

FIELD BODY TEMPERATURES OF CAIMANS IN THE PANTANAL, BRAZIL

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Body temperatures of 51 caimans in the Pantanal were monitored by radio telemetry in cool (dry season) and warm (dry and wet seasons) seasons in an area with isolated lakes and an area with intermittent rivers. Cloacal temperatures of 739 caimans of different sizes captured between 1830 hrs and 2200 hrs were measured with a digital thermometer between August 1996 and September 1999 in the same area. The masses of caimans monitored ranged from 3 to 42 kg, and caiman size affected the amplitude of body temperatures. Small caimans generally had lower mean body temperatures than larger caimans only at the beginning of the night in the cool season before body temperatures equilibrated with water temperatures. Mean body temperature was 25.7 °C in the cool season and 30.1 °C in the warm season, with a minimum of 16.9 °C and a maximum of 37.9 °C. In the warm season, caimans spent more time in shady areas, on land or in the water, than exposed directly to sunlight, and body temperatures only slightly exceeded water temperatures. In the cool season, caimans basked in the sun, both on land and in water, and caimans on land achieved body temperatures up to 15 °C above water temperatures, but body temperatures of caimans on land rarely exceeded air temperatures during daylight hours. Gravid females did not have higher temperatures than females that were not gravid. The caimans appeared to vary from near thermoconformity in the warm season to active thermoregulation when water temperatures were less than about 28 °C. However, caimans often appeared to give low priority to thermoregulation, and much shuttling behavior may occur for reasons unrelated to thermoregulation.

Key words: behaviour, *Caiman crocodilus yacare*, temperature, thermoregulation, behaviour

INTRODUCTION

Crocodylians are large semi-aquatic reptiles that thermoregulate actively by shuttling between air and water, and between places exposed to sun and places in the shade (Seebacher *et al.*, 1999). However, the significance of shuttling to the temperature relations of individuals may not be simple. *Alligator mississippiensis*, a temperate-zone species, basks to raise its temperature, but many species of crocodylians apparently leave the water to cool (Lang, 1987a; Thorbjarnarson, 1995). In *Crocodylus johnstoni*, some animals maintain temperatures similar to that of the water at all times of year, and others only achieve temperatures distinct from that of the water in some seasons (Seebacher & Grigg, 1997).

Although most species of crocodylians “bask” in the sun during the day (Lang, 1987a), it is not known whether this generally results in their attaining higher temperatures than they would have if they remained in water. As individuals may display shuttling behaviour as a result of social interactions (Lang, 1987b; Seebacher & Grigg, 1997), shuttling does not necessarily result in individuals attaining preferred body temperatures. Studies on turtles suggest that basking has other advantages, such as retarding growth of epiphytes and fungi on the skin (Moll & Legler, 1971), and may also be a strategy for the synthesis of vitamin D (Pritchard & Greenwood, 1968).

Tropical crocodylians avoid high ambient temperatures during much of the year, and Lang (1987a) considered them to be thermoconformers. However, detailed evaluation of the significance of behavioural changes often requires information on operative temperatures (Bakken & Gates, 1975; Tracy, 1982; O'Connor & Spotila, 1992; Hertz *et al.*, 1993), and studies on large numbers of wild individuals have been undertaken only on species of the genus *Crocodylus* (Grigg & Seebacher, 2001). Even in warm climates, seasonal changes in temperature can result in changes in shuttling behaviour and mean temperatures. Preferred temperatures also may change seasonally (Seebacher and Grigg, 1997). Habitat may also affect body temperatures in crocodylians (Loveridge, 1984), and female reptiles often seek higher temperatures when gravid (Shine, 1985).

Independent of the motivation for shuttling and whether the organism is actively thermoregulating, crocodylian size will affect body temperatures because large reptiles heat and cool slowly while smaller individuals warm and cool quickly (Spotila *et al.*, 1973; Smith, 1979; Grigg *et al.*, 1979; Stevenson, 1985; Seebacher, 1999; Seebacher *et al.*, 1999; Seebacher, 2000). During the day, small individuals could compensate for a lower thermal inertia by shuttling more frequently, or adopting heat-accumulating postures (Seebacher, 1999). However, crocodylians are aquatic, primarily-nocturnal predators. Heat loss is expected to be greatest at the beginning of the night when foraging

crocodilians return to the water, and opportunities to thermoregulate are limited. Due to their higher surface area to mass ratio, and the high specific heat of water, smaller crocodilians should lose heat much more quickly than large crocodilians when they return to the water at the beginning of the night and the water starts to cool (Grigg & Seebacher, 2001).

Although much information is available on the thermal relations of North American *Alligator mississippiensis* and Australian species of the genus *Crocodylus* (Grigg & Seebacher, 2001), little information is available on thermal relations in the wild for species from other regions. Shuttling behaviour has been described for *Caiman crocodilus crocodilus* in Venezuela (Stanton and Dixon, 1975; Marcellini, 1979; Ayarzagüena, 1983; Thorbjarnarson 1995), but the body temperatures of the animals in different situations were not recorded.

In this paper we describe the behaviour and body temperatures of *Caiman crocodilus yacare* in the Brazilian Pantanal. *C. c. yacare* is one of the most abundant crocodilians (Coutinho & Campos, 1996; Mourão *et al.*, 2000), but there is no published information on its thermal relations. We used temperature-sensitive radio transmitters and direct measurements of cloacal temperature to investigate whether body temperature in *C. c. yacare* varies between seasons, between habitats, between animals of different reproductive states, and/or between animals of different sizes.

