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# Body Temperature Null Distributions in Reptiles with Nonzero Heat Capacity: Seasonal Thermoregulation in the American Alligator (*Alligator mississippiensis*)

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## ABSTRACT

Regulation of body temperature may increase fitness of animals by ensuring that biochemical and physiological processes proceed at an optimal rate. The validity of current methods of testing whether or not thermoregulation in reptiles occurs is often limited to very small species that have near zero heat capacity. The aim of this study was to develop a method that allows estimation of body temperature null distributions of large reptiles and to investigate seasonal thermoregulation in the American alligator (*Alligator mississippiensis*). Continuous body temperature records of wild alligators were obtained from implanted dataloggers in winter ( $n = 7$ , mass range: 1.6–53.6 kg) and summer ( $n = 7$ , mass range: 1.9–54.5 kg). Body temperature null distributions were calculated by randomising behavioural postures, thereby randomly altering relative animal surface areas exposed to different avenues of heat transfer. Core body temperatures were predicted by calculations of transient heat transfer by conduction and blood flow. Alligator body temperatures follow regular oscillations during the day. Occasionally, body temperature steadied during the day to fall within a relatively narrow range. Rather than indicating shuttling thermoregulation, however, this pattern could be predicted from random movements. Average daily body temperature increases with body mass in winter but not in summer. Daily amplitudes of body temperature decrease with increasing body mass in summer but not in winter. These patterns result

from differential exposure to heat transfer mechanisms at different seasons. In summer, alligators are significantly cooler than predictions for a randomly moving animal, and the reverse is the case in winter. Theoretical predictions show, however, that alligators can be warmer in winter if they maximised their sun exposure. We concluded that alligators may not rely exclusively on regulation of body temperature but that they may also acclimatise biochemically to seasonally changing environmental conditions.

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## Introduction

Regulation of body temperature plays an important role in ensuring that biochemical and cellular processes can proceed at a rate that is near optimal for an animal, thereby maximising its fitness (Segal and Crawford 1994; Feder et al. 2000). Ectotherms exchange heat with their environment by physical mechanisms (radiation, convection, and conduction), whereas the heat produced by the metabolic breakdown of energy-rich substances obtained in food is negligible. It is widely accepted that reptiles behaviourally control heat exchange with their environment in such a way that body temperature remains within a narrow range at which physiological processes are optimal (Huey 1974; Huey and Bennett 1987).

It is also possible, however, that animals respond to changing environmental conditions by modifying their biochemical characteristics, for example, rather than always attempting to maintain stable body temperatures. Such adaptive phenotypic responses (acclimatisation) are well known to occur seasonally in aquatic ectothermic invertebrates and vertebrates (Crawford et al. 1999; Wilson and Franklin 1999; Guderley et al. 2001) that live in thermally homogenous environments that preclude behavioural thermoregulation. It may not be valid, therefore, to assume a priori that animals, particularly ectotherms with their negligible metabolic heat production, always regulate body temperature to attain a single “preferred” or “selected” temperature range. Instead, it is appropriate to ask whether or not organisms regulate body temperature at all. This question is by no means novel, and since the seminal work by Heath (1964), numerous investigations have aimed to identify the occurrence of thermoregulation by comparing measured body temperatures to null distributions representing body temperature dis-

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tributions of nonthermoregulating, randomly moving hypothetical animals.

The methodology most commonly employed in studies on thermoregulation of reptiles is that proposed by Hertz (1992) and Hertz et al. (1993), which compares field body temperatures and random operative temperatures (either calculated or measured with physical models) with the "selected" body temperature of the study organism determined in a laboratory thermal gradient (e.g., Webb and Shine 1998; Christian et al. 1999; Angilletta 2001; Blouin-Demers and Weatherhead 2001; Niewiarowski 2001; Shine and Kearney 2001). Although it is excellent for small species, a major problem is that the methodology is inappropriate for larger animals because random operative temperature distributions do not represent the potentially attainable body temperatures of animals with non-negligible heat capacity (see Bakken 1992). As body mass increases, internal thermal gradients and their rate of change become increasingly important in defining body temperatures and heat exchange with the environment (Turner 1987; O'Connor 2000), and operative temperatures (which are defined for animals with zero heat capacity; Bakken and Gates 1975) represent animal surface temperatures. To estimate potentially available (core) body temperatures (i.e., random null distributions) of animals with nonzero heat capacity, it is necessary to consider transient temperatures rather than surface or equilibrium temperatures (Seebacher 2000). If an animal with nonzero heat capacity remained long enough in a thermally homogenous environment, its internal body temperature gradients and the rate of change of those gradients would approach zero as the animal reaches equilibrium (steady state) with its thermal environment. At equilibrium, core body temperatures would equal surface temperatures, and both could be represented by operative temperatures (*sensu* Bakken and Gates 1975). It is, however, unlikely that terrestrial animals with nonzero heat capacity often reach thermal equilibrium with their environment, because of animal movement, and temporal changes in the thermal environment during the solar day. Hence, equilibrium temperatures, regardless of how they were calculated or measured, will rarely represent the potentially available body temperatures of active animals in the wild.

It was the aim of this study to develop a method that allows calculations of random transient body temperature null distributions for animals of nonzero heat capacity. We investigated whether or not a large reptile, the alligator (*Alligator mississippiensis*), regulates its body temperature seasonally by measuring body temperatures in the field. Field body temperatures were compared with calculated random body temperature distributions in order to assess whether or not thermoregulation occurred and how the thermal response may change with season.

Alligators are an excellent study organism for this investigation because they are a large reptile and the most temperate modern crocodylian, which makes it likely that thermal ad-

aptations, either behavioural and/or physiological, have evolved in this species. Moreover, their relative temperate distribution raises the question of how their thermal biology compares with tropical species. Limited data available on body temperatures of free-ranging alligators (Spotila 1974; Smith 1975) indicate that their patterns of body temperature may be fundamentally different from that of similar-sized crocodiles, which has led to speculations that there may be phylogenetic differences between the two families (Grigg and Seebacher 2001). Small tropical crocodiles (*Crocodylus johnstoni*) thermoregulate behaviourally by shuttling between water and sun so that their body temperature forms a more or less stable plateau during the day, although there are nonetheless significant differences between winter and summer (Seebacher and Grigg 1997). The larger *Crocodylus porosus* does not display the shuttling behaviour seen in the smaller species; it changes its behaviour patterns over a longer time period, between night and day and between seasons, so that body temperatures fluctuate sinusoidally during the day rather than forming a plateau (Grigg et al. 1998; Seebacher et al. 1999). The data available from *A. mississippiensis* (Spotila 1974; Smith 1975) indicate that the body temperature patterns even of small individuals are similar to those of the larger *C. porosus* rather than to the similar-sized *C. johnstoni*.

