1,16} = 2.2; p = 0.089$	$t_{1,16} = 1.8; p = 0.094$	$t_{1,16} = -0.5; p = 0.604$
5 - Sept. 21 to 30, 2000	$t_{1,16} = 2.8; p = 0.038$	$t_{1,16} = 1.8; p = 0.124$	$t_{1,16} = 0.6; p = 0.570$
6 - Oct. 1 to 10, 2000	$t_{1,16} = 1.9; p = 0.114$	$t_{1,16} = 2.5; p = 0.034$	$t_{1,16} = 0.7; p = 0.512$
7 - Oct. 11 to 20, 2000	$t_{1,16} = 1.5; p = 0.163$	$t_{1,16} = 0.1; p = 0.878$	$t_{1,16} = 0.1; p = 0.882$
8 - Oct. 21 to 31, 2000	$t_{1,16} = 2.3; p = 0.037$	$t_{1,16} = 2.4; p = 0.029$	$t_{1,16} = 0.8; p = 0.437$
9 - Nov. 1 to 10, 2000	$t_{1,16} = 0.04; p = 0.044$	$t_{1,16} = 2.5; p = 0.025$	$t_{1,16} = 0.8; p = 0.415$
10 - Nov. 11 to 20, 2000	$t_{1,16} = 1.8; p = 0.097$	$t_{1,16} = 1; p = 0.321$	$t_{1,16} = 0.7; p = 0.465$
11 - Nov. 21 to 30, 2000	$t_{1,16} = 1.2; p = 0.247$	$t_{1,16} = 0.4; p = 0.681$	$t_{1,16} = 1.2; p = 0.250$
12 - Dec. 1 to 10, 2000	$t_{1,16} = 0.6; p = 0.562$	$t_{1,16} = 0.3; p = 0.746$	$t_{1,16} = -0.2; p = 0.818$
13 - Dec. 11 to 20, 2000	$t_{1,16} = 0.5; p = 0.609$	$t_{1,16} = 0.1; p = 0.907$	$t_{1,16} = 0.2; p = 0.843$
14 - Dec. 21 to 31, 2000	$t_{1,16} = 0.3; p = 0.720$	$t_{1,16} = -0.3; p = 0.774$	$t_{1,16} = -0.08; p = 0.943$
15 - Jan. 1 to 10, 2001	$t_{1,16} = 0.5; p = 0.623$	$t_{1,16} = -0.4; p = 0.670$	$t_{1,16} = 0.6; p = 0.585$
16 - Jan. 11 to 20, 2001	$t_{1,16} = 0.4; p = 0.664$	$t_{1,16} = 0.2; p = 0.818$	$t_{1,16} = -0.3; p = 0.740$
17 - Jan. 21 to 31, 2001	$t_{1,16} = 0.4; p = 0.671$	$t_{1,16} = 0.2; p = 0.826$	$t_{1,16} = 0.6; p = 0.545$