MATERIALS AND METHODS

STUDY AREA

The Pantanal is located in the upper Paraguay River basin, near the geographical centre of South America. The Pantanal covers almost 140,000 km², and is characterized by a mosaic of seasonally flooded fields and slightly higher islands that do not flood. The climate is classified as AW (savanna) according to the Köppen system. The climate is markedly seasonal, with rain concentrated in late spring and summer (October to April). Winter and early spring (May to September) are generally warm and dry, except when cold fronts from the south cause abrupt falls in air temperature. The mean annual air temperature between 1986 and 1999 varied from 22 to 26 °C, and rainfall from 800 to 1200 mm/year (Soreano, 1997). Environmental temperatures during the study reflected the seasonally unpredictable temperatures in the Pantanal. From May to September, temperatures fluctuated widely. Hot days often alternated with cold days because of cold fronts from the south. Mean air temperatures were low in May 1998 (20.4 °C) and September 1996 (21.2 °C), but in September 1999 the mean air temperature was above 30 °C and the mean air temperature in April 1998 was 28 °C. In the remaining months of the year, mean air temperatures remained around 30 °C. The study was undertaken in the Nhecolândia region, located in the Taquari River alluvial fan in the south-west of the Pantanal.

Major habitats and the monitoring of ambient temperatures. One part of the study area (Campo Dora Ranch) is within the drainage basin of intermittent rivers and has few lakes, and the other part (Nhumirim Ranch) is in an area characterized by small shallow (<2.0 m) lakes. The river area is covered by open pastures and mosaics of gallery forest. The lake area is covered mainly by forest, but has some pastures. The lakes support a diverse aquatic plant community, but coverage, composition and biomass of macrophytes vary among lakes (Pott, 1994). During the rainy season, pastures are flooded, but during the dry season water remains only in larger lakes and in pools formed in the intermittent rivers.

Air and water temperatures were measured with StowAway^{Temp} data-loggers (Onset®). They were programmed to take readings at the times that body temperatures were monitored. Water temperature was measured by the data-loggers near the surface (10-15 cm) and at 60 cm depth. Air temperature (TAR) was registered with data-loggers in shady places on the margins of lakes and rivers at 100 cm above ground level. In the river area, between October and November 1999, no data loggers were available, and air temperatures were registered in the Nhumirim Meteorological Station at 0800, 1400 and 2000 hrs. Operative temperatures were not measured. However, air and water temperatures probably indicate minimum temperatures available to caimans. We assumed that evaporative cooling would not be sufficient to maintain these large reptiles at temperatures much less than air temperature, and that evaporative cooling would not occur when the caimans were in water.

RADIO TELEMETRY EQUIPMENT AND TEMPERATURE-SENSITIVE DATA LOGGERS

Caimans were located at night with spotlights, and approached from small boats in the pools in the river area, or on foot from the shore in the lake area, and captured with nooses attached to long poles. The caimans were taken to a laboratory at Nhumirim Ranch. The next morning, radio transmitters or data loggers were surgically implanted in the peritoneal cavity under sterile conditions.

During surgery, cooling was used for immobilization and 2 ml of Xylocaine for local anesthesia. Before initiating surgery, the incision area was washed with running water and neutral soap and sterilized with iodized alcohol. To cool the caimans, they were rolled in cloth, their legs tied, the mouth and eyes sealed with duct tape and they were placed in a freezer until their body temperatures dropped to about 19 °C (60-90 mins, depending on the size of the caiman). A surgical incision was made in the flank in front of the left hind leg. The radio transmitter was sterilized with iodized alcohol and introduced in the peritoneal cavity. The 47 cm antenna of the transmitter remained inside the body cavity. The peritoneal membrane and musculature were closed with absorbable sutures (catgut) in continuous points. The external inci-

sion was closed with cotton or nylon sutures, in individual points. All procedures followed ethical practices for animals recommended by EMBRAPA veterinarians. The animals did not show signs of stress and were released the same day at the site of capture.

The temperature-sensitive radio transmitters (Sirtrack®) measured approximately $3 \times 2 \times 2$ cm, weighed 50 g, and had external 47 cm antennas. The data loggers (Onset® StowAway^{tidbit}) measured 4 cm by 3 cm and weighed approximately 30 g. All radio transmitters and data loggers were encapsulated with resin at the factory. Radio transmitters had different frequencies in the 164 to 166 MHz range, and a predicted useful life of 6 months. The radios and data loggers were previously calibrated against a mercury bulb thermometer and readings were accurate to within 0.3 °C.

The radio signals were detected with a TR2-Scanner and a TR4 receiver (Telonics®). Radio transmitters could usually be detected at distances up to 500 m, especially when caimans were on banks or swimming at the surface of the water. A Sirtemp encoder® was used for body temperature reading.

The body temperatures of 739 caimans of different sizes captured between 1830 hr and 2200 hrs were measured with a digital thermometer between August 1996 and September 1999. Caimans were caught with a noose mounted on a pole and their cloacal temperatures were measured within 5 mins of capture.

DATES AND LOCATIONS OF MONITORING

The diel and seasonal variation in body temperatures of 51 caimans were monitored by temperature-sensitive radio transmitters and data loggers. In the lake area, one adult male was used to test the use of radio transmitters attached to the tail, implanted in the peritoneal cavity, and in the stomach in May 1995. We monitored body temperatures of one female from June to August 1997, 12 caimans (7 males and 5 females) from May to October 1998, 9 caimans (5 males and 4 females) from November to March 1998, and 5 caimans (2 males and 3 females) from May to August 1999. In the river area, we monitored body temperatures of 10 caimans (8 males and 2 females) from June to July 1999, and 14 caimans (7 males and 7 females) from October to November 1999.

