

CROCODILES AS DINOSAURS: BEHAVIOURAL THERMOREGULATION IN VERY LARGE ECTOTHERMS LEADS TO HIGH AND STABLE BODY TEMPERATURES

FRANK SEEBACHER*, GORDON C. GRIGG AND LYN A. BEARD

Department of Zoology, University of Queensland, Brisbane, QLD 4072, Australia

*e-mail: fseebacher@zoology.uq.edu.au

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Summary

Empirical field data describing daily and seasonal cycles in body temperature (T_b) of free-ranging *Crocodylus porosus* (32–1010 kg) can be predicted by a mathematical analysis. The analysis provides a mechanistic explanation for the decreased amplitude of daily cycles in T_b and the increase in ‘average’ T_b with increasing mass. Assessments of ‘average’ daily T_b were made by dividing the integral of the difference between measured values of T_b and minimum operative temperature by the period of integration, to yield a thermal index expressing relative ‘warmth’ of crocodiles. The average daily T_b of a 1010 kg crocodile was 3.7 °C warmer than that of a 42 kg individual in summer and 1.9 °C warmer than that of a 32 kg individual in winter. The success of this mathematical approach confirms that crocodiles are simple ectotherms and that there is unlikely to be a significant contribution to their thermal biology from physiological mechanisms. Behaviour, however, is very important even in large individuals. Crocodiles in the field typically move daily between land and water in cycles that vary seasonally. We predicted T_b for the reverse of these behavioural cycles, which more than doubled seasonal fluctuations in T_b

compared with the observed fluctuations. We were also able to predict the T_b of very large, dinosaur-sized crocodiles in a similar climate to that at our study site. A 10 000 kg ‘crocodile’, for example, would be expected to have a T_b of 31 °C in winter, varying by less than 0.1 °C during a day when operative temperatures varied by nearly 20 °C, from 20 to 38 °C. The study confirms that, in low latitudes at least, large dinosaurs must have had an essentially high and stable value of T_b , without any need for endothermy. Also, access to shade or water must have been crucial for the survival of large dinosaurs at low latitudes. Furthermore, the finding of increasing ‘average’ T_b as ectotherms grow larger may have implications for the metabolic rates of very large reptiles, because the Q_{10} effect could counteract the downscaling of metabolic rate with mass, an effect that seems not to have been recognised previously.

Key words: crocodile, *Crocodylus porosus*, body temperature, operative temperature, heat transfer, mathematical prediction, behaviour, dinosaurs.

Introduction

Twenty years ago Grigg (1977) speculated that *Crocodylus porosus* would become warmer with increasing mass and show increased stability in body temperature (T_b). Recently, both these predictions have been confirmed empirically by Grigg et al. (1998), who showed that the daily variability in T_b of *C. porosus* decreased with increasing mass and that there was an indication that the level around which daily T_b fluctuated also increased with mass. The present paper will provide mechanistic explanations for these two phenomena using mathematical analyses of field data gathered from crocodiles over a large mass range (32–1010 kg). We have also been able to assess quantitatively the effects of seasonally changing patterns of daily movements of crocodiles between water and land on the observed patterns of T_b . Because *C. porosus* is the largest of the living archosaurs and may grow to 7 m in length, equal to the mass of a medium-sized dinosaur, these questions are relevant

to ideas about the thermal relationships of dinosaurs. A recent review by Reid (1996) provides a good synthesis of the present state of our knowledge of dinosaur thermal relationships, which we hope to supplement with our analysis of crocodile T_b .

Other authors too have taken a mathematical approach to speculations about the thermal relationships of dinosaurs. Spotila et al. (1973) used a mathematical model predicting T_b and thermal time constants in dinosaurs, concluding that the time constant of a cylindrical dinosaur with a diameter of 1 m would be approximately 48 h, long enough for the animal not to respond to daily fluctuations in environmental temperature. The conclusion that medium- to large-sized dinosaurs had a stable T_b over the period of 1 day was confirmed using mathematical models by Dunham et al. (1989) and Spotila et al. (1991). However, both studies emphasised that even large dinosaurs with typically reptilian metabolism would show considerable

seasonal fluctuations in T_b . Previous studies have been limited by the absence of empirical data with which to validate models, and the effects of daily and seasonal changes in behaviour have not been considered. In our study, we have access to a large body of empirical data collected in the field, including behavioural data, and we have made predictions about patterns of T_b in animals larger than those in our study only after having validated the mathematical representations against the field observations.

Some types of behaviour, such as basking and shuttling between land and water, have long been recognised to be of thermal significance in crocodiles (Cott, 1961; Modha, 1968), but their effect on T_b in large individuals has never been quantified. Smaller crocodiles (*C. johnstoni*), up to approximately 20 kg, are known to thermoregulate by shuttling frequently between land and water during the day (Seebacher and Grigg, 1997; Seebacher, 1999). Their frequency of movement between land and water decreased as mass increased, and data from *C. johnstoni* effectively predicted what was observed subsequently in *C. porosus* heavier than 30 kg, in which a single daily T_b cycle was observed (Grigg et al., 1998). However, *C. porosus* showed marked changes in behaviour between winter and summer. They basked frequently during the day in winter and spent the night in the water. In summer, however, they typically spent the day in the water and the night on land. Our analysis and mathematical predictions gave us an opportunity to examine quantitatively the effects of these long-term behavioural cycles on T_b .