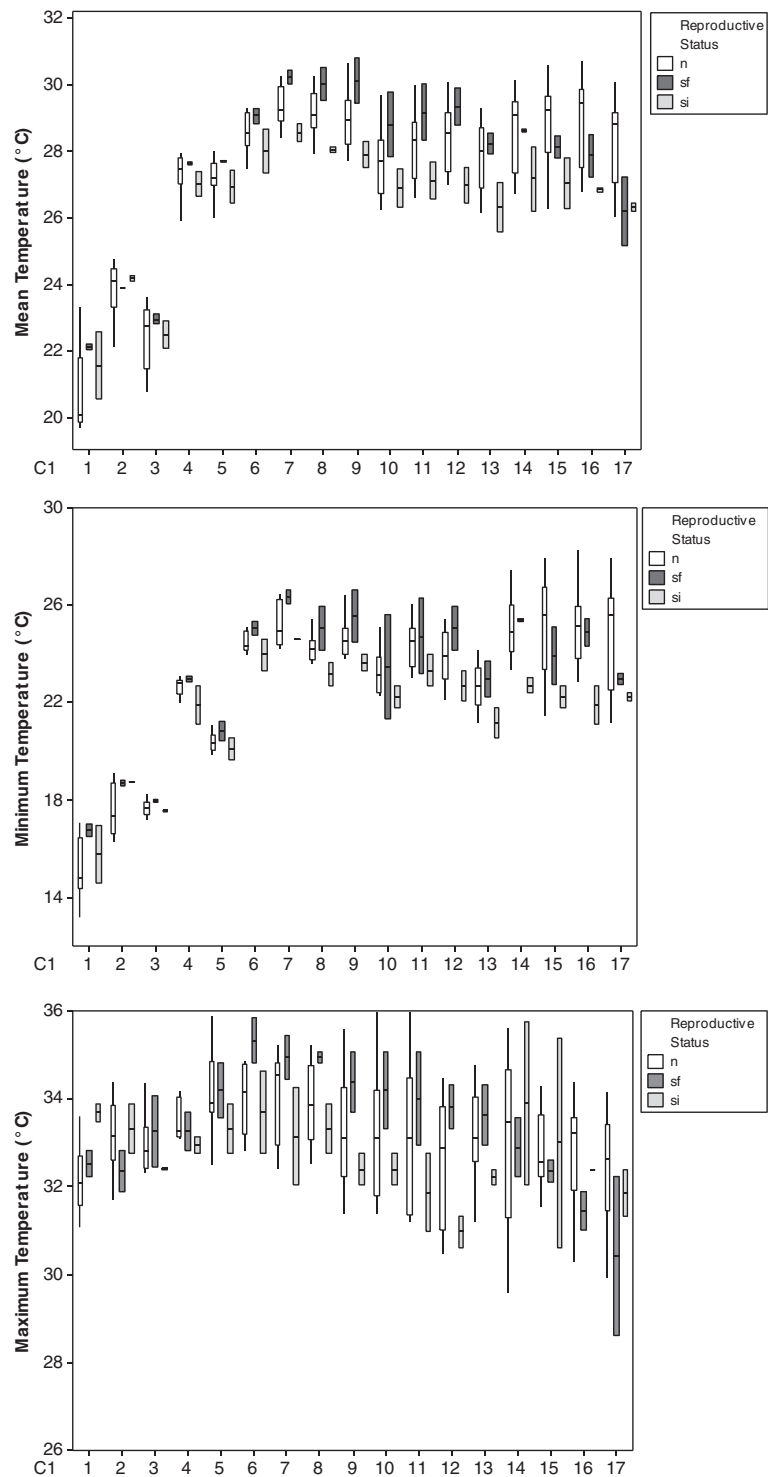


Figure 3 Comparison of body temperature among female captive adult broad-snouted caimans. n, non-reproductive female; sf, female laying fertile eggs; si, female laying infertile eggs. 1 - Aug. 10 to 20, 2000; 2 - Aug. 21 to 31, 2000; 3 - Sept. 1 to 10, 2000; 4 - Sept. 11 to 20, 2000; 5 - Sept. 21 to 30, 2000; 6 - Oct. 1 to 10, 2000; 7 - Oct. 11 to 20, 2000; 8 - Oct. 21 to 31, 2000; 9 - Nov. 1 to 10, 2000; 10 - Nov. 11 to 20, 2000; 11 - Nov. 21 to 30, 2000; 12 - Dec. 1 to 10, 2000; 13 - Dec. 11 to 20, 2000; 14 - Dec. 21 to 31, 2000; 15 - Jan. 1 to 10, 2001; 16 - Jan. 11 to 20, 2001; 17 - Jan. 21 to 31, 2001.

si, female laying infertile eggs). A Tukey HSD test was used to verify possible differences between these treatments. All the analyses were performed in MINITAB 13 (Minitab 2000).

Results

The animals showed a clear diel variation in T_b during the study period (August 2000 through January 2001), with a minimum temperature of 17°C to 23°C in the morning (0900 to 1000 hours) and a maximum temperature of 32°C to 35°C in the afternoon (1400 to 1700 hours). This pattern coincides with temperature variation among the different microhabitats of the animals' facilities (water surface, pool bottom, and ground) selectively used by the animals during the day (Figure 1). The water temperature varied from approximately 21°C at 09:00 hours to 29°C at 14:30 hours at the surface and from 22.5°C at 08:30 hours to 30°C at 16:00 hours at a depth of 100 cm. The air temperature varied from 17°C at 07:00 hours to 38°C at 14:00 hours at the ground level by the pool margin.

No relationship was found between body mass and snout-vent length (body mass 23.9 to 64.8 kg, snout-vent length 85 to 123 cm; Table 2) and T_b (mean, minimum, and maximum temperatures) of broad-snouted caiman. However, females presented a higher minimum temperature than males from October to early November (Figure 2; Table 3). In addition, reproductive females (i.e., those that laid fertile eggs) had higher T_b than those that laid infertile eggs in the same period (Figure 3; Table 4).