In the lake area, monitoring was done over 3-4 consecutive days, at intervals of one hour in the cool season (May - September) and in the warm season (October - March). In the intermittent-river area, monitoring was done during 7 to 9 consecutive days, at intervals of 1 hour in the cool season (June - July) and in the warm season (October - November).

REPRODUCTIVE STATE

No attempt was made to determine the reproductive state of males, but five of the females had pre-ovulatory follicles in advanced stages of development as evidenced by the flaccid cloaca, swollen flanks and increased body weight.

OBSERVATIONS OF CAIMAN BEHAVIOUR

Free-ranging caimans with radio transmitters were marked individually with coloured collars to facilitate observations of basking behaviour. At the same time that body temperatures of caimans were recorded, observations were made of basking behaviour of the caimans with radio transmitters. Each hour, the positions of the caimans (on land or in water, and in sun or in shade) were recorded. In the river area, which had open margins without vegetation, caimans with radio transmitters could be observed when in water or on land. In the lake area, basking caimans could not be observed due to aquatic vegetation. In this area, caimans were rarely found on the margins of the lakes, but rested on floating vegetation when out of the water. All analyses were done in the Systat version 8.0 program (Wilkinson, 1998).

RESULTS

SEASONAL VARIATION IN BODY TEMPERATURE

In this study, we registered 17661 body temperatures by radio telemetry and data loggers from 51 individuals over three years (Table 1). The minimum temperature registered was 16.9 °C and the maximum 37.4 °C. The mean water and air temperatures were more strongly correlated in the warm ($r=0.96$) season than in the cool ($r=0.80$) season when cold fronts from the south often resulted in short-term abrupt changes in air temperature that were reflected only weakly by water temperatures. The only cold front that passed through the study site during a monitoring period occurred in September, and resulted in caiman body temperatures well below those recorded in other months in the warm or cool seasons (Fig. 1).

The mean body temperature in the cool season was 25.7 °C (Median=25.7, SD=0.86), and the mean monthly body temperature varied from 23.8 to 28.3 °C. In the warm season, mean body temperature was 30.1 °C (Median=30.3, SD=0.66), and mean monthly temperatures varied from 28.5 to 31.3 °C. Mean monthly body temperatures were significantly ($t_{49}=20.6$, $P<0.001$) lower in the cool season than in the warm season (Fig. 1). This difference persisted ($t_{39}=17.3$, $P<0.001$) when we excluded September, the month in which data recording coincided with the passage of a cold front.

Maximum body temperatures registered for each individual were also significantly ($t_{49}=2.57$, $P=0.013$) lower in the cool season (mean=34.2 °C, median=34.2, min=31.5, max=37.2) than in the warm season (mean=35.1 °C, median=35.4, min=31.5, max=37.4), but there was no significant difference ($t_{39}=1.49$, $P=0.145$) between maximum temperatures in the cool season (mean_{max}=34.4 °C, median=34.3, min=31.5, max=37.2) and the warm season (mean_{max}=35.1 °C, median=35.4, min=31.5, max=37.4) when we excluded September, the month in which data recording coincided with the passage of a cold front.

TABLE 1. Snout-vent lengths (SVL), and body temperatures (BT - °C) of caimans in the lake (L) and river (R) areas in cool (C) and warm (H) seasons.