## Material and Methods

### Field Study

Alligators were captured by noose in the wild at the Rockefeller Wildlife Refuge, Louisiana (29°40'N, 92°50'W), during June/July 2001 (summer) and February 2002 (winter). In each season, 20 animals were implanted with temperature loggers (iButton thermocron, Dallas Semiconductor), and seven of those animals were also implanted with a temperature-sensitive radio transmitter. Radio telemetry proved to be ineffective because of the unexpectedly high salinity of the water. Of the 20 animals implanted with loggers each season, data were obtained from seven animals recaptured in summer and from seven in winter (note that there was no overlap of study animals between winter and summer). The loggers, which were flat disks with a diameter of 18 mm, were programmed to record temperature every 10 or 15 min, and we obtained continuous body temperature data for an average of 10.3 d ( $\pm 1.3$  SE, range 8–17 d) from each recaptured animal in summer and for 7.6 d ( $\pm 1.3$  SE, range 5–13 d) in winter. However, except for descriptive representations, only those days for which all study animals per season were sampled concurrently were analysed to avoid bias owing to climatic differences between days; this resulted in a sample size of 5 d from each study animal in summer and in winter, except for two animals for which only 4 d were available in summer. Body mass of the study animals ranged from 1.59 to 53.64 kg (mean  $14.97 \pm 7.11$  SE) in winter (three female and four male) and from 1.93 to 54.54 kg (mean  $15.90 \pm 6.87$  SE) in summer (four female and three male). Total length ranged

Table 1: Variables used in the analysis, as well as their symbols and units

Symbol	Variable	Units
$\alpha$	Thermal diffusivity	$\text{m}^2 \text{s}^{-1}$
$\zeta_n$	Root of transcendental equation	
$\theta$	Dimensionless temperature	
$\nu$	Kinematic viscosity	$\text{m}^2 \text{s}^{-1}$
$A$	Surface area	$\text{m}^2$
Fo	Fourier number	
$h_a$	Convection coefficient (air)	$\text{W m}^{-2} \text{K}^{-1}$
$h_w$	Convection coefficient (water)	$\text{W m}^{-2} \text{K}^{-1}$
$J_n$	Solutions for Bessel equations	
$k$	Thermal conductivity	$\text{W m}^{-1} \text{K}^{-1}$
$l$	Length	m
$L$	Skin thickness	m
$L'$	Characteristic dimension	m
Nu	Nusselt number	
Pr	Prandtl number	
$Q_{\text{abs}}$	Absorbed solar radiation	$\text{W m}^{-2}$
$r$	Radius	m
$r^*$	Dimensionless spatial variable	
Re	Reynolds number	
$t$	Time	
$T_a$	Air temperature	$^{\circ}\text{C}$
$T_c$	Operative temperature	$^{\circ}\text{C}$
$T_g$	Ground temperature	$^{\circ}\text{C}$
$T_w$	Water temperature	$^{\circ}\text{C}$
$\nu$	Fluid speed	$\text{m s}^{-1}$

from 0.84 to 2.45 m (mean  $1.46 \pm 0.22$  SE) in winter and from 0.89 to 2.44 m (mean  $1.55 \pm 0.19$  SE) in summer.

Dataloggers and transmitters were surgically implanted into the peritoneal body cavity via a 3–4-cm incision in the right flank of the alligators, just anterior to the hind leg. Surgery was performed using sterile techniques and a local anaesthetic (Xylocaine). Similar procedures used in crocodiles and lizards previously did not have any detrimental side effects (Seebacher and Grigg 1997, 2001). Data from the first 2 d after animals were released were not used in the analysis. Solar radiation, shallow and deep water temperatures, air temperature, and wind speed were measured every 5 min during fieldwork by sensors (Sol Data [Denmark] pyranometer, LM335 semiconductor temperature sensors, and a Pacific Data Systems [Australia] anemometer) connected to a multichannel datalogger (Data Electronics, Australia).

### Theoretical Analysis

Changes in behavioural postures alter the proportions of animal surface area exposed to different avenues of heat transfer (convection in air, convection in water, conduction to the ground,

and absorption of solar radiation) and, thereby, change operative temperatures experienced by animals (Seebacher 1999). Behavioural thermoregulation presumes that animals behave nonrandomly with respect to their thermal environment (i.e., expose themselves nonrandomly to different mechanisms of heat transfer) so that if behavioural thermoregulation occurred, body temperature distributions should be different from those of a randomly moving animal in a heterogeneous thermal environment. Here, we calculated body temperature null distributions of a randomly moving animal by randomising relative proportions of alligator surface area exposed to different heat transfer mechanisms (=behaviour). Operative temperatures, that is, animal surface temperatures, were calculated for each random “behavioural” posture, and core body temperatures were calculated from the operative (surface) temperatures by transient heat transfer analysis incorporating conduction through the body wall as well as convection by blood flow. Note that the term “operative temperature” is used here in the sense of Bakken and Gates (1975, p. 261), who defined it as “the temperature of an inanimate object of zero heat capacity, with the same size, shape, and radiative properties as the animal and exposed to the same microclimate,” or, in other words, the surface temperature of an animal with nonzero heat capacity.