Other authors have not addressed Grigg's (1977) other initial proposal that the 'mean' daily T_b of large ectotherms should increase with mass. As it turned out, the prediction was correct but, as we will show, the reasoning behind it was incorrect. Reptiles may heat up faster than they cool down (Bartholomew, 1982; Grigg and Alchin, 1976; Grigg et al., 1979) and, according to Grigg (1977), this heating/cooling hysteresis would enable crocodilians with a large body mass to retain more heat during cooling compared with smaller individuals, leading ultimately to higher 'mean' T_b at higher body mass. It has been shown subsequently, however, that heating and cooling hysteresis is most effective in animals with a body mass of approximately 5 kg, with effectiveness decreasing in larger animals (Turner and Tracy, 1986). Although Turner and Tracy's (1986) theoretical predictions need to be confirmed by field data, it seems likely that cardiovascular adjustments will be ineffective in altering rates of heating and cooling in crocodiles much heavier than 5 kg. Hence, Grigg's (1977) reasoning for proposing that large (>1000 kg) *C. porosus* should have a 'high' T_b is probably flawed. Interestingly, however, the empirical data indicated that the 'mean' T_b of crocodiles did increase with mass (Grigg et al., 1998), and in this study we provide a more plausible explanation for this observation.

Materials and methods

Study site

The study was conducted at the Edward River Crocodile Farm on Cape York Peninsula, Queensland, Australia

(14°55'S, 141°35'E). Study animals (Table 1) were free-ranging either in an enclosed, natural lagoon (area approximately 0.3 km²), where they were part of a total population of approximately 150 crocodiles, or in a smaller separate enclosure (pen, area approximately 2000 m²) consisting of a pond (70–80% of the area) surrounded by grassy banks with some bushes and trees. There were approximately 20 animals in the pen.

Study animals

Because of the size and the number of crocodiles in the lagoon and the pen, it was impractical to capture the study animals for measuring and weighing. Accordingly, we measured their length from imprints left on sandy ground after they had moved away or, if this was not possible, we estimated length visually with the assistance of experienced farm staff. Body mass was then predicted from total length using allometric relationships derived from morphometric data of 190 *Crocodylus porosus* (Schneider) ranging from 8 to 120 kg (F. Seebacher, unpublished data) and from data in Webb and Messel (1979). The length and mass of the study animals, sample sizes (number of days sampled), the month of sampling (Summer=November–December 1993; Winter=June–July 1993) and the site of sampling (Lagoon or Pen) are shown in Table 1 (from Grigg et al., 1998).

Signals from crocodile 11 were received infrequently in summer, and we were not able to calculate daily amplitudes in T_b . However, it was possible to determine mean hourly differences between T_b and minimum T_e ($T_{e,min}$ see below). To extend the size range to very small crocodiles, we also included data (identified) from two *Crocodylus johnstoni* (2.6 kg and 3.5 kg) sampled for 7 and 10 days in July 1992 and November 1991, respectively, in the wild at another location in North Queensland (17°07'S, 144.03°03'E) (Seebacher and Grigg, 1997; F. Seebacher, unpublished data).

Table 1. Sample sizes, month of sampling, study site, total length and mass of the study animals

Crocodile	<i>N</i>	Month	Site	Total length (m)	Mass (kg)
1	6	Summer	Pen	2.1	32
2	10	Winter	Pen	2.3	42
3	12	Summer	Lagoon	2.7	77
4	14	Winter	Pen	3.7	233
5	4	Winter	Lagoon	4.2	383
6	9	Winter	Pen	4.3	408
7	5	Summer	Lagoon	4.6	520
8	13	Winter	Lagoon	4.6	520
9	4	Summer	Lagoon	4.9	660
10	15	Summer	Lagoon	5.2	820
11	30	Winter	Lagoon	5.5	1010
	11	Summer	Lagoon	5.5	1010

N is the number of days of sampling.

Data from Grigg et al. (1998).

Sampling methods

We measured air and ground temperatures using calibrated temperature sensors (National Semiconductor LM335, accurate to 0.3 °C) suspended in the shade next to the lagoon (air) and covered lightly with sand in an open space within the lagoon enclosure (ground). Solar radiation was measured using a tube solarimeter (Irricrop Technologies, Narrabri, Australia). All sensors were connected to a datalogger (Data Electronics, Melbourne, Australia), and measurements were taken every 30 min. We measured water temperature using calibrated temperature-sensitive radio transmitters (Sirtrack, Havelock North, New Zealand; accurate to 0.2 °C) suspended in the water column at three different places in the lagoon. Water temperatures did not vary substantially within the lagoon and, in the analysis, we used the water temperature measured in an area frequented by most of the study animals.