Sex	SVL (cm)	Mass (kg)	Season	Year	$O_{TB} \pm SD$	Minimum	Maximum	N	Habitat
F	61.0	4.8	C	1999	26.0 ± 3.3	20.5	34.3	315	L
F	62.5	5.1	C	1998	26.2 ± 4.1	17.3	33.8	490	L
F	63.0	5.2	C	1998	28.3 ± 4.1	17.3	35.6	443	L
F	68.0	6.4	H	1998	30.9 ± 2.1	26.8	36.2	221	L
F	69.0	7.5	H	1998	28.5 ± 3.6	24.9	33.5	610	L
F	70.0	7.0	C	1997	25.2 ± 3.0	19.8	34.3	85	L
F	72.0	7.6	H	1998	31.3 ± 2.1	25.9	36.9	224	L
F	72.0	7.4	H	1998	30.9 ± 1.9	26.4	36.0	231	L
F	73.5	8.0	C	1999	25.7 ± 3.0	21.3	34.6	295	L
F	77.0	10.0	C	1999	23.8 ± 2.6	20.1	31.5	91	L
F	77.0	11.5	C	1998	26.1 ± 3.4	17.6	33.5	486	L
F	78.0	12.0	C	1998	26.1 ± 3.4	17.6	33.6	490	L
F	83.0	13.0	C	1998	30.7 ± 1.6	26.5	35.9	240	L
M	55.0	3.3	C	1999	20.7 ± 3.1	20.7	33.6	302	L
M	60.0	4.3	C	1998	25.5 ± 3.3	17.6	32.9	490	L
M	63.0	4.7	C	1998	26.2 ± 3.8	17.0	34.4	487	L
M	64.0	5.5	C	1998	25.5 ± 2.1	21.0	31.9	256	L
M	75.0	7.8	H	1998	30.5 ± 1.5	26.3	34.4	241	L
M	82.0	11.0	C	1999	25.2 ± 2.9	20.2	34.0	281	L
M	83.0	12.0	H	1998	30.6 ± 1.7	26.5	35.5	249	L
M	85.0	13.0	C	1998	26.1 ± 3.5	17.8	32.9	465	L
M	86.0	15.0	C	1998	25.7 ± 3.6	17.2	33.4	489	L
M	94.5	19.5	H	1998	30.5 ± 1.5	27.1	34.7	223	L
M	95.5	20.0	C	1998	25.9 ± 3.2	17.8	32.8	490	L
M	106.0	27.0	H	1998	30.6 ± 1.4	26.6	33.8	207	L
M	106.0	25.0	H	1998	29.7 ± 3.7	17.9	37.4	4420	L
M	113.0	31.5	C	1998	25.5 ± 3.3	17.6	32.9	482	L
F	60.0	5.0	H	1999	30.2 ± 3.2	22.9	36.3	212	R
F	69.0	8.0	C	1999	28.3 ± 4.1	20.5	34.2	223	R
F	72.0	9.5	H	1999	29.8 ± 3.1	22.2	35.9	228	R
F	74.0	8.0	C	1999	24.7 ± 3.9	16.9	35.8	289	R
F	77.5	13.0	H	1999	28.8 ± 3.1	23.9	33.3	31	R
F	81.0	14.0	H	1999	30.9 ± 2.3	26.5	35.7	139	R
F	84.0	15.0	H	1999	30.3 ± 2.6	24.8	34.7	114	R
F	89.0	19.0	H	1999	29.9 ± 2.6	24.2	34.6	198	R
F	90.0	17.0	H	1999	29.2 ± 2.3	24.2	34.7	133	R
M	57.0	3.9	C	1999	25.0 ± 3.9	19.4	35.4	176	R
M	58.0	4.0	C	1999	25.2 ± 4.8	17.4	37.2	139	R
M	63.5	6.0	C	1999	25.4 ± 4.1	17.4	35.1	272	R
M	75.0	10.0	H	1999	30.3 ± 2.7	23.4	36.2	167	R
M	79.0	10.0	C	1999	27.3 ± 5.4	19.2	35.1	16	R
M	80.5	13.0	H	1999	29.8 ± 2.1	24.0	35.1	209	R
M	83.5	15.0	H	1999	29.9 ± 3.1	23.6	35.7	162	R
M	88.5	16.5	H	1999	29.8 ± 2.8	23.0	35.1	227	R
M	89.0	12.0	C	1999	25.2 ± 3.6	20.0	36.1	188	R
M	99.0	22.0	C	1999	24.9 ± 3.7	17.4	33.7	326	R
M	101.0	22.5	H	1999	30.2 ± 2.9	23.6	35.4	166	R
M	105.0	29.0	H	1999	29.7 ± 2.8	23.5	35.3	218	R
M	111.0	28.0	C	1999	24.5 ± 3.9	17.6	34.2	301	R
M	115.0	39.0	H	1999	29.7 ± 2.7	24.1	35.8	213	R
M	122.0	42.0	C	1999	30.4 ± 1.2	27.5	31.5	11	R

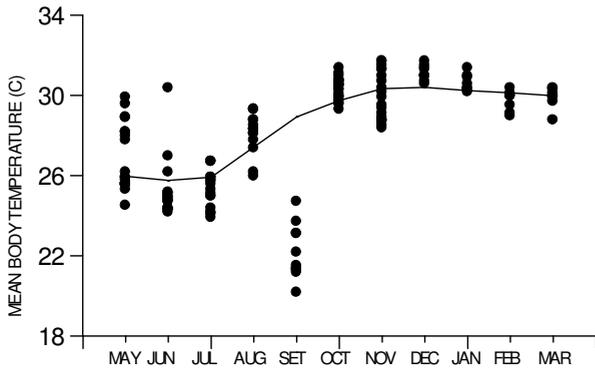


FIG. 1. Mean monthly body temperatures of individual caimans. The curve is a LOWESS regression (tension=0.5).

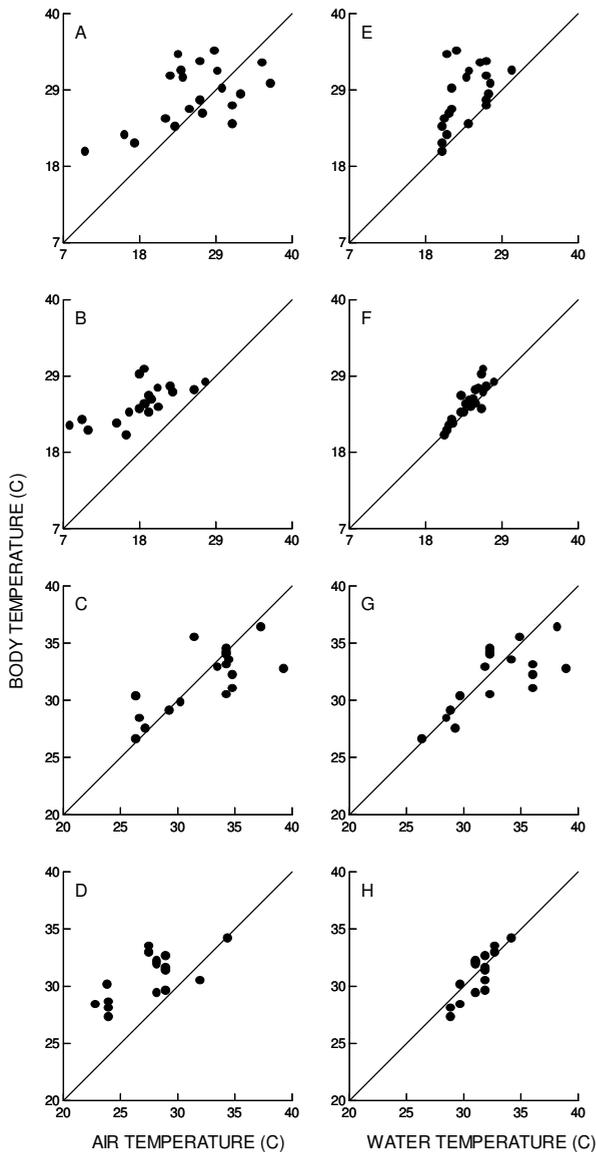


FIG. 2. Relationship between body temperature and air temperatures during the day (A) and during the night (B) in the cool season, and during the day (C) and during the night (D) in the warm season. Relationship between body temperature and surface water temperature during the day (E) and during the night (F) in the cool season, and during the day (G) and during the night (H) in the warm season.