Random behavioural postures were determined by randomising the relative proportion of alligator surface area out of the water and then determining the relative importance of different heat transfer mechanisms acting at the animal surface in such a way that the overall posture was consistent with physical reality. Null (random) distributions of body temperature were calculated from operative temperatures, which were based on behavioural postures that were determined every 5 min, that is, with each new measurement of environmental parameters, by randomly assigning (using a random number generator) the proportion (0 to 1) of total possible alligator surface area exposed above water. Note that the maximum possible alligator surface area that can be exposed to air is two-thirds (0.67) of the total surface area, because the ventral side must be in contact with the ground or water (Muth 1977). For example, a randomly assigned proportion of 0.8 of total possible surface area exposed to air indicates that  $0.8 \times 0.67 \times$  total surface area is exposed to convection in air. Furthermore, solar radiation is absorbed over the silhouette area (0.33) of the exposed area (Muth 1977), so that in the previous example, radiation would be absorbed over  $0.8 \times 0.67 \times 0.33 \times$  total surface area. The environment at the study site, extensive marsh, was such that there were no tall shading trees or shrubs, and it was assumed that any parts of the alligators out of the water were exposed to sun. Moreover, behavioural observations showed that alligators commonly rested on dense floating vegetation so that the underside would be in contact with water rather than with the ground. In the calculations of operative temperatures, it was therefore assumed that the underside of alligators was in

contact with the ground only when they were fully out of water (proportion exposed = 1, i.e.,  $0.67 \times$  total surface area exposed to air, and  $0.33 \times$  total surface area in contact with the ground); otherwise, the proportion of alligators not exposed from water was assumed to exchange heat by convection in water.

In addition to estimating body temperature null distributions of randomly moving alligators when alligators were “allowed” to move between being fully submerged in water and basking on land (range of proportions of surface areas exposed = 0–1) at any time of day, some simulations were aimed at testing more specific hypotheses. Hence, to estimate whether or not alligators maximised heat gain in winter, simulations were conducted where the random proportions of exposed surface area were constrained to fall within 0.75 to 1 during the day, and alligators were assumed to remain in water when water temperatures exceeded operative temperatures on land at night.

Surface areas of alligators were calculated using the “polynomial” technique described in Seebacher et al. (1999) and Seebacher (2001). All simulations of random body temperature were repeated 100 times, and the means of the 100 random simulations were used in the analysis comparing measured body temperatures to null distributions.

Operative temperatures were determined for each randomised posture using environmental parameters measured in the field at that time. Operative temperatures were calculated by solving a steady state energy balance equation (Bakken and Gates 1975; Tracy 1982). The resulting equation was

$$T_e = \frac{Q_{\text{abs}} + h_w AT_w + h_a AT_a + k/LAT_g}{h_w A + h_a A + k/LA},$$

where  $Q_{\text{abs}}$  = absorbed solar radiation,  $h_a$  = convection coefficient in air,  $h_w$  = convection coefficient in water,  $A$  = body surface area,  $T_a$  = air temperature,  $T_w$  = water temperature,  $T_g$  = ground temperature,  $k$  = thermal conductivity (tissue, including muscle and blood =  $0.5 \text{ W m}^{-1} \text{ K}^{-1}$  [Bowman et al. 1978]), and  $L$  = skin thickness. Convection coefficients were calculated according to Churchill and Bernstein’s (1977) definition of the Nusselt number:

$$\text{Nu} = 0.3 + \frac{0.62\text{Re}^{0.5}\text{Pr}^{0.33}}{[1 + (0.4/\text{Pr})^{0.67}]^{0.25}[1 + (\text{Re}/282,000)^{0.625}]^{0.8}},$$

where  $\text{Re}$  = Reynolds number ( $\text{Re} = vL/\nu$ , where  $v$  = fluid speed,  $L$  = characteristic dimension of solid, and  $\nu$  = kinematic viscosity of the fluid: air =  $15.89 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $300^\circ\text{K}$ , water =  $85.24 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $300^\circ\text{K}$ ) and  $\text{Pr}$  = the Prandtl number ( $\text{Pr} = \nu/\alpha$ , where  $\alpha$  = thermal diffusivity:

air =  $22.50 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $300^\circ\text{K}$ , water =  $1.47 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  at  $300^\circ\text{K}$ ). Convection coefficients can be calculated from

$$\text{Nu} = \frac{hL}{k},$$

where  $h$  = convection coefficient and  $k$  = thermal conductivity (air =  $0.026 \text{ W m}^{-1} \text{ K}^{-1}$  at  $300^\circ\text{K}$ , water =  $0.61 \text{ W m}^{-1} \text{ K}^{-1}$  at  $300^\circ\text{K}$  [Incropera and DeWitt 1996]). Note that convection coefficients were calculated separately for air and water.

Surface conditions (operative temperature) were related to core body temperature by calculating transient heat transfer through the body between the core and the surface. Heat transfer was calculated by considering heat transfer by transient conduction and by blood flow according to methods given in Seebacher (2000). Briefly, heat conduction was calculated by nondimensional analysis for an infinite cylinder. The initial equation was (Incropera and DeWitt 1996)

$$\frac{\partial^2 \theta}{\partial (r^*)^2} = \frac{\partial \theta}{\partial \text{Fo}},$$

where  $\theta$  is the dimensionless temperature  $(T_b - T_e)/(T_i - T_e)$  (where  $T_i$  = initial  $T_b$ ),  $r^* = r/l$  (where  $r$  = radius and  $l$  = length of cylinder), and  $\text{Fo}$  = Fourier number ( $\text{Fo} = \alpha t/r^2$ , where  $t$  = time). This equation has a series solution for the cylinder midline temperature (Schneider 1955):

$$\theta_0 = \sum C_n e^{(-\zeta_n^2 \text{Fo})},$$

where the coefficient

$$C_n = \frac{2}{\zeta_n \{J_1(\zeta_n)/[J_0^2(\zeta_n) + J_1^2(\zeta_n)]\}}$$

and  $\zeta_n$  are the positive roots of the transcendental equation

$$\text{Bi} = \zeta_n \left[ \frac{J_1(\zeta_n)}{J_0(\zeta_n)} \right],$$

where  $\text{Bi}$  = Biot number (Incropera and DeWitt 1996). The series solution of the Bessel functions,  $J_0$  and  $J_1$ , were evaluated for the first five roots of  $\zeta_n$  (British Association for the Advancement of Science 1958), and the series converged after 25 terms (Piaggio 1965). Note that the biological validity of the transient heat transfer model has been tested extensively against a large set of field data (Seebacher 2000), and all variables are summarised in Table 1.