Two females died during the sampling period. These animals presented symptoms of infection and had relatively

higher minimum T_b than healthy animals (minimum temperature - healthy: 24.2°C ± 1.8°C, sick: 27.4°C ± 0.6°C, $t_{1,18} = 5.1$; $p = 0.014$; mean temperature - healthy: 28.1°C ± 1.4°C, sick: 30.1°C ± 0.6°C, $t_{1,18} = 3.2$; $p = 0.082$; maximum temperature- healthy: 32.4°C ± 1.6°C, sick: 33.4°C ± 1.2°C, $t_{1,18} = 1$; $p = 0.473$). Both died before the end of the study.

Discussion

The diel T_b variation of the broad-snouted caiman reflects the thermal variation in the environment used by the species (the water surface, pool bottom, and ground). The ground showed a wide temperature range in comparison to the other environments, followed by the water surface and the pool bottom (Figure 1). These observations show that the available environments provided a wide spectrum of temperatures to be exploited by the animals to thermoregulate. Broad-snouted caiman hatchlings in greenhouses move through the environment during the day, choosing the most suitable temperatures available in the different environments (Verdade et al. 1994). A similar pattern has been described for the American alligator (Lang 1987).

Most of the animals were found in the pool during the morning, but moved out of the water to sunbathe during the hottest hours of the day. This behavioral thermoregulation by moving in and out of the water is consistent with the previous studies for the same species (Molina and Sajdak 1993; Verdade et al. 2006) and for the Nile crocodile (*C. niloticus*) (Downs et al. 2008).

In nature, female crocodilians can be more sedentary than males (Goodwin and Marion 1979) and, consequently,

Table 4 Statistical values of comparison of body temperature among female captive adult broad-snouted caimans

	Mean temperature	Minimum temperature	Maximum temperature
1 - Aug. 10 to 20, 2000	$F_{2,16} = 0.8$; $p = 0.477$	$F_{2,16} = 1.9$; $p = 0.172$	$F_{2,16} = 4.3$; $p = 0.025$
2 - Aug. 21 to 31, 2000	$F_{2,16} = 1.9$; $p = 0.171$	$F_{2,16} = 1.1$; $p = 0.382$	$F_{2,16} = 0.7$; $p = 0.561$
3 - Sept. 1 to 10, 2000	$F_{2,16} = 1.9$; $p = 0.900$	$F_{2,16} = 1.3$; $p = 0.300$	$F_{2,16} = 0.6$; $p = 0.625$
4 - Sept. 11 to 20, 2000	$F_{2,16} = 2$; $p = 0.158$	$F_{2,16} = 2.9$; $p = 0.074$	$F_{2,16} = 0.3$; $p = 0.827$
5 - Sept. 21 to 30, 2000	$F_{2,16} = 3$; $p = 0.069$	$F_{2,16} = 2.1$; $p = 0.149$	$F_{2,16} = 0.6$; $p = 0.604$
6 - Oct. 1 to 10, 2000	$F_{2,16} = 2.1$; $p = 0.145$	$F_{2,16} = 3.4$; $p = 0.050$	$F_{2,16} = 1.7$; $p = 0.203$
7 - Oct. 11 to 20, 2000	$F_{2,16} = 3.8$; $p = 0.037$	$F_{2,16} = 1.9$; $p = 0.172$	$F_{2,16} = 1.1$; $p = 0.364$
8 - Oct. 21 to 31, 2000	$F_{2,16} = 4.7$; $p = 0.020$	$F_{2,16} = 4.2$; $p = 0.026$	$F_{2,16} = 1.4$; $p = 0.279$
9 - Nov. 1 to 10, 2000	$F_{2,16} = 3.4$; $p = 0.048$	$F_{2,16} = 2.9$; $p = 0.074$	$F_{2,16} = 1.1$; $p = 0.365$
10 - Nov. 11 to 20, 2000	$F_{2,16} = 1.9$; $p = 0.170$	$F_{2,16} = 0.6$; $p = 0.588$	$F_{2,16} = 0.79$; $p = 0.519$
11 - Nov. 21 to 30, 2000	$F_{2,16} = 1.8$; $p = 0.185$	$F_{2,16} = 0.6$; $p = 0.588$	$F_{2,16} = 0.9$; $p = 0.431$
12 - Dec. 1 to 10, 2000	$F_{2,16} = 1.8$; $p = 0.181$	$F_{2,16} = 1.3$; $p = 0.293$	$F_{2,16} = 1.4$; $p = 0.274$
13 - Dec. 11 to 20, 2000	$F_{2,16} = 1.2$; $p = 0.348$	$F_{2,16} = 1$; $p = 0.413$	$F_{2,16} = 0.4$; $p = 0.735$
14 - Dec. 21 to 31, 2000	$F_{2,16} = 0.7$; $p = 0.551$	$F_{2,16} = 1.6$; $p = 0.223$	$F_{2,16} = 0.1$; $p = 0.946$
15 - Jan. 1 to 10, 2001	$F_{2,16} = 0.7$; $p = 0.529$	$F_{2,16} = 1$; $p = 0.407$	$F_{2,16} = 0.2$; $p = 0.881$
16 - Jan. 11 to 20, 2001	$F_{2,16} = 1.2$; $p = 0.321$	$F_{2,16} = 2.5$; $p = 0.143$	$F_{2,16} = 0.6$; $p = 0.609$
17 - Jan. 21 to 31, 2001	$F_{2,16} = 1.1$; $p = 0.366$	$F_{2,16} = 0.7$; $p = 0.546$	$F_{2,16} = 0.8$; $p = 0.514$

