Thermal relations of large crocodiles, *Crocodylus porosus*, free-ranging in a naturalistic situation

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We monitored behaviour and environmental and body temperatures (T_b) in summer and winter in 11 salt-water crocodiles (*Crocodylus porosus*), of body mass 32–1010 kg, free-ranging in naturalistic captivity in northern Australia. We found pronounced daily cycles in air and water temperatures in both winter (16–33 °C and 20–31 °C, respectively) and summer (21–45 °C and 24–36 °C, respectively). In winter, crocodiles exposed themselves to the sun during the day and stayed in the water at night. In summer, they remained in the water during the day and emerged onto land at night. Body temperature showed a daily cycle the amplitude of which decreased with increasing mass, from 3.5 °C (mass 32 kg) to 1.0 °C (660 kg) in summer, and from 3.5 °C (42 kg) to 1.4 °C (1010 kg) in winter. Underlying the daily cycles in T_b were intermediate (10–13 day, tidal?) and seasonal cycles. Overall, values of modal T_b ranged from 25.1 to 28.7 °C in winter and from 28.4 to 33.6 °C in summer, trending upwards with body size. This pattern of continuous oscillations in T_b , with no daily plateau, is conspicuously different from that seen in crocodilians of small sizes and from the pattern usually regarded as typical of reptiles in general.

Keywords: crocodiles; body temperature; behaviour; operative temperature

1. INTRODUCTION

Our understanding of reptilian thermoregulation comes predominantly from data on lizards and other small and mainly terrestrial diurnal species, in which behavioural events often achieve regulation at a plateau or 'preferred' body temperature (T_b) during their daytime activity period (Diaz 1994; Christian & Weavers 1996; Tosini & Avery 1996). For these short-term behavioural adjustments to be effective in changing and regulating T_b , an animal needs to be of a small size, i.e. have a short thermal time constant (Grigg *et al.* 1979; Robertson & Smith 1981; Diaz *et al.* 1996). Common sense dictates that large reptiles would be unable to show similar patterns because of their long thermal time constants, but there are little or no data available.

The largest living reptiles are the crocodilians, with the possible exception of the wholly aquatic leatherback turtles (*Dermochelys coriacea*). Their conspicuous sun-basking behaviour has long been assumed to be of thermal significance (Cott 1961; Cloudsley-Thompson 1964; Modha 1968), and thermal attribution of their daily movements between water and land go back to the writings of Herodotus and Pliny the Elder. The recognition that behaviour is an important facet of crocodilian thermal relations, as in lizards, has now been confirmed by measurements, mainly from individuals in captivity (see Lang (1987) and Grigg & Gans (1993) for a review). Interestingly, however, a field study by Seebacher &

Grigg (1997) showed that *Crocodylus johnstoni* individuals weighing up to 20 kg are able to maintain their T_b within a narrow range for much of the day by shuttling between water and land, in a pattern reminiscent of many lizards.

Nevertheless, the adults of most crocodilians are much larger than 20 kg and much too large for the 'typical' lizard pattern to prevail. This is because an increase in the thermal time constant with mass (Smith 1976; Grigg *et al.* 1979) means that short-term behavioural adjustments will be ineffective in promoting short-term changes in T_b . However, the nature of the daily and seasonal patterns of T_b that are typical of the crocodilians are, to date, unknown.

In addition, at a particularly large size, a reptile could even be thermostable. This concept is known variously as 'inertial or mass homeothermy' (Colbert *et al.* 1946, 1947; McNab & Auffenberg 1976) and 'gigantothermy' (Paladino *et al.* 1990), and it has received a lot of theoretical attention (Spotila *et al.* 1973, 1991; Dunham *et al.* 1989), particularly in speculation about the thermal relations of dinosaurs. Crocodiles, the largest extant reptiles and the last of the archosaurs, offer opportunities to test theory against empirical data.

With these points in mind, we determined to monitor thermal relations of the salt-water crocodile, *Crocodylus porosus*.