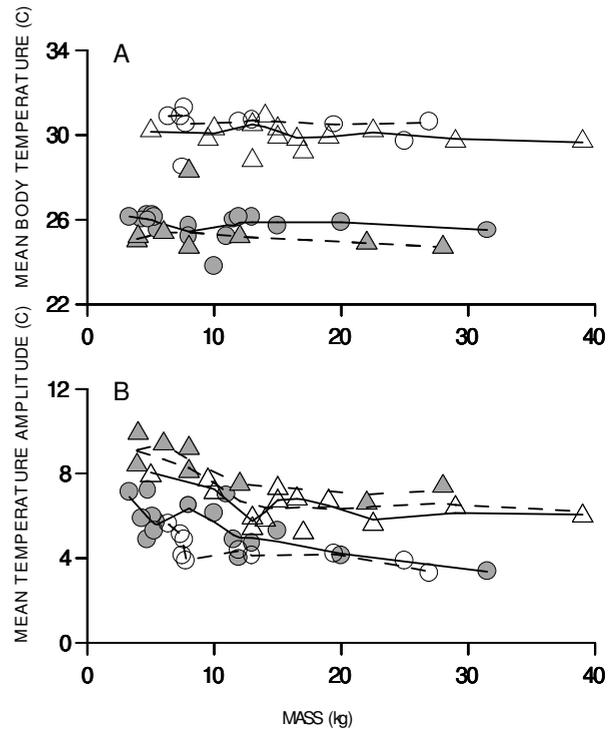


FIG. 3. Relationship between mass and body temperature ($^{\circ}\text{C}$) (A), and mean daily amplitude in temperature ($^{\circ}\text{C}$) (B) for caimans in cool (filled circles) and warm (open circles) seasons in the lake area, and cool (filled triangles) and warm (open triangles) seasons in the river area.

MEAN DIURNAL AND NOCTURNAL TEMPERATURES

Hourly records of body temperatures obtained by radio telemetry, coupled with hourly records of air and water temperatures, were available for 21 caimans in the cool season and 18 caimans in the warm season. Mean body temperature was correlated with mean air ($r=0.51$) and mean water ($r=0.55$) temperature during the day, and mean air ($r=0.88$) and mean water ($r=0.70$) temperature during the night in the cool season; and mean air ($r=0.74$) and mean water ($r=0.76$) temperature during the day, and mean air ($r=0.85$) and mean water ($r=0.70$) temperature at night in the warm season (Fig. 2). Mean temperatures higher than those of the water were obtained mainly during the day in the cool season. The mean body temperature at night varied from 24.9 to 33 $^{\circ}\text{C}$. Over the whole study period, mean monthly temperature of caimans at night was strongly correlated with mean monthly air ($r=0.83$, $N=10$) and water ($r=0.97$, $N=10$) temperatures.

EFFECTS OF BODY MASS AND HABITAT ON BODY TEMPERATURE

The body mass of the caimans monitored by radio telemetry ranged from 3.3 to 42 kg (Table 1) and was log transformed for statistical analyses. Analysis of covariance (ANCOVA) included site (lake or river) and season (cool or warm), as categorical variables. Mean body temperature (Fig. 3A) was affected by season ($F_{1,47}=378.6$, $P<0.001$) but not site ($F_{1,47}=1.01$, $P=0.319$) or $\text{Log}_{10}\text{Mass}$ ($F_{1,47}=1.15$, $P=0.289$). The