We measured T_b using calibrated temperature-sensitive radio transmitters (Sirtrack, Havelock North, New Zealand; accurate to 0.2 °C) which were sewn into chickens and fed to selected crocodiles. Crocodiles retained the transmitters in their stomach for varying periods, and the number of days we were able to sample each crocodile is shown in Table 1. T_b of crocodiles in the lagoon was monitored manually by timing the intervals between pulses using a stopwatch from approximately 06:30 to 22:00 h each day from 29 June 1993 to 29 July 1993 (winter) and from 16 November 1993 to 7 December 1993 (summer). Measurements were taken at least as frequently as once every 1–1.5 h, and our objectives were to obtain fairly continuous daily T_b records as well as recording the ‘turning points’ when daily T_b minima and maxima occurred. We were able to measure T_b of animals in the pen by a remote sampling system which recorded each frequency at 65 min intervals (Grigg et al., 1992). The remote sampling system could not be used in the much larger lagoon where crocodiles were often beyond the range of a permanently installed sampling station. Because of the reduced range of the transmitters, being contained within such large animals, we had to follow individuals in the lagoon to receive radio signals. Safety considerations put certain constraints on manual data gathering.

Mathematical analysis

Operative environmental temperatures (T_e) represent the mean surface temperature of an animal taking all heat transfer mechanisms acting at the animal surface into account (Bakken and Gates, 1975). We calculated T_e by solving a steady energy budget equation for T_b as described by Tracy (1982), taking changes in behaviour into account by varying the proportion of body surface exposed to the ground, the air and the water described by Grigg et al. (1998) and Seebacher (1999). Briefly, from behavioural observations (Grigg et al., 1998), we estimated that in winter daytime crocodiles typically exposed 75 % of their surface area to air (and radiation) and 25 % to water; 10 % of the body surface was in contact with the ground. At night, crocodiles were 90 % in water with only 10 % exposed to air. We estimated that in summer daytime 25 % of their surface area was exposed to radiation, with 75 % in the water, while 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).

Heat is conducted from the surface of the crocodile to the core, and we calculated heat conduction and T_b of crocodiles assuming that the animal was made up of two thermally distinct layers (Turner, 1987): an outer layer made up of muscle and fat and with a thickness of 15 % of the total radius (see below), and an inner core consisting of bone, tissue and fat with a thickness of 85 % of the total radius. Applying Fourier’s law to the temperature distributions (Incropera and DeWitt, 1996), of each layer gives the following conduction equations:

$$C_c dT_c/dt = -K_c(T_b - T_s) \quad (1)$$

and

$$C_s dT_s/dt = K_c(T_b - T_s) - K_s(T_s - T_e) \quad (2)$$

for the core (equation 1) and outer (equation 2) layers, where C_c and C_s are the heat capacities for the core and outer layer, respectively, K_c and K_s are the conductances through the core and outer layer, respectively, T_c and T_s are the core and outer layer temperatures, respectively, and t is time. More information on conductance and its relationship to heat capacity can be found in Incropera and DeWitt (1996). Substituting for T_s gives a non-homogeneous linear second-order differential equation:

$$(C_s C_c / K_c K_s) d^2 T_b / dt^2 + (C_c / K_s + C_c / K_c) dT_b / dt + T_b = T_e, \quad (3)$$

which can be solved using the method of undetermined coefficients (Stewart, 1991). As the particular solution of this equation, we chose a trigonometric function because the shape of the daily and seasonal T_b and T_e curves are periodic functions determined by fluctuations in environmental temperatures and solar radiation but, rather than simple harmonic oscillation (Stevenson, 1985), they are of a sawtooth shape owing to the asymmetry of the solar day (Grigg et al., 1998), and we solved equation 3 for a Fourier series with three terms of the form:

$$T_e = T - A \sin[(2Pt) + \phi] + c_1 A \sin[(4Pt) + \phi] - c_2 A \sin[(6Pt) + \phi], \quad (4)$$

where T is mean temperature, A is amplitude, P is period, t is time, ϕ is phase angle, and c_1 and c_2 are constants determining the ‘sawtooth’ of the periodic motion (Halliday and Resnick, 1978) and which we determined empirically to be 0.305 and 0.109, respectively.