2. MATERIALS AND METHODS

We studied 11 crocodiles over an estimated size range of 2.1 to 5.5 m (32–1010 kg) (table 1), captive in naturalistic surroundings

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Table 1. *The study animals and sampling details*

crocodile	number of days observed	month	season	study site	total length (m)	mass (kg)
1	6	Dec. 1993	summer	pen	2.1	32
2	10	July 1993	winter	pen	2.3	42
3	12	Nov./Dec. 1993	summer	lagoon	2.7	77
4	14	June/July 1993	winter	pen	3.7	233
5	4	July 1993	winter	lagoon	4.2	383
6	9	June/July 1993	winter	pen	4.3	408
7	5	Dec. 1993	summer	lagoon	4.6	520
8	13	July 1993	winter	lagoon	4.6	520
9	4	Dec. 1993	summer	lagoon	4.9	660
10	15	Nov./Dec. 1993	summer	lagoon	5.2	820
11	7	Nov. 1992	summer	lagoon	5.5	1010
11	30	June/July 1993	winter	lagoon	5.5	1010
11	11	Nov./Dec. 1993	summer	lagoon	5.5	1010

at the Edward River Crocodile Farm on Cape York Peninsula, Australia (14°55' S, 141°35' E). Seven individuals were in a large, fenced, natural area comprising a lagoon bordered by grassland and mangroves (lagoon, *ca.* 0.3 km²) containing *ca.* 150 crocodiles of both sexes. Four individuals were studied in a smaller enclosure (pen, *ca.* 2000 m²), housing *ca.* 20 crocodiles, which comprised a pond (70–80% of the area) surrounded by grassy banks with some bushes and trees.

Weighing individuals was not practicable and so we calculated mass from measurements and/or estimates of total body length, using an allometric relationship derived from 190 *C. porosus* ranging from 8 to 120 kg (F. Seebacher, unpublished data). Total lengths were determined by measuring the distance between marks on the ground after a crocodile had moved away, or by estimation in consultation with experienced farm staff (table 1).

We measured air and ground temperatures with calibrated temperature sensors (National Semiconductor LM335, accurate to 0.3 °C) suspended in the shade next to the lagoon, or covered lightly with sand in an open space within the lagoon enclosure. Solar radiation was measured using a tube solarimeter (Irricrop Technologies, Narrabri, Australia). All sensors were connected to a data-logger (Data Electronics, Melbourne, Australia) and measurements were taken every 30 min. We measured water temperature (T_w) with calibrated temperature-sensitive radio transmitters (Sirtrack, accurate to 0.2 °C) suspended in the water at three different places in the lagoon but, in the analysis, we used T_w from the area most frequented by the study animals. We calculated operative environmental temperatures (T_e) as described by Seebacher & Grigg (1997). For this, we estimated (see below) that in winter daytime, crocodiles typically exposed 75% of their surface area to air (and radiation), 25% to water, and had 10% in contact with the ground. At night, crocodiles were 90% submerged in water with only 10% of their surface area exposed to air. We estimated that in summer daytime, 25% of their surface area was exposed to radiation, with 75% in the water, whereas crocodiles moved more onto land at night, with 75% of their surface area exposed to air and 25% in the water. Note that when a crocodile is, for example, 75% exposed to air, it absorbs radiation on the silhouette area of 75% of its body (Muth 1977).

Body temperature was measured using calibrated temperature-sensitive radio transmitters (Sirtrack, New Zealand) placed into chickens and fed to selected crocodiles as pseudogastroliths.

In the lagoon, T_b was measured manually by timing intervals between pulses with a stopwatch. Crocodiles in the pen had less range of movement and we were able to record T_b with a remote sampling system (Grigg *et al.* 1992). During the most intensive sampling period, T_b was measured between approximately 0630 and 2200 from 29 June 1993 to 29 July 1993 (winter) and from 16 November 1993 to 7 December 1993 (summer). An emphasis was placed on obtaining the 'turning points', when the daily T_b minima and maxima occurred. It should be recognized that data acquisition from larger crocodiles in the lagoon was not always straightforward because the observer had to approach close to the animals, often on foot, to get near enough to gain a good signal. This was potentially dangerous and not always possible, therefore, explaining occasional gaps in the data. In addition, crocodiles periodically regurgitated transmitters, which resulted in unequal sample sizes.

We monitored the movement of crocodiles between the water and land in the lagoon by using a scan-sampling methodology (Martin & Bateson 1993). The water surface and shoreline were scanned with binoculars four times per day during the July and November 1993 study periods (period ranges 0600–0700, 0930–1000, 1230–1300 and 1730–1800). All scans were done by the same observer (F.S.) who recorded the number of crocodiles less than 25% emerged from the water, 25–75% emerged, and more than 75% emerged. Scan samples included all crocodiles in the lagoon. Behavioural notes were made whenever possible.