show different T_b than males. However, Verdade et al. (2006) have reported a consistent individual variation of space use by the broad-snouted caiman in captivity, possibly due to the lack of intermale competition for territories as those captive groups had single males. Nevertheless, the difference in T_b between males and females in this study may be due to their distinct reproductive biology. In addition, in this study, we found no relationship between body mass and snout-vent length and T_b . Similar patterns have been previously described for crocodylians (Diefenbach 1975a; Downs et al. 2008; Smith 1979). However, future studies should include a broader range of body sizes, as well as different periods of the year.

The period during which the T_b of the fertile females (i.e., those that laid fertile eggs) was higher than that of the non-fertile ones (i.e., those that laid infertile eggs) apparently coincided with the ovulation period. Changes in T_b due to the reproductive condition of females are relatively well documented in reptiles (Blazquez 1995; Charland 1995; Daut and Andrews 1993; Rock et al. 2000; Rosen 1991; Tu and Hutchison 1994). It is likely that the temperature increase during gestation results in an increase of the rate of embryonic development (Shine 1983).

Social behavior significantly affects crocodylians' thermoregulation (Seebacher et al. 1999). The social hierarchy of females may have influenced the results of the present study because it directly affects reproductive success (Joanen and McNease 1989; Lang 1987, 1989; Verdade 1992b). Social dominance can be related to the use of habitat and available resources (Alcock 1993; Krebs 1985; Krebs and Davis 1991; Verdade 1992b). Cardeilhac (1989, 1990) states that competition for areas suitable for sunbathing during the pre-ovulation period can affect the gonadal development of females with a low hierarchical position, preventing them from entering ovulation or even achieving the minimum follicular development required for ovulation.

The behavioral change associated with nesting and nest protection by the reproductive females may have influenced the present results, because possible disputes over nesting sites may affect the thermoregulatory behavior of the subordinate animals. These animals could be excluded from the best nesting habitats, which could also restrict their basking sites, thus affecting their thermoregulatory behavior (Verdade 1992b). Agonistic displays by adults, especially during the reproductive period, are common in crocodylians (Ayarzaguena 1983; Garrick and Lang 1977; Lang 1987; Verdade 1992b, 1999; Vliet 1989). Agonistic interactions among females involving thermoregulatory behavior were also observed during this study.

The animals that died from bite wounds (possibly associated with infectious diseases) presented a higher minimum T_b than healthy animals during a certain period.

Behavioral fever resulting from infections has been previously reported for diverse ectothermic taxa, including turtles (do Amaral et al. 2002), lizards (Firth et al. 1980; Merchant et al. 2008; Ortega et al. 1991), and crocodylians (Lang 1987; Merchant et al. 2007). American alligators in controlled experiments exhibited 2 days of fever after inoculation with an infectious agent. The increase in T_b relative to that of a control group was 2.6°C on the first day and 3.5°C on the second day (Merchant et al. 2007). Fever is a component of the physiological defense of the host against invading agents (microbial or non-microbial) recognized as foreign bodies by the host's immune system (Zeisberger 1999). In the present study, the individuals suffering from infections appeared to seek hotter areas for sunbathing.

Conclusions

The results of this study show that sex, reproductive status, and health condition can affect the T_b of adult broad-snouted caiman in captivity. Crocodylians are intensively managed for sustainable use of their meat and leather. Future studies should focus on the relationships between thermoregulatory behavior and management both in captivity (e.g., the design of the captive facilities; see Verdade and Piña 2006) and in the wild (e.g., the influence of hunting pressure on social behavior; see Verdade 1996), as environmental anthropic pressures can affect individuals' growth rate and reproductive performance.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

LABB carried out the experiments and wrote the preliminary draft of this manuscript. LMV, TSM, AM, and CIP gave advice in the statistical analysis and revised the manuscript. LMV carried out the design and coordination of the study. All authors have approved the final version of the manuscript.

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