Body dimensions

An important requirement for estimating heat transfer in animals is a realistic expression of body shape. Typically, the dimensions of animals have been approximated by a cylinder or a sphere. However, crocodiles look neither like a cylinder nor like a sphere and, furthermore, volumes and surface areas of crocodiles are overestimated by the volume of a cylinder of equal length and radius as the crocodile and underestimated by a sphere of the same radius as a crocodile (Fig. 1). Looking at

a crocodile from the side, its shape is such that the maximum height occurs at mid-body and decreases fairly evenly towards the head and towards the tail. We determined the outline of crocodiles by measuring the height of crocodile carcasses from the head to the tip of the tail every 15 cm (F. Seebacher, unpublished results) and fitted a polynomial to these measurements [$f(x)=R+0.000819x-0.00045x^2$, where R is the maximum height at the centre of the body) (Fig. 1A). Hence, the polynomial represents the dorsal boundary of the crocodile, the x -axis represents the ventral boundary and the points where the polynomial intersects the x -axis represent -0.5 and $+0.5$ total length (Fig. 1A). We estimated crocodile dimensions by integration: we calculated crocodile surface area (A_c) as half the surface area of the volume of revolution plus the flat ventral area, and the volume (V_c) of the crocodile was calculated as half the volume of revolution:

$$V_c = 0.5 \{ \pi \int [f(x)]^2 dx \}, \quad (5)$$

$$A_c = 0.5 [2\pi \int f(x) dx] + 4 \int f(x) dx. \quad (6)$$

Note that the area of a surface of revolution (S) is calculated as $S=2\pi \int f(x) \{ 1+[f'(x)]^2 \}^{1/2} dx$, but in the present case $\{ 1+[f'(x)]^2 \}^{1/2}$ approximates 1 (Stewart, 1991); the second integral in equation 6 represents the ventral area of a crocodile. We tested the validity of this method by calculating the volume of crocodiles of known dimensions, multiplying the calculated volume by density (assumed to be 1036 kg m^{-3}) to give an

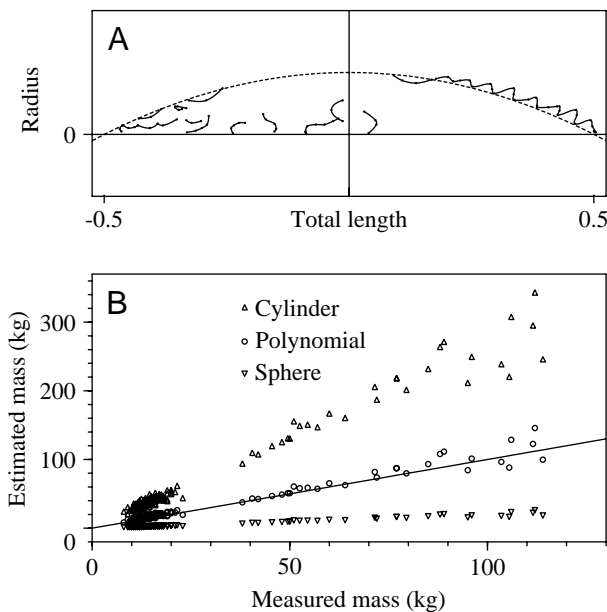


Fig. 1. Comparison between different estimates of crocodile shape. We estimated the shape of crocodiles by integrating a polynomial equation (broken line), coefficients of which were determined from measurements on crocodile carcasses (A). The measured mass of 190 *Crocodylus porosus* was estimated from the calculated dimensions of a cylinder (Δ), a sphere (∇) and the polynomial method (\circ). Representing a crocodile by a cylinder or a sphere over- or underestimates the measured mass, respectively, while the integrated polynomial gave a relatively accurate estimate of measured mass.

estimate of mass, and then comparing the calculated mass with the measured mass of the crocodile (Fig. 1B). We did this for 190 *C. porosus* for which total length, mass and height were measured on the fresh carcass (F. Seebacher, unpublished data). The mass estimated from the 'polynomial' method was close to the measured mass, the cylinder geometry overestimated the mass, while the sphere underestimated the mass (Fig. 1B). We used the maximum height described above in all calculations rather than a mean height, which would improve the cylinder estimate but make the sphere estimate worse; another advantage of our method lies in the fact that the necessary parameters (height) can be measured directly on the animal.

Results

Magnitude and variation of T_b

As reported in Grigg et al. (1998), T_b became more stable as mass increased from 32 kg to 1010 kg, as seen in the representative examples shown in Fig. 2 (from Grigg et al., 1998); T_b of the 1010 kg animals fluctuated by less than 2°C despite T_e fluctuations of nearly 20°C ; in contrast, T_b of the 32 kg and the 42 kg crocodiles tracked T_e much more closely both in winter and summer although, even in these small animals, there was a noticeable lag between T_b and T_e . Note also the increase in T_e between the 42 kg and the 1010 kg crocodiles sampled in winter. Overall, this decreased variability in T_b was reflected in the decrease of T_b amplitude with mass shown in Fig. 3, where we plotted the ratio $T_b:T_e$ against mass. Plotting the $T_b:T_e$ ratio eliminated the bias of increasing T_e with mass (see below) and standardised data