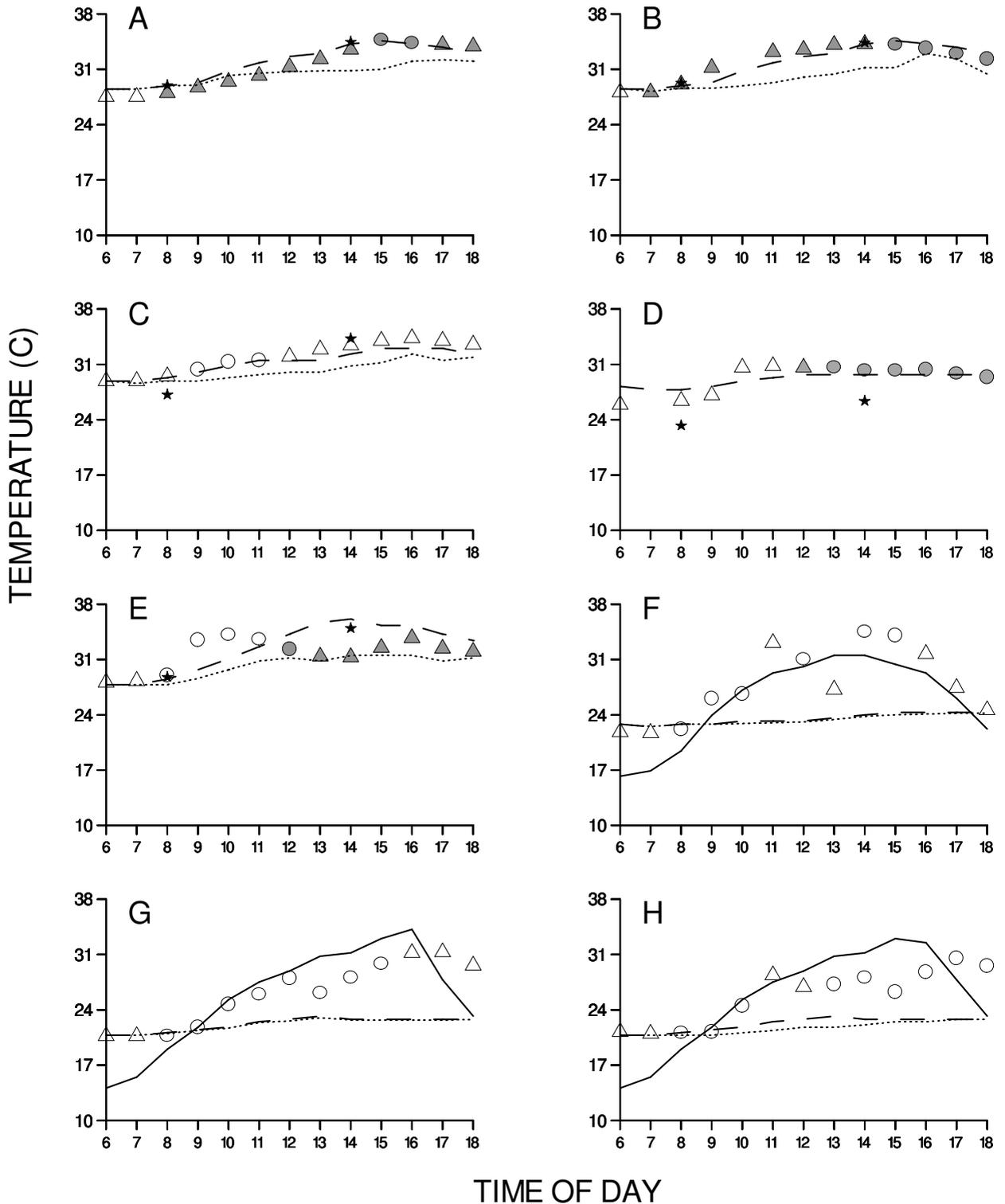


FIG. 4. Relationship between body temperature (circles and triangles), air temperature (asterisks or solid line), water temperature at 60 cm depth (dotted line), surface water temperature (dashed line), and time of day. Triangles indicate that the individual was in the water and circles indicate that it was on land. Open symbols indicate that the individual was exposed to the sun, and closed symbols indicate that it was in the shade.

mean daily amplitude (Fig. 3B) of body temperature was affected significantly by season ($F_{1,47}=12.6, P=0.001$), site ($F_{1,47}=59.4, P<0.001$) and $\text{Log}_{10}\text{Mass}$ ($F_{1,47}=0.14.0, P<0.001$).

DIURNAL PATTERNS IN BODY TEMPERATURES

In the river area, eight caimans were observed between 0600 and 1800 hrs. In the warm season, five

caimans (two females and three males) had similar patterns of terrestrial-aquatic movements and body temperatures, which were close to surface water temperatures (Fig. 4A, B, C, E, F). Body temperatures during the warm season were around 28 °C in the early morning and usually approached 35 °C at midday. The two females remained in water or on land in the shade (Fig. 4A, B). However, the males (Fig. 4C, D, E) re-

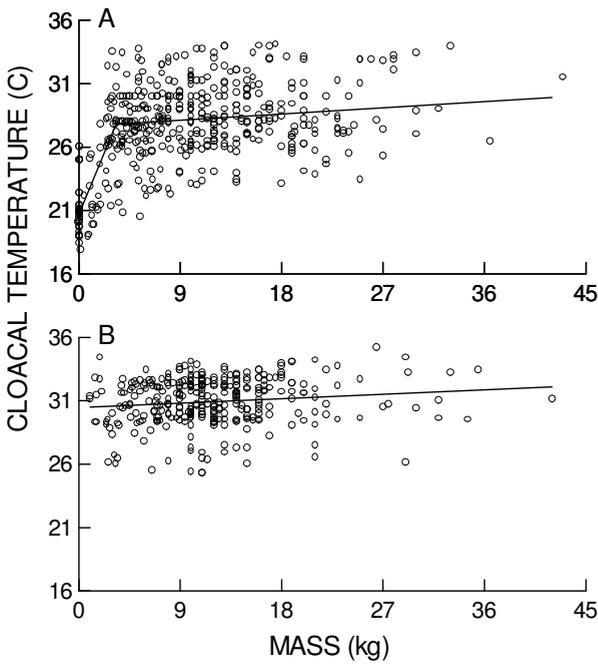


FIG. 5. Relationship between cloacal temperature and mass of caimans in the early hours of the night (1830-2200 hrs) during the cool (A) and warm (B) seasons.

mained in the water exposed to sun in the early morning, and alternated between land and water after 1200 hrs. During the warm season, body temperatures of caimans were similar to surface water temperatures, independent of whether they were in the shade or exposed to sun, or whether they were on land or in the water.

In the cool season, the body temperatures of the three caimans were closer to air temperature than water temperature during daylight hours, and the animals spent more time exposed to the sun, on land and in water (Fig. 4 F, G, H). The mean body temperature in the morning in the cool season was around 23 °C, rising to over 30 °C, for a few hours at midday.