Convection of heat via blood flow changes with heart rate, and heat transfer was calculated for flow between the core and a three-dimensional microvascular network situated just beneath the animal surface. Convective heat transfer by blood

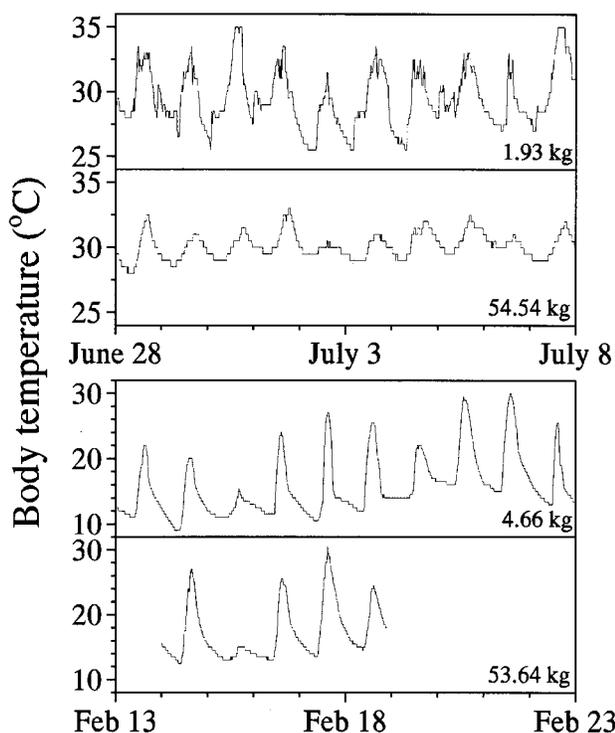


Figure 1. Representative examples of body temperature records from alligators in summer (first panel, 1.93-kg alligator; second panel, 54.54-kg alligator) and in winter (third panel, 4.66-kg alligator; fourth panel, 53.64-kg alligator).

flow was calculated for internal flow through a circular cylinder (blood vessel) with constant surface temperature (Incropera and DeWitt 1996), as described in Seebacher (2000). Heart rate and blood flow are functionally related (Morgareidge and White 1969; Grigg and Alchin 1976), and heart rates were estimated from measurements on crocodiles (*Crocodylus porosus*; C. E. Franklin and F. Seebacher, unpublished data). Hence, heart rate of a 1-kg alligator with a body temperature of 30°C was assumed to be 35 beats  $\text{min}^{-1}$ , and heart rate scaled allometrically with body mass with an exponent of  $-0.25$  and changed with temperature with  $Q_{10} = 2$ . Average daily body temperatures were calculated as the integral of the daily measurements or predictions (Seebacher and Grigg 2001).

## Results

### Field Data

Body temperatures of alligators showed daily oscillations reminiscent of a sinusoidal function (Fig. 1). Body temperatures oscillated regularly with a period of 24 h, and there was little evidence of behavioural thermoregulation in the sense that body temperature formed a more or less stable plateau during

the day as a result of, for example, the animals shuttling between water and land.

There were pronounced seasonal changes in body temperature and in environmental conditions (Figs. 1, 2). Body temperatures of alligators in summer were near water temperatures, which were around 30°C. Maximum operative temperatures (i.e., for an animal fully exposed to sun) were between 30° and 60°C for 12 h during the day (0700–1900 hours) in summer (Fig. 2). In winter, body temperatures were elevated from water temperatures for part of the day, when maximum operative temperatures were high. In contrast to summer, however, operative temperatures in winter exceeded 30°C for 6–7 h only, and water temperatures were considerably cooler, between 12° and 16°C (Fig. 2).

Average daily body temperatures for all alligators were 29.92°C ( $\pm 0.20$  SE) in summer and 15.66°C ( $\pm 0.31$  SE) in winter. In summer, there was no relationship between average daily body temperature and body mass (linear regression:

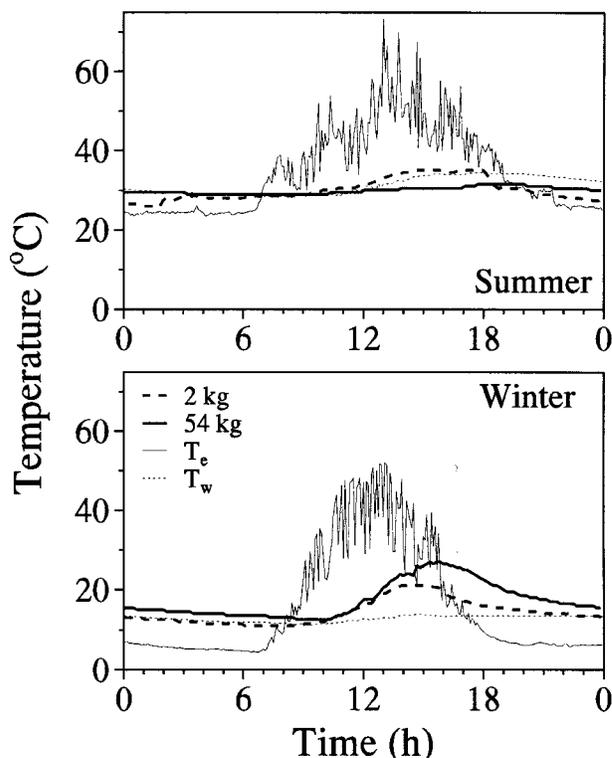


Figure 2. Representative examples of daily fluctuations of maximum (for animals fully exposed in sun on land) operative temperatures ( $T_o$ ) and water temperatures ( $T_w$ ) in summer (top, June 30) and winter (bottom, February 14). For comparison, body temperatures for the same day of the smallest (2 kg = 1.9 kg in summer and 1.6 kg in winter) and the largest (54 kg = 54.5 kg in summer and 53.6 kg in winter) study animals are also shown. Maximum operative temperatures exceeded 30°C for 12 h in summer but only for 6–7 h in winter. Water temperatures were between 26° and 30°C in summer and between 12° and 16°C in winter.