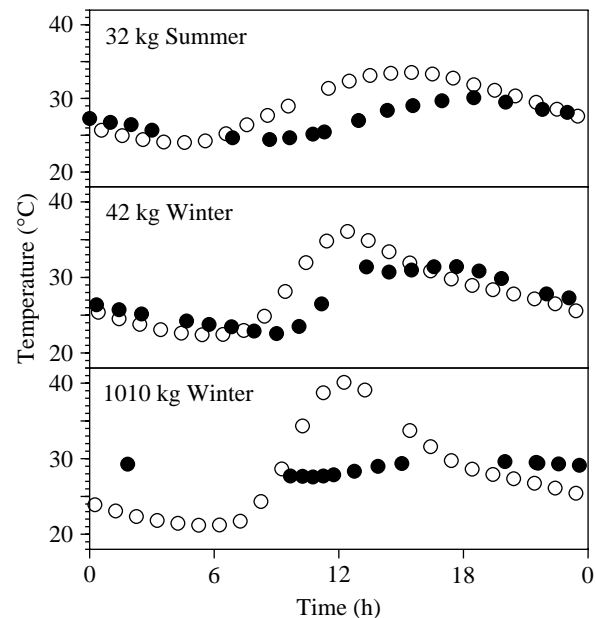


Fig. 2. Representative examples of daily body temperature (\bullet) (T_b) and minimum operative temperature (\circ) (T_e) patterns of differently sized crocodiles at different seasons (from Grigg et al., 1998).

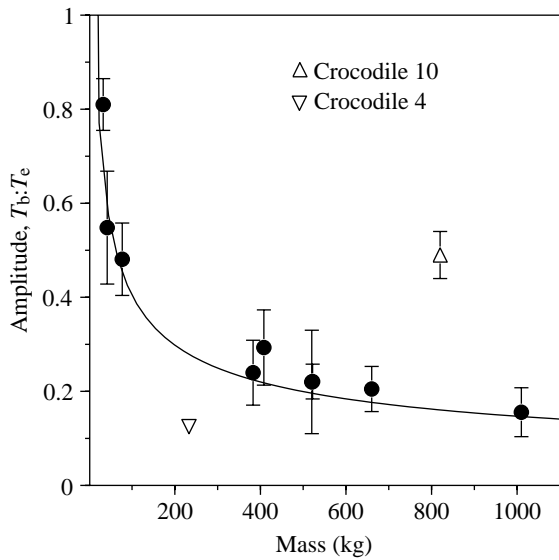


Fig. 3. Body temperature amplitudes, expressed as the ratio of body temperature (T_b) to minimum operative temperature (T_e) to overcome bias from environmental conditions and the increase in T_e with mass, decrease allometrically with crocodile mass. The outliers (open symbols, crocodiles 4 and 10) are from males subjected to intraspecific aggression. Values are means \pm S.E.M., N as in Table 1.

sampled at different times of year, allowing us to plot data from both seasons together (Fig. 3). At a ratio of 1, T_b equals T_e , while a ratio of zero indicates complete independence of T_b from fluctuations in T_e . The decrease in the amplitude ratio was described by a negative power relationship ($3.051M^{-0.4389}$, where M is body mass; $r^2=0.91$). Amplitudes of crocodiles 4 and 10 did not fit the general pattern. As pointed out by Grigg et al. (1998), these crocodiles were the second largest males in the lagoon (crocodile 10) and in the pen (crocodile 4) and each had frequent aggressive encounters with dominant males (crocodiles 11 and 6 in the lagoon and pen, respectively). Position in the social hierarchy can have a very distinct effect on thermal relationships of crocodiles (Seebacher and Grigg, 1997), which could explain the discrepancy between the T_b amplitude of those crocodiles and that of the other animals. Patterns of T_b of the study animals are described in depth by Grigg et al. (1998).

We were able to predict the amplitude of daily changes in T_b mathematically by solving equation 3 for T_b (Fig. 4). Predicted and measured amplitudes were not significantly different from each other (paired t -test excluding data from crocodiles 4 and 10, $t=-0.31$, d.f.=8, $P=0.76$), confirming the validity of our analysis in predicting field T_b (Fig. 4). Note that the decrease in the amplitude of the T_b cycle reflects an increase in thermal time constants, which is represented as the ratio between heat capacity and conductance (C/K) in equation 3 (Incropera and DeWitt, 1996). Again, T_b amplitudes of crocodiles 4 and 10 did not follow the general pattern, presumably because their behaviour differed from that of the other crocodiles as a result of their position in the social