NOCTURNAL CLOACAL TEMPERATURES

The body temperatures of 739 caimans of different sizes were measured at night (1830-2200 hrs) between August 1996 and September 1999. The snout-vent lengths of the caimans captured ranged from 14.5 to 120 cm (mean=74.0, SD=20.4) and mass varied from 0.04 to 43.0 kg (mean=10.7, SD=6.9). During the cool season (May to September), there was a nonlinear relationship between mean cloacal temperature (CT) and body mass (Fig. 5A). Piecewise regression indi-

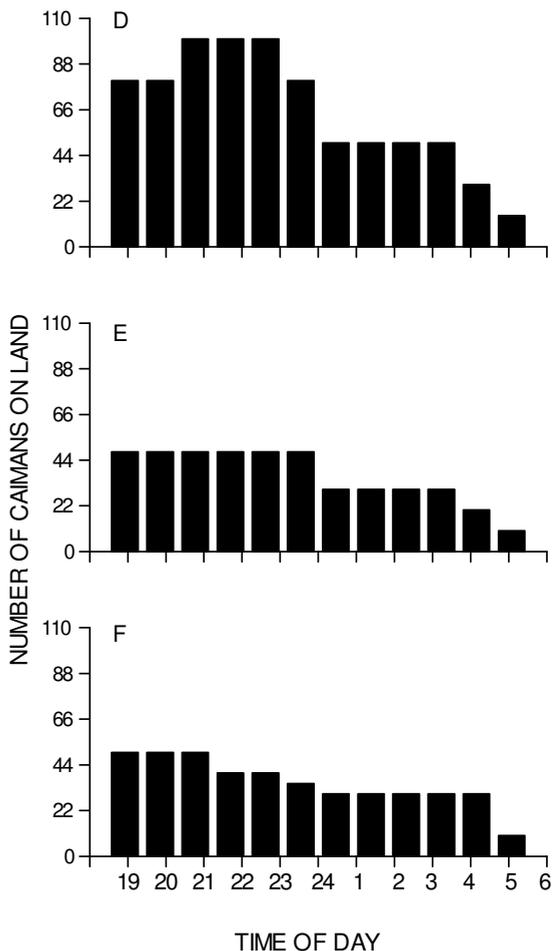
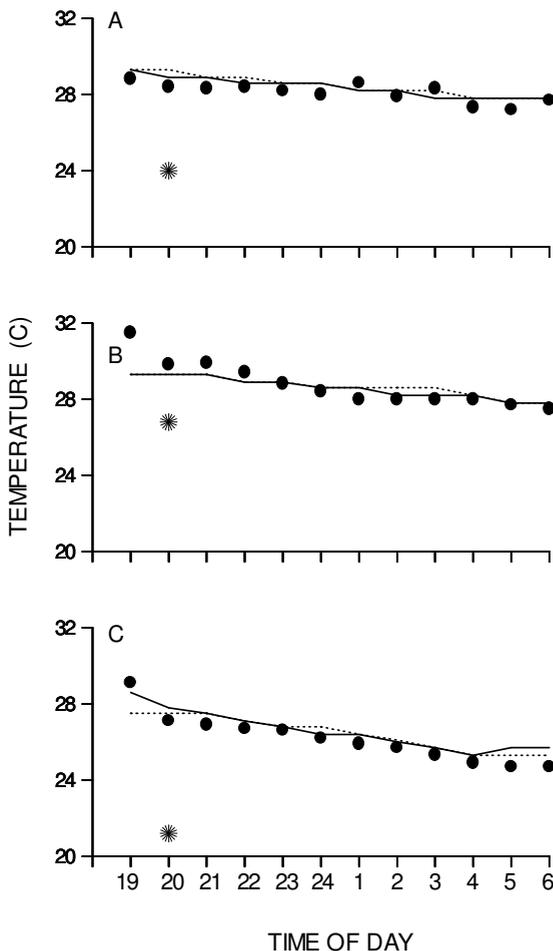


FIG. 6. Mean body temperatures of 14 caimans in a pool in the river (filled circles), air temperature (asterisks), water temperature at the surface (solid line), and water temperature at 60 cm depth (dotted line) between 1900 hrs and 0600 hrs on 28 October (A), 29 October (B), and 6 November 1999. Numbers of caimans on land beside the pool at hourly intervals on 28 October (D), 29 October (E), and 6 November 1999 (F).

cated a very strong relationship between mass and temperature for caimans with masses of <3.3 kg ($CT=20.7+2.167 \times \text{mass}$, $r^2=0.494$, $N=73$, $P<0.001$), and a much smaller effect of mass on mean nocturnal temperature for larger animals ($CT=27.6+0.055 \times \text{mass}$, $r^2=0.020$; $N=358$, $P=0.008$).

In the warm season (October to April), there were no hatchlings in the population and individuals with body masses <3.3 kg had temperatures similar to those of adults (Fig. 5B). In this season, body mass explained only about 1.5% of the variation in nocturnal body temperatures ($CT=30.6+0.035 \times \text{mass}$, $r^2=0.015$, $N=316$, $P=0.035$).

SHUTTling BEHAVIOUR AT NIGHT

Caimans in a pool in the river area were observed at night on 28-29 October, and 6 November 1999. The number of caimans on land was estimated at hourly intervals. As the caimans had to be illuminated with a spotlight during counts, the number of caimans was estimated quickly in intervals of 10 to avoid disturbance. The caimans undertook movements between water and land similar to those undertaken during the day, and there were large numbers of caimans on land throughout the night, until about 0500 hrs (Fig. 6D, E, F). Fewer caimans were seen on land on the second and third nights, but it is not known whether this resulted from a reduction in number of caimans using the pool, or a reduction in the proportion leaving the water.