$R^2 = 0.01$ ,  $F_{1,6} = 0.85$ ,  $P = 0.85$ ; Fig. 3). In winter, however, average daily body temperatures increased significantly with increasing body mass (nonlinear regression:  $R^2 = 0.72$ ,  $F_{1,6} = 11.50$ ,  $P < 0.02$ ;  $Y = 14.17 \times \text{mass}^{0.048}$ ), and the 53-kg animal was on average more than 2°C warmer than 2–3-kg alligators (Fig. 3).

Daily amplitude of body temperature (Fig. 4) decreased significantly with increasing body mass in summer (nonlinear regression:  $R^2 = 0.85$ ,  $F_{1,6} = 12.33$ ,  $P < 0.02$ ;  $Y = 4.49 \times \text{mass}^{-0.26}$ ) but not in winter (linear regression:  $R^2 = 0.026$ ,  $F_{1,6} = 0.13$ ,  $P = 0.73$ ).

#### Theoretical Analysis

Simulations of body temperature distributions of randomly moving alligators (null distributions) resembled the shape of the measured body temperature curves (Fig. 5), but in summer, null distributions were warmer than measured body temperatures (Fig. 5, *left*), while the reverse was the case in winter when measured body temperatures exceeded null distributions (Fig. 5, *right*). Overall, measured average daily body temperatures were significantly less than those predicted by the null distributions in summer (Fig. 6; two-sample  $t$ -test:  $t = 12.69$ ,  $df = 32$ ,  $P < 0.0001$ ), but average daily body temperatures pre-

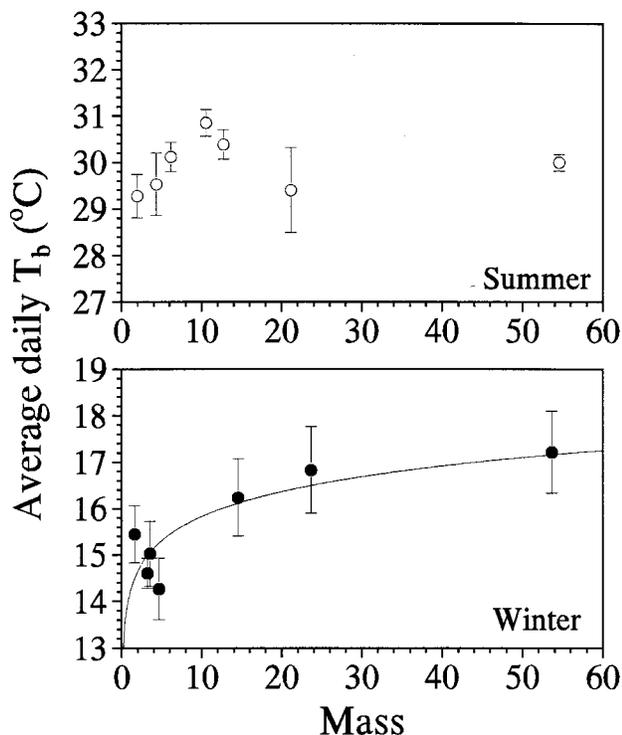


Figure 3. Average daily body temperatures did not change with body mass in summer (average for all alligators: 29.9°C; *top*), but there was a significant increase in average daily body temperatures with increasing body mass in winter (*bottom*).

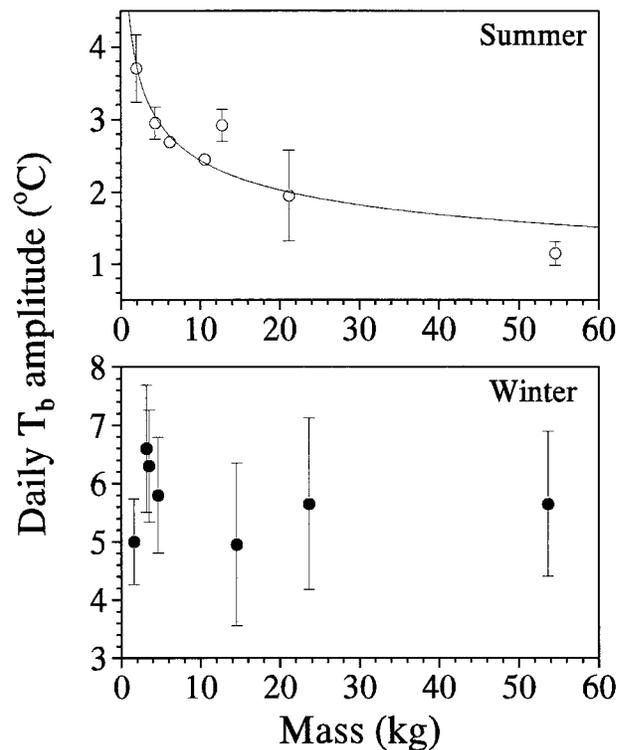


Figure 4. Daily amplitudes of body temperature decreased significantly with increasing body mass in summer (*top*), but it did not change with mass in winter (*bottom*).

dicted by the null distributions were significantly less than measured body temperatures in winter (Fig. 6; two-sample  $t$ -test:  $t = 6.25$ ,  $P < 0.0001$ ).

Interestingly, however, body temperatures measured in winter were significantly less than those predicted for alligators that maximised their sun exposure during the day (i.e., random exposures constrained to within 0.75–1 during the day; Fig. 7). Measured body temperatures were in between those predicted for a randomly moving animal and those of an alligator maximising its sun exposure (Fig. 7, *top*), and average measured daily body temperatures were significantly less than those predicted for alligators maximising their sun exposure ( $t = 7.2$ ,  $df = 34$ ,  $P < 0.0001$ ; Fig. 7, *bottom*).