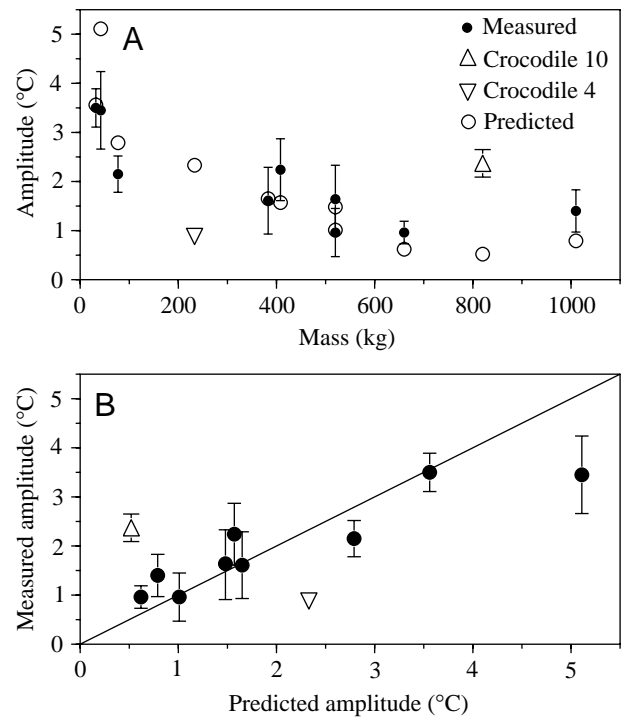


Fig. 4. Measured and predicted body temperature (T_b) amplitudes plotted against mass (A); note that increased variation in amplitudes compared with Fig. 3 is due to seasonal variation. Measured T_b amplitudes are plotted against predicted T_b amplitudes in B, and the solid line shows the line of equality. Predicted amplitudes were not significantly different from measured amplitudes (paired t -test; $t=-0.31$, d.f.=8, $P=0.76$). Values are means \pm S.E.M., N as in Table 1.

hierarchy. Data from these crocodiles (4 and 10) was therefore omitted from the following analyses. Also, the predicted amplitude for the 42 kg crocodile (crocodile 2) varied somewhat more from the measured amplitude compared with the other crocodiles, but we have no observations explaining this and therefore retained this data point in the analysis.

The field data indicated not only that amplitudes decreased and that T_b become more stable with increasing mass, but that larger crocodiles were also warmer than small ones (Grigg et al., 1998). We sought a more detailed representation and an explanation of this phenomenon. It is difficult to find a meaningful measure of the average 'warmth' of crocodiles because arithmetic means and other measures of central tendency derived from continuous T_b data are confounded by the dependence of the measurements. Also, because of differences in environmental conditions, comparisons may be invalid if T_b data are compared when they were not measured at exactly the same time. To overcome this problem, we standardised T_b measurements, eliminating bias from sampling different crocodiles on different days, by subtracting minimum daily T_e ($T_{e,min}$) from daily T_b measurements ($T_b - T_{e,min} = dT_b$). This describes T_b relative to the T_e range available during the day and, similar to the raw data, mean hourly dT_b showed a periodic, slightly sawtoothed daily oscillation (Fig. 5). The

magnitudes of the dT_b curves depend on mass and maximum T_e as follows. Intuitively, it would be easy to assume that T_b oscillates around the same daily 'average' temperature in all crocodiles. If this were the case, one would expect the decrease in T_b amplitude with mass to lead to an increase in the daily minimum T_b and a decrease in the daily maximum T_b as crocodile mass increased. There was, indeed, a significant (one-way analyses of variance followed by Tukey tests) increase in the daily minimum dT_b with increasing mass in both winter ($F_{4,60}=21.78$, $P<0.0001$) and summer ($F_{3,26}=20.24$, $P<0.0001$), but daily maximum dT_b did not vary among crocodiles in either winter ($F_{4,55}=0.84$, $P=0.50$) or summer ($F_{3,25}=2.94$, $P=0.056$). The reason for this departure from the expected pattern is that the 'average' temperature around which T_b oscillated was not the same for all crocodiles, but increased with mass. This increase is due to the diminishing importance of convective heat transfer in larger individuals (resulting from an increase in the width of the surface boundary layer), leading to greater input of solar radiation in the overall heat exchange between animal and environment as mass increases. Therefore, maximum daily T_e , which is determined primarily by shortwave solar radiation, increases with mass in individuals experiencing identical climatic conditions, leading to higher 'average' T_b in larger crocodiles. In the absence of solar radiation, such as at night, T_e does not vary with mass.