3. RESULTS

(a) *The thermal environment*

Air temperatures in the shade ranged daily from 16 to 33 °C in winter and from 21 to 42.5 °C in summer (figure 1). Water temperatures were 20–31 °C in winter and 24–36 °C in summer (figure 1). Incident solar radiation was slightly less in summer, presumably because of high humidity (figure 1). An unexpected find was a cycle in environmental temperatures with a period of 10–13 days and an amplitude of 1–2 °C. Our working hypothesis is that this derives from the (somewhat irregular) tidal cycle in the Gulf of Carpentaria: at neap tides, extensive mud-flats are exposed (1–2 km wide), which may modify the temperature of the onshore breeze as it blows over the sun-exposed mud-flat.

Figure 1. Air temperatures (open circles) and water temperatures (filled circles) and solar radiation (lines) for (a) the June/July 1993 sampling period (italic scale of x-axis) and (b) the November/December 1993 sampling period. Note daily (period = 1 day) and intermediate (period = 10–13 days) cycles in air and water temperatures.

Figure 2. Daily basking behaviour in winter and summer (counting all crocodiles in the lagoon).

(b) Movement between water and land

There were significant differences in emergence from water, i.e. exposure to sun, between the time of day, time of year and their interaction (log-linear model, total d.f. = 190, all $p < 0.001$). Most crocodiles were 25–75% or more than 75% exposed to sun in winter, except during the early morning hours (figure 2, winter) when operative temperatures were still low (see below). Conversely, in summer few crocodiles were seen with more than 25% of their body exposed to sun during the day (figure 2, summer).

We noted that at night crocodiles stayed submerged in water in winter, but moved onto land in summer.

Figure 3. Examples of daily patterns of body temperature (filled circles) and operative temperature (open circles) for crocodile 1 (32 kg) in summer, crocodile 2 (42 kg) in winter and crocodile 11 (1010 kg) in winter.

(c) Body temperature

Body temperature cycled daily within the range of T_e (figure 3) but, although the amplitude of T_e increased with the mass of the crocodiles, T_b amplitude decreased. Operative and, hence, body temperatures did not oscillate as a symmetric sinusoidal wave over the daily period of 24 h. Rather, the relatively short interval from sunrise to the solar zenith (6–7 h in winter and 7–8 h in summer) causes a short heating phase in the morning followed by a longer cooling phase; this asymmetry in the daily cycle of T_b and T_e is best described by a Fourier series (figure 3).

The daily T_b amplitude of small crocodiles (32 kg and 42 kg, figure 3) approached that of the relevant T_e , whereas the T_b of our largest crocodile (1010 kg, figure 3) remained nearly stable despite T_e fluctuations of more than 20 °C. During both winter and summer, T_b amplitude decreased allometrically with mass (figure 4), except in two crocodiles (4 and 10). Interestingly, each of these crocodiles was the second largest male in its respective enclosure and was subjected to frequent aggression by the dominant male (crocodiles 6 and 11 in the pen and lagoon, respectively). In the case of crocodile 4, these encounters led to it being chased back into the water whenever it emerged. Body temperature tracked water temperature much more closely in this crocodile, explaining its low T_b (figure 8) and T_b amplitude (figure 4). Similarly, crocodile 10 was challenged whenever it attempted to enter the main part of the lagoon. This may have compromised its thermal behaviour but, because the animal was usually obscured by mangroves, we were unable to observe its behaviour.

Underlying daily oscillations, the T_b of all crocodiles cycled over a period of 10–13 days (figure 5). The amplitude of these oscillations (1.2–1.4 °C) was independent of mass, and even the 1010 kg crocodile had a time constant too short to dampen oscillations within such a long period. Similarly, T_b fluctuated seasonally, as is demonstrated by

Figure 4. Daily amplitudes of cycles in body temperature ($\pm 95\%$ confidence intervals) seen in crocodiles in winter (open circles) and summer (filled circles). Crocodiles 4 (open triangle) and 10 (filled triangle) are identified separately because their behaviour differed from that of the other crocodiles (see text). Amplitudes decreased allometrically: winter, $y = 9.698x^{-0.276}$, $R^2 = 0.92$; summer, $y = 16.859x^{-0.459}$, $R^2 = 0.98$.

Figure 5. Examples of daily and intermediate oscillations in body temperature (open circles) and operative temperature (lines) for crocodile 8 (520 kg) in winter and crocodile 3 (77 kg) in summer.

data from our largest crocodile (crocodile 11) (figure 6). Body temperature was warmer in summer (figure 6), but the spread of T_b data is considerably less than the range of the T_e experienced by the animal, and the seasonal modal T_b values are within 5°C of each other (figure 8).