Occasionally, measured body temperature curves appeared to flatten during the day (e.g., Fig. 1, *first panel*) in a pattern reminiscent of that described for typical “shuttling thermoregulators” (Huey and Slatkin 1976; Seebacher and Grigg 1997). While we performed simulations to predict body temperature distributions of randomly moving animals, it became clear, however, that those patterns may occur simply as a result of the physics of the response in body temperature to fluctuations in the thermal environment. For example, the stable phase observed in the 1.93-kg alligator in summer (Fig. 1, *first panel*;

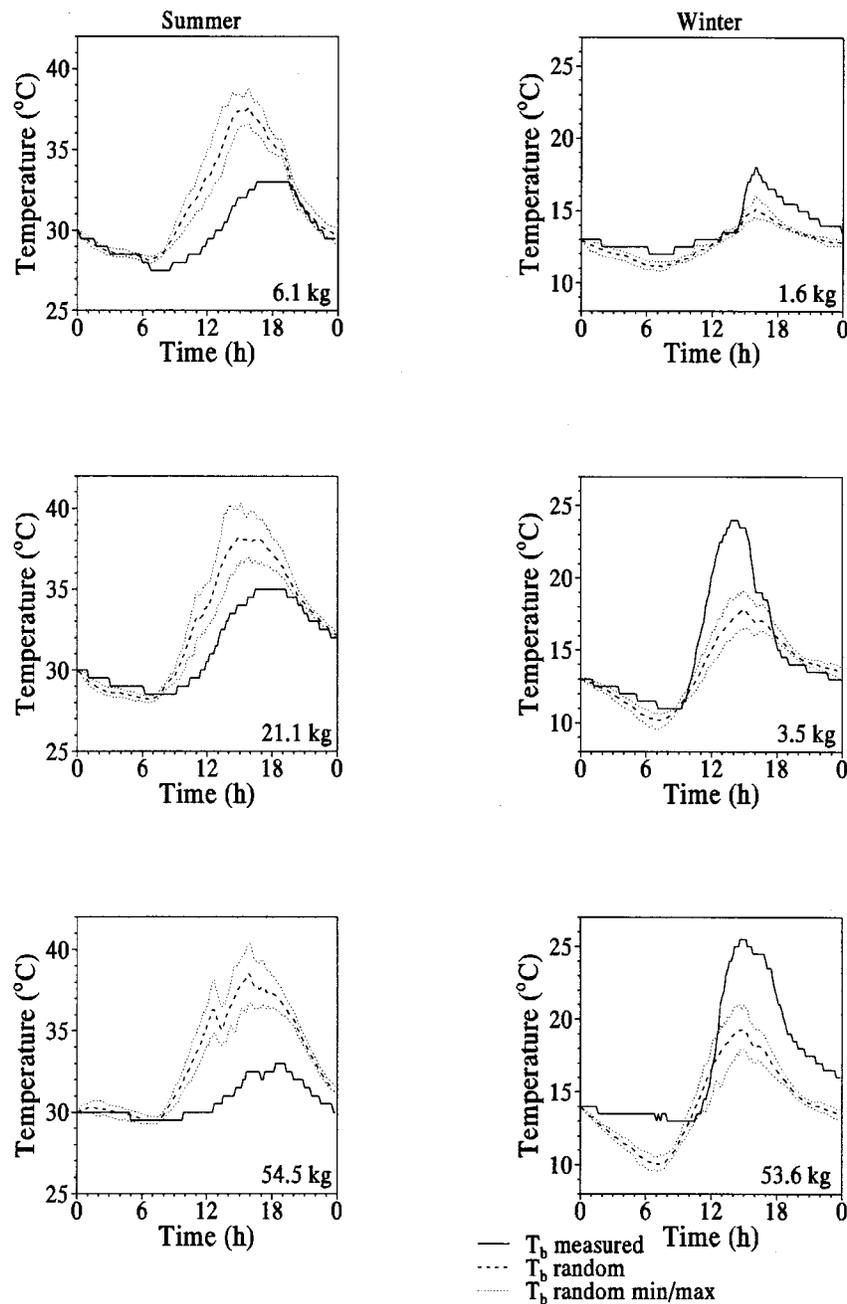


Figure 5. Representative examples of measured daily body temperature records and of null distributions of a randomly moving animal calculated for the same day and the same body mass as the study animal (*left*, summer; *right*, winter; body mass is shown in each panel). Null distributions show the mean of 100 simulations ( $T_b$ , random) as well as the minimum and maximum predictions ( $T_b$ , random min/max). In summer, measured body temperatures were significantly greater than those predicted for a randomly moving animal, while measured body temperatures were significantly less than random in winter.

July 3) was reflected also in the computer simulation when maximum daily exposure was restricted to 0.8 or less to coincide with the measured body temperature magnitude (Fig. 8).

#### Discussion

The patterns of body temperature recorded in this study confirm previous observations that the body temperatures of al-

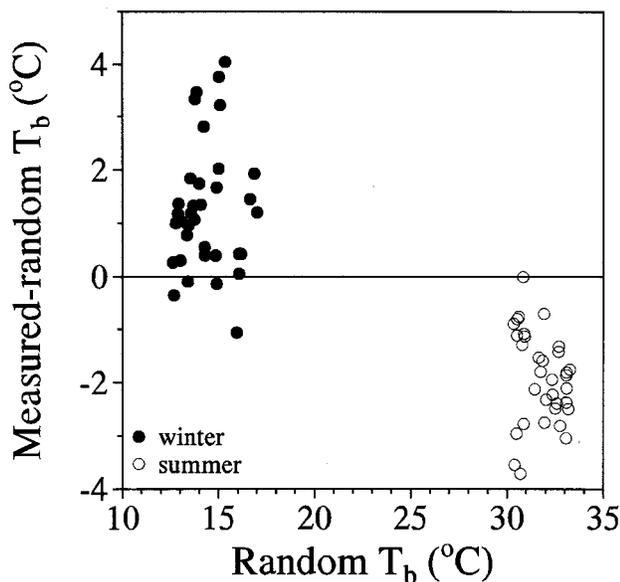


Figure 6. Difference between average daily measured body temperatures and the average daily predicted body temperature of randomly moving animals for winter (filled circles) and summer (open circles). Average daily body temperatures were significantly warmer than random in winter and significantly cooler than random in summer.

alligators fluctuate more or less regularly with a period of 1 d (Spotila 1974; Smith 1975). At least in smaller alligators (<20 kg), this pattern is in contrast to crocodiles (*Crocodylus johnstoni*), which display characteristic shuttling behaviour between basking in the sun and the water (Seebacher and Grigg 1997; Seebacher 1999) that often results in a plateau of body temperature during the day. In larger crocodiles (*Crocodylus porosus*, >30 kg), slower rates of heat transfer render shuttling behaviour between thermally different microhabitats during the day ineffective, and the body temperature of these animals follows harmonic oscillations similar to those observed in alligators in this study (Grigg et al. 1998; Seebacher et al. 1999). There may be fundamental differences in the thermal behaviour between alligators and crocodiles (Grigg and Seebacher 2001). Our data support this notion at least for small alligators (<20 kg) whose body temperature patterns are different from those observed in similar-sized *C. johnstoni*. However, the environment at our study site was very different (extensive, continuous marshes) from *C. johnstoni* habitat (distinct rivers) so that, although alligators have been observed to bask on land, access to terrestrial habitat may be limited, which may at least in part explain differences in body temperature pattern.