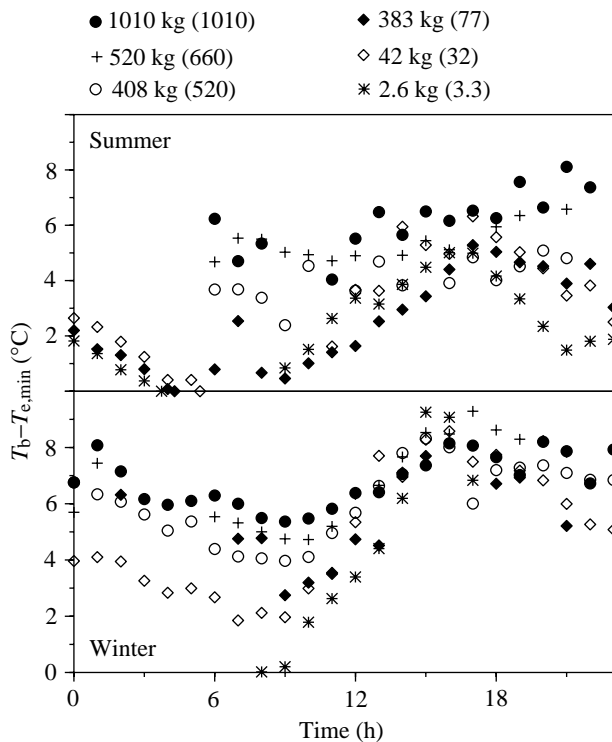


Fig. 5. Difference between mean hourly body temperature (T_b) and mean hourly minimum operative temperature ($T_{e,min}$) for all study animals, as well as for two *Crocodylus johnstoni* (2.6 kg and 3.5 kg), for winter and summer (mass in parentheses in the legend). All standard errors were less than 1.0°C except for crocodile 11 in summer (mass 1010 kg, when maximum S.E.M. was 1.90).

We expressed 'average' daily T_b ('warmth') of crocodiles by integrating the daily mean dT_b curves shown in Fig. 5 and dividing the integral by the period (24 h), resulting in a thermal index, which is conceptually – but not mathematically – similar to a mean daily T_b or, in the present case, the mean daily elevation of T_b above $T_{e,min}$ (Fig. 6).

Thermal indices (TI) increased with mass (M) following allometric relationships ($TI_{WINTER}=3.0528M^{0.120}$, $r^2=0.92$; $TI_{SUMMER}=0.9815M^{0.258}$, $r^2=0.91$; Fig. 6A) and were higher in winter than in summer, because during winter crocodiles behaviourally exposed themselves more to sun. We expressed the decrease in the relative importance of convective heat transfer with mass by calculating the dimensionless Biot number (Fig. 6B). The Biot number represents the ratio of internal thermal resistance of the body to the boundary layer resistance at the surface of the animal (Incropera and DeWitt, 1996), and larger Biot numbers indicate less dependence of T_b change on convective heat exchanges at the surface. Thermal indices increase linearly with Biot numbers (B) ($TI_{WINTER}=2.144+1.139B$, $r^2=0.92$; $TI_{SUMMER}=-1.425+0.757B$, $r^2=0.86$), which were higher in summer because of the greater exposure of the crocodiles to water and the high convection coefficient associated with water.

Having explained the increase in T_b with mass observed in our field data, we were interested to find a scaling relationship

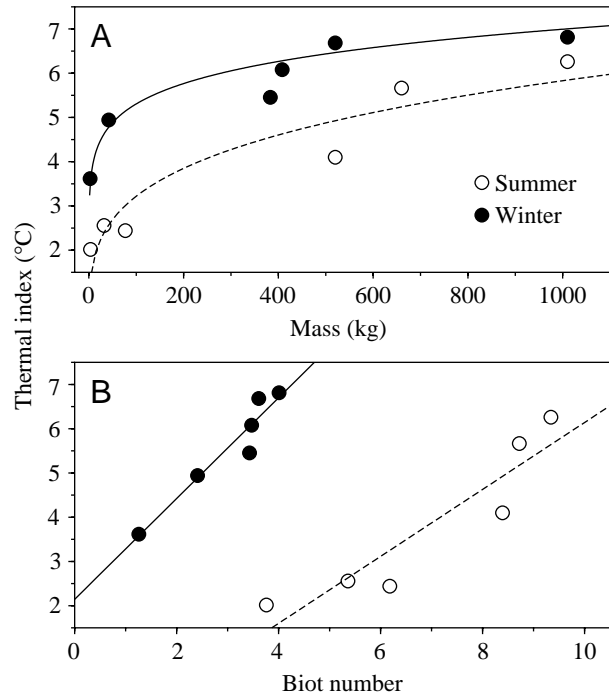


Fig. 6. 'Mean' body temperature (T_b) (expressed as thermal indices) increased allometrically with mass in both winter and summer (A), and there was a linear relationship between thermal indices and the dimensionless Biot number (B). Equations are given in the text. Differences in thermal indices and Biot numbers between winter and summer are due to seasonal differences in crocodile behaviour altering the convective environment.

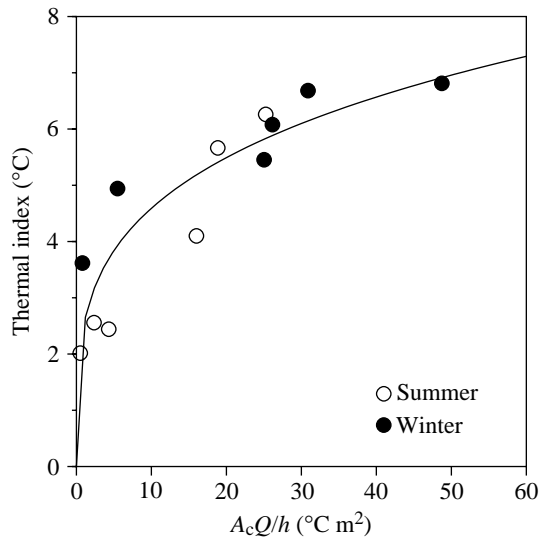


Fig. 7. The thermal index (TI) scaled proportionally with crocodile surface area (A_c) and solar radiation intensity (Q), and inversely with the total convection coefficient (h). $TI=2.533(A_c Q/h)^{0.2583}$, $r^2=0.81$. Crocodile behaviour influenced thermal indices by altering convection coefficients; for example, total convection coefficients increase, and the thermal index decreases, the more a crocodile is submerged in water.