The body temperatures of 14 caimans in the pool were monitored by radio telemetry during the observation period. We could not distinguish individual caimans at night, but assume that the monitored caimans showed similar shuttling behaviour to the other individuals. Air temperatures were well below water temperatures at the beginning of the night, and the difference probably increased throughout the night. The mean temperature of the 14 caimans was similar to water temperatures, and decreased slowly over the night (Fig. 6A, B, C).

TEMPERATURES OF GRAVID FEMALES

Five females with well developed ovarian follicles were monitored in the warm season. Mean body temperatures ($t_{4.3}=-0.412$, $P=0.70$) and standard deviations of body temperature ($t_{7.2}=-1.533$, $P=0.168$) of those females were similar to those of other females.

DISCUSSION

Body temperatures of free ranging *Caiman crocodilus yacare* varied strongly throughout the year, in concert with ambient temperatures, and the range of temperatures recorded (16.9-37.4 °C) was similar to those recorded in the literature for captive and free ranging crocodilians (Colbert *et al.*, 1946; Cott, 1961; Johnson *et al.*, 1976; Diefenbach, 1975; Grigg *et al.*, 1998). In the cool months, with alternating cold and hot days, the mean body temperature of caimans (26 °C) was lower than in the hotter part of the year (30 °C). Pre-

ferred temperatures may change seasonally in *Crocodylus johnstoni* (Seebacher & Grigg, 1997). We did not record operative temperatures, and therefore cannot address preferred temperatures in the Pantanal caiman. However, excluding one period in which a strong cold front passed through the study site, maximum temperatures did not vary between the warm and cool seasons, suggesting that the caimans were attempting to attain similar temperatures in both seasons.

Several authors have discussed the effect of body mass on temperature patterns shown by crocodilians (Smith, 1979; Diefenbach, 1975), but only Grigg *et al.* (1998) demonstrated an effect, and then only for very large (>100 kg) individuals. Variation in mass of caimans (3 to 42 kg) was not significantly related to the mean temperature of caimans, but significantly affected the amplitude of temperature fluctuations. Temperatures of small caimans fluctuated more than those of large caimans. The smaller fluctuation of body temperatures of large individuals has been attributed to thermal inertia in large lizards, turtles and crocodilians (Read *et al.*, 1996; Grigg *et al.*, 1998).

Although mass generally had a negligible effect on mean body temperatures of caimans, it was important in specific periods. At the beginning of the night, body temperatures of small caimans were lower than large caimans, especially in the cool season, probably due to the high specific heat of water, and the larger surface area to mass ratio of small caimans (Grigg & Seebacher 2001). As caimans forage principally at night (Lang, 1987a), differences in body temperature could have a disproportionate effect on fitness during this period.

In the river area, the amplitude of daily temperature fluctuations was greater than in the lake area. Habitat affects survival of eggs and sex ratios of hatchlings (Campos, 1993), but little is known of the effect of habitat on survival and growth of caimans post hatching. As the lakes have more cover, lower densities of large caimans, and lower temperature fluctuations, they may be important resources for small caimans, especially in the dry season.

Water has a fundamental role in thermoregulation of crocodilians (Lang, 1987b), because thermal conductance and specific heat of water are higher than those of the air. Caimans left the water during the day and the night during both seasons. However, they obtained temperatures well above those of the water only during the day in the cool season. During the warm season, body temperatures were similar to water temperatures, independent of whether the caimans were on land or in the water, and whether they were in the sun or in the shade. As the effect of shuttling onto land on body temperatures was minimal during this season, much of the shuttling may have taken place for reasons other than thermoregulation. Caimans possibly moved between the water and land for social reasons (Lang, 1987a; Seebacher & Grigg, 1997) and/or to reduce the growth of fungi, algae or bacteria on the skin (Moll & Legler, 1971; Pritchard & Greenhood, 1968). In the months of

October and November, the lakes and pools in the rivers become very shallow and algae and bacteria accumulate due to the high density of caimans and dying fish (Campos *et al.*, 1994).

When brooding eggs, *Python molurus* can regulate its body temperature, and the temperature of its eggs, by increasing metabolic rate through muscular contractions (Van Mierop & Barnard, 1976). Female lizards may decrease their body temperatures when gravid (Tosini & Avery, 1996). However, in this study, the body temperatures of five female caimans in the river area with large ovarian follicles were similar to those of female caimans without well developed ovarian follicles. Gravid female lizards may seek higher temperatures because the eggs are kept in the oviducts for long periods after fertilization and females can control the temperature of embryos (Yaron, 1985). Embryos of crocodylians are less advanced at the time of laying than those of most lizards and snakes (Hubert, 1985), with most development occurring in the nest (Ferguson, 1987). It is the nest that keeps the temperatures of eggs relatively high and constant (Magnusson *et al.*, 1990).

The caimans seemed to be largely thermoconformers in the warm season when air and water temperatures generally were above 28 °C. In the cool season, when water temperatures were around 20 °C, the caimans alternated between the water and the air depending on which was hotter. It is probable that the majority of the crocodylians are usually thermoconformers, in the sense that thermoregulation has a lower priority than activities such as hunting, social interactions, and the need to avoid parasites in the water, when available water temperatures are above 28 °C. However, the caimans seemed to thermoregulate actively, selecting warmer positions when water temperatures were below 28 °C. It is probable that the capacity to accept relatively low temperatures is necessary for nocturnal aquatic predators that have few options to thermoregulate during their period of greatest foraging activity.

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