There were occasions when body temperatures of alligators steadied during the day to oscillate within a relatively narrow range ( $\pm 1^\circ\text{C}$ ; Fig. 1), which is reminiscent of patterns observed in *C. johnstoni* (Seebacher and Grigg 1997). However, similar fluctuations were reproduced in the random computer simu-

lations, which indicates that such a pattern does not necessarily reflect directed thermoregulatory behaviour but, rather, that it may simply be the result of heat transfer characteristics of the animal with its environment and operative temperature distributions. Note that the random simulations were constrained by a maximum exposure of 0.8, which implies that alligators thermoregulated by avoiding full exposure to sun. Nonetheless, the data imply that while animals may thermoregulate by avoiding extreme environments, predictable and nonrandom shuttling between sun and water is not necessary to produce “preferred body temperature” patterns as observed in *C. johnstoni* (Seebacher and Grigg 1997). This is not to say that “shuttling” behaviour never occurs, but the example serves as a caution when inferring mechanisms from observed patterns. As Heath (1964) has demonstrated very elegantly, thermoregulation can be inferred only when thermoregulatory behaviour has been observed explicitly or when it has been demonstrated that patterns of body temperature are nonrandom.

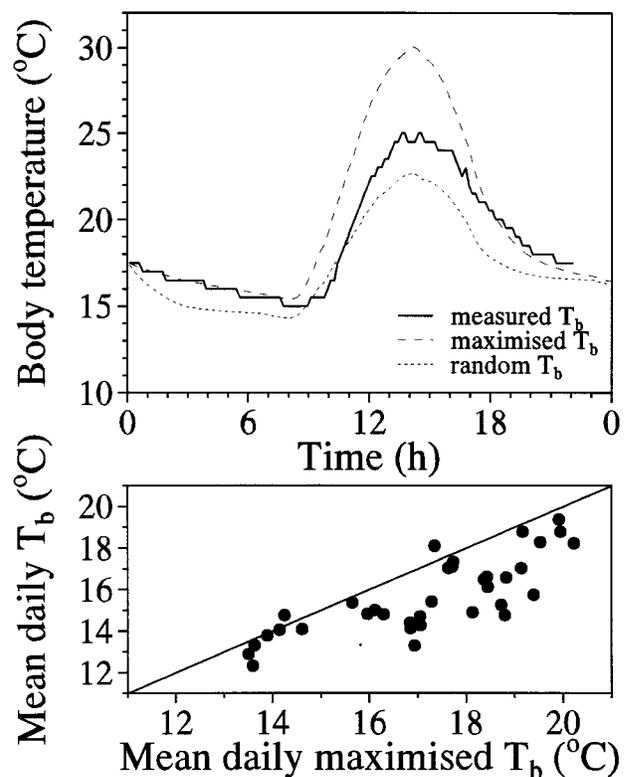


Figure 7. Example of predictions for a daily body temperature record of an alligator in winter that maximised its exposure to sun (i.e., it exposed 0.75–1 of total surface area to sun during the day (maximised  $T_b$ ; top). For comparison, measured body temperature for an animal of the same size (23.6 kg; measured  $T_b$ ) and random body temperature (exposure 0–1; random  $T_b$ ) are also shown. Measured body temperature fell between random and maximised body temperature predictions. Overall, measured average daily body temperatures were significantly less than those predicted for maximised sun exposure (bottom).

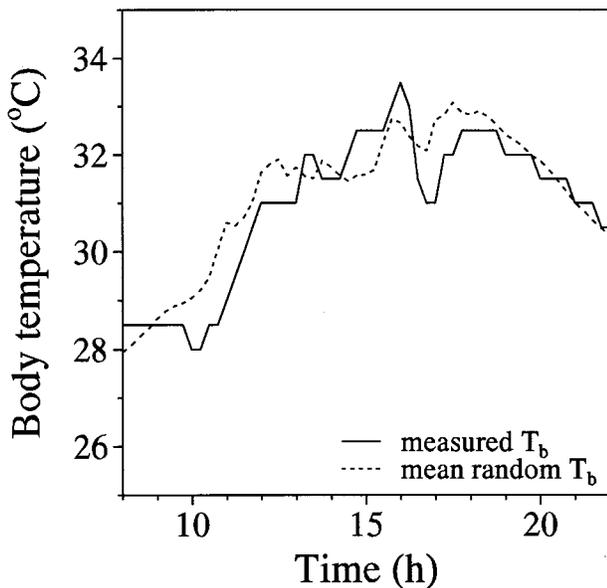


Figure 8. Example of a “plateau” of body temperature fluctuating around 32°C observed in a 1.93-kg alligator in summer (measured  $T_b$ ) and the corresponding prediction of a randomly moving animal (mean of 100 simulations with the constraint that maximum exposure = 0.8; mean random  $T_b$ ) that showed a plateau similar to the “real” alligator.

An increase in average daily body temperature with increasing mass has previously been reported in a crocodile (Seebacher et al. 1999) and in a snake (R. Shine, unpublished data). This phenomenon is explained by the increase in the convective boundary layer thickness as animal size increases (Stevenson 1985; Incropera and DeWitt 1996). Convective heat loss therefore decreases with increasing size and, if animals also absorb heat from shortwave solar radiation, average body temperature will increase (Seebacher et al. 1999), but the increase in body temperature will be modified to a certain extent by the concurrent decrease in relative surface area as animals grow larger. Average daily body temperatures increased in alligators in winter, because animals were exposed to solar radiation, but not in summer, when animals remained mainly in water.

Differences in behaviour may also explain why daily body temperature amplitudes decreased with increasing mass in summer but not in winter. Different-sized animals would experience very similar operative temperatures in summer when mainly submerged in water, so body temperature amplitudes would decrease with increasing mass as a result of decreased convective heat transfer. When exposed to solar radiation in winter, however, the range of operative temperatures experienced by alligators increases with increasing mass, which may counteract mass-related decreases in convective heat transfer so that amplitudes would remain the same, at least over the mass range

of our study animals and assuming that all alligators displayed similar behaviour patterns within a season.

Our data show that reptiles do not always regulate their body temperature within a narrow range (Huey 1974; Huey and Slatkin 1976; Huey and Bennett 1987). We show that alligators behaved nonrandomly with respect to their thermal environment but that they nonetheless displayed marked seasonal differences in body temperature while remaining active. Several species of reptile display seasonal differences in body temperatures (Christian et al. 1983; Seebacher and Grigg 1997), although temperate species are usually inactive during the coldest months (Case 1976; Van Damme et al. 1987), while lower winter temperatures in tropical species may be linked to drier environmental conditions (Christian and Bedford 1996). Water was, however, not restricted at any time of year at our study site. The body temperature of alligators in summer was significantly less than that of randomly moving animals, but in winter, it was significantly greater than random. Nonetheless, summer temperatures were markedly higher than winter temperatures, and in winter, alligators could have been warmer if they maximised their sun exposure during the day. Casual behavioural observations showed that alligators were not inactive in winter; they were observed feeding and moving onto land where terrestrial habitat was available, and all study animals were in very good condition, as indicated by subcutaneous fat stores (revealed during transmitter implantation surgery). How did they manage? A possible explanation is that rather than exclusively relying on regulation of body temperature to a constant level, which in any case would not have been possible because of environmental constraints (see Fig. 7), alligators may acclimatise to seasonal changes in their thermal environment by shifting the thermal sensitivity of physiological/biochemical processes. Such shifts in the thermal sensitivity of physiological performance occur in fish and other aquatic animals. The specific activity of enzymes changes proportionally to temperature, and seasonally constant metabolic rate may be maintained by production of more enzyme at cooler temperatures (Graves and Somero 1982; St. Pierre et al. 1998; Crawford et al. 1999). For example, a teleost fish (*Fundulus heteroclitus*) subjected to the clinal variation in water temperature along the Atlantic coast of North America shows concomitant changes in metabolic enzyme concentration; populations in the colder north have about twice as much enzyme as southern populations so that constant reaction velocity is maintained (Crawford and Powers 1989). Similar patterns may occur in response to seasonally changing thermal conditions (Thibault et al. 1997; Guderley et al. 2001). This hypothesis remains largely untested in reptiles, although metabolic enzyme activity may change with season and winter dormancy in a freshwater turtle (Olson 1987).

In recent years, most studies on reptiles have used the protocol of Hertz et al. (1993) to assess whether or not thermo-regulation occurs (e.g., Angilletta 2001; Blouin-Demers and

Weatherhead 2001). Thermoregulation is assessed by comparing body temperatures and operative temperatures measured in the field to the “selected” body temperature of the study species determined in a thermal gradient. This protocol has been criticised for its use of thermal gradients to determine “selected” body temperatures (Currin and Alexander 1999; Wills and Beaupre 2000) on the grounds that data obtained in the artificial environment of a thermal gradient are not comparable with preferences in the field. In addition, reptiles may not regulate their body temperature within a selected range, or the selected range may change with season, as in alligators in this study and also in crocodiles (Seebacher and Grigg 1997). Employing similar reasoning as forms the basis for Hertz et al.’s (1993) method, it may also be necessary to demonstrate that animals move nonrandomly in thermal gradients, which, of course, leads to a circular argument; if animals moved randomly in a linear thermal gradient, it would be expected that their body temperature coincided with the midpoint temperature of the gradient.

Wills and Beaupre (2000) suggested an alternative protocol that uses a posteriori randomization of field operative temperatures. Measured mean hourly differences between body temperatures and operative temperatures were compared with randomised distributions of such differences to determine whether the observed differences were sufficiently large to be statistically significant. This protocol, as well as Hertz et al.’s (1993), relies on physical models, randomly distributed within the environment, to measure operative temperatures, and operative temperatures are assumed to represent the potentially attainable body temperatures of the organisms under study. By definition, operative temperatures (Bakken and Gates 1975) represent the body temperature of an animal with the same physical characteristics as the study organism but with zero heat capacity. This means that operative temperatures, or equilibrium temperatures, do not represent potentially attainable body temperatures of animals with nonzero heat capacity since they would overestimate the range of available body temperatures. Many studies that have used Hertz et al.’s (1993) protocol have not appreciated this fact so that at least some of their conclusions are rendered invalid. Some workers have accounted for nonzero heat capacity by using water-filled models to represent their study organism (e.g., Wills and Beaupre 2000; Blouin-Demers and Weatherhead 2001). Such models cannot be assumed to respond instantaneously to changing thermal conditions, and their internal temperature is determined by their thermal history. The internal temperature of models (and animals) of nonzero heat capacity varies with the dimension of time on two levels: by the temporal (daily, seasonal) change in climatic conditions and by the movement and behaviour of the animal. Although models may be placed randomly within an environment, their thermal histories would often not be random (unless they are moved regularly and randomly) so

that an a posteriori randomisation procedure is essential (Wills and Beaupre 2000).

We have approached the difficulty of generating null distributions of body temperature for animals of nonzero heat capacity by calculations, rather than by the employment of physical models, and by a priori randomisation, that is, randomising behaviour first and then calculating body temperatures. Physical models of organisms as large as alligators are impractical so that heat transfer calculation are of obvious advantage. This method also differs from other approaches in that the thermal history of each simulation is based on random behavioural sequences, and it allows for predictions of continuous body temperature profiles for any given set of environmental conditions and behavioural constraints. The predictive power of our model, which was based on calculations that have been rigorously tested to accurately represent thermal relations of reptiles in the field (Seebacher 2000), thereby constitutes a powerful tool to explore hypotheses in thermal biology.

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