A summary of T_b oscillation is provided in figure 7, which shows data from crocodile 8 (daily and intermediate

Figure 6. Relationships between body temperature and operative temperature of crocodile 11 (1010 kg) in different seasons. The panels are in temporal sequence left to right: November 1992, June/July 1993 and November/December 1993. Lines of equality between T_b and T_e are shown in each panel.

Figure 7. Daily, intermediate and seasonal cycles in body temperature; data from crocodile 8 (520 kg; daily and intermediate cycles) and crocodile 11 (1010 kg; seasonal cycle, 1993 data).

cycles) and crocodile 11 (seasonal cycle). Daily oscillations follow a Fourier series with short heating and longer cooling episodes (figure 7, daily cycle), which were superimposed onto an intermediate, 10–13 day oscillation (figure 7, intermediate cycle). The intermediate oscillation is clearly reflected in the daily T_b means (means of daily minima and maxima) plotted in figure 7. Finally, both daily and intermediate oscillations are superimposed onto seasonal oscillations (figure 7, seasonal cycle), and all three together form the thermal profile of a crocodile.

Modal T_b was several degrees warmer in summer than in winter in crocodiles of a similar size (figure 8). There was a slight increase in modal T_b with mass, with a

Figure 8. Relationship between modal body temperature and body temperature range in individual crocodiles in winter (filled circles) and summer (open circles). Data from crocodiles 4 (inverted triangle) and 10 (upright triangle) are identified separately because their behaviour differed from that of other individuals (see text).

significant regression in winter ($y = 25.54 + 0.00305x$, $R^2 = 0.41$, $F = 2.11$, $p < 0.001$) but not in summer ($y = 29.88 + 0.00215x$, $R^2 = 0.29$, $F = 1.68$, $p = 0.26$) (figure 8). Exceptions to this general pattern were, again, crocodiles 4 and 10, as explained above.

Raw data showing the patterns described above are shown in figure 9. Operative temperatures in winter (42 kg, 520 kg and 1010 kg individuals) had a much greater range than those in summer (77 kg, 520 kg and 1010 kg individuals) because of the greater sun exposure chosen by crocodiles, and T_e markedly increased with mass. Despite the greater difference between T_b and T_e in larger animals, T_b became more dissociated from daily fluctuations in T_e as mass increased. The series of data points showing T_b at around 24 °C in figure 9 (winter; 1010 kg) are from one unseasonally cloudy and rainy day.

4. DISCUSSION

Little is known about the patterns of T_b of free-ranging crocodilians, except for *Crocodylus johnstoni* of a mass of up to 20 kg (Seebacher & Grigg 1997). There are some data on the T_b of small *C. niloticus* in the wild (Loveridge 1984) and of free-ranging, small- to medium-sized alligators (Spotila 1974; Smith 1975; Lang 1979). However, most data available on the T_b of crocodilians are single measurements or brief T_b episodes from single individuals, or means of T_b from many individuals. Taken as a whole, previously published data on crocodilian T_b do not elucidate patterns of T_b and have not provided a framework within which to conceptualize crocodilian thermal relations. Most notably, there have been no data relating T_b to body mass, which is clearly a shortfall when one considers that, during growth to adulthood, the mass of the largest crocodilians changes by five orders of magnitude.

Lang (1987) contrasted the thermal relations of *A. mississippiensis* and *C. porosus* based heavily, apparently,

on unpublished material and made some puzzling generalizations about both of them. He reported that alligators move onto land in the morning to warm, choose exposed positions during the day, maintain their T_b at 31–33 °C during the afternoon, and cool overnight to a temperature close to that of the water. Without referring to the location, the season, or the body size of the animals under consideration, this information is of limited value. In contrast to alligators, he reported that *C. porosus* avoid daytime heating by remaining under water for most of the day and cool on land at night, except in 'the southern parts of their range, in mid-winter, where they may remain out of water for longer periods during the day and, in cooler areas, all day'. He went on to say that 'body temperatures rise slowly from 28 °C at sunrise to 30 °C at sunset, and then drop at night', concluding that '*C. porosus* T_b s are low and variable during the day whereas *A. mississippiensis* T_b s tend to be stable and at levels considerably above ambient air and water temperatures'. The source of these generalizations about *C. porosus* is unknown, along with the latitudes at which they were made, the season(s?) and the sizes of the individuals studied, making them difficult to compare with the present work. Lang went on to suggest that 'a crocodilian's thermal preference is inversely related to its thermal environment. Thermoregulation is pronounced in species living in thermally-variable habitats whereas a strategy of thermoconformity typifies forms living in thermally-equable habitats'. However, the present study shows clearly that there are marked seasonal changes of behaviour which have thermal significance to *C. porosus*, and it could be that differences between seasons and/or between different geographic areas within its range are of comparable magnitude to the differences judged by Lang to be interspecific. It would be interesting to make detailed comparisons of (similar sized) *A. mississippiensis* and *C. porosus* in thermally similar habitats. The former occurs in higher latitudes and certainly copes with cooler winters (Spotila 1974; Brisbin *et al.* 1982), so there may be good reason to suspect a familial difference between them.