of thermal indices in order to predict 'average' T_b beyond the conditions under which our field data were collected. Such a scaling relationship should incorporate animal size, behaviour and climatic conditions, and a very simple relationship was found to predict thermal indices adequately: $A_c Q/h$ (Fig. 7), where A_c is the animal surface area (m^2), Q is the mean daily solar radiation, again calculated as the integral of continuous measurements divided by the period of integration ($W m^{-2}$), and h is the combined convection coefficient of air and water ($W m^{-2} \text{ } ^\circ C^{-1}$). Area, rather than mass, was chosen to represent animal size because heat transfer with the environment occurs at the animal surface, and a decrease in A_c causes a decrease in the thermal index. The ratio Q/h expresses the relationship between animal behaviour and environmental conditions, so that as h increases, for example as a result of increasing surface area in water, the thermal index decreases, and *vice versa*. An increase in radiation intensity, Q , causes an increase in the thermal index.

Mathematical predictions

We tested the validity of our mathematical calculations by predicting field T_b taking crocodile behaviour and environmental conditions measured in the field into account (Fig. 8). The representative examples in Fig. 8 confirm that we were able to predict the T_b of crocodiles across a size range of 32–1010 kg. Encouraged by this, we proceeded to predict the effects on T_b of seasonally altered behavioural patterns.

Grigg et al. (1998) reported that crocodiles behaved differently in winter and summer: they were mostly exposed to the sun during the day and remained in water at night in

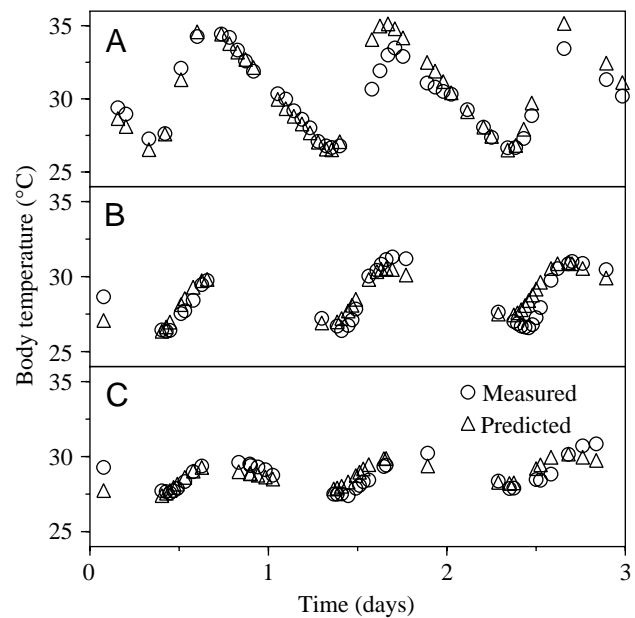


Fig. 8. Representative examples of the mathematical model predicting body temperature (T_b) measured in differently sized crocodiles in the field (A, 32 kg summer; B, 520 kg winter; C, 1010 kg winter).

winter, while remaining largely in water during the day and emerging onto land at night in summer. We were able to determine the extent to which these seasonal changes in behaviour had an impact on the patterns of T_b in each season by predicting T_b with hypothetically reversed behaviour, i.e. crocodiles in a winter climate behaved as if in summer, and *vice versa*. In Fig. 9, we plotted 3 days of measured T_b for two crocodiles of equal size (520 kg), one in summer (crocodile 7) and one in winter (crocodile 8), as well as the T_b predicted for the same 3 days with the behaviour reversed. Behaviour had a pronounced effect on T_b , even in these large crocodiles, and reversing seasonal behaviour patterns led to a considerable increase in annual T_b fluctuations, varying by more than $10^\circ C$ winter to summer (Fig. 9). In contrast, patterns of behaviour observed in the field led to warmer T_b in winter and cooler T_b in summer, reducing the differences in T_b between winter and summer, which resulted in much more stable annual T_b , fluctuating by only $5^\circ C$, compared with that predicted for the reversed behaviour (Fig. 9).

Finally, we predicted daily T_b profiles of very large reptiles (dinosaurs) with the same shape and behaviour, and in the same climate as crocodiles at Edward River (winter minimum T_e $20^\circ C$, amplitude $9.0^\circ C$ for mass 1000 kg; summer minimum T_e $26.5^\circ C$, amplitude $4.8^\circ C$ for mass 1000 kg) (Fig. 10). The 10 000 kg 'crocodile