Our data show that T_b patterns are composed of several superimposed cycles: an asymmetric oscillation (Fourier series) over the period of one day superimposed on simple harmonic oscillations with periods of 10–13 days and 365 days. Intermediate cycles may be unusual, but they show nicely the responsiveness of T_b to the ambient thermal conditions. The amplitudes of the daily T_b cycles decreased with mass, whereas crocodiles of all sizes reduced variations in T_b between summer and winter by changing their behaviour seasonally. We confirmed the observations of previous authors (Modha 1968; Smith 1975), that crocodiles move between land and water in a daily cycle, but extend them with the observation that daily cycles in behaviour change with season in a thermally significant way.

It is interesting to observe the way behavioural interactions between individuals affect T_b . Two large males were chased frequently by the dominant males and, in both, T_b values were either cooler in winter or more variable in summer than the pattern established by the other study animals. Although we were not able to quantify this observation thoroughly, it agrees with data presented by Seebacher & Grigg (1997) on *C. johnstoni*, some of which were prevented from reaching their preferred T_b range as

Figure 9. Influence of season and body size on body temperature (open circles), in relation to operative temperature (filled circles), exemplified by raw data from crocodiles 2, 8 and 11 in winter and crocodiles 3, 7 and 11 in summer.

a result of being chased from their basking sites by other crocodiles.

How do thermal relations of crocodiles compare to other reptiles? In a comprehensive review, Avery (1982) remarked that our knowledge of reptile thermoregulation is to a large extent based on field data from diurnal lizards, with comparatively little data from other families. Hence, there is the danger that our current thinking, indeed our current paradigm, of body temperature and energetics in reptiles is biased against other groups. Crocodylians are an important component of any general picture of reptilian thermal relations because of their great ontogenetic size range and their evolutionary status as one of the last living archosaurs, yet Avery (1982) found crocodylians were particularly under-represented.

Small crocodylians, certainly, may show lizard-like patterns. *Crocodylus johnstoni* of up to 20 kg, small crocodiles but a large reptile nevertheless, regulated T_b to a plateau during the day by shuttling between a basking site and the water (Seebacher & Grigg 1997). The range of body sizes over which short-term behavioural thermoregulation (shuttling) can be effective is much larger in the aquatic habitat, because heat transfer between body and environment increases by an order of magnitude between air and water.

Figure 10. The number of basking bouts performed per day ($\pm 95\%$ confidence intervals) by *Crocodylus johnstoni* over a size range from 2.6 kg to 20.5 kg (open circles), showing a decrease that predicts a single bout per day (i.e. a continuous daily oscillation in T_b) at higher body mass, as seen in the present study (solid circle = 32 kg *C. porosus*). Data from Seebacher (unpublished; refer to Seebacher & Grigg (1997) for details). The fitted curve shows a logistic growth function with asymptote 1 ($y = 1/(1 - 0.884e^{-0.0255x})$, $R^2 = 0.92$).

However, as mass increases, as seen in *C. porosus*, time constants become too large to make short-term shuttling behaviour effective for thermoregulation, even with access to water. Behavioural patterns of larger individuals change over a much longer time-scale, between day and night, and between seasons, and T_b forms a continuous cycle rather than a daily plateau. We speculate that this shift in the pattern of T_b occurs somewhere between a mass of 20 and 30 kg; we know that *C. johnstoni* of up to 20 kg show the typical shuttling pattern during the day, but that the number of basking bouts decreases with mass (figure 10). The T_b of a 32 kg *C. porosus* in this study followed a continuous oscillation, and we predict that the pattern of T_b changes between the size of the largest *C. johnstoni* in figure 10 (20.5 kg) and our smallest *C. porosus* (32 kg).

We are grateful to the management and staff of the Edward River Crocodile Farms Pty Ltd whose cooperation and assistance made this research possible. All animal handling and experimentation procedures had the approval of the University of Queensland's Animal Experimentation Ethics Committee (approval number ZOO/579/93/ARC). The research was funded by a grant from the Australian Research Council to G.C.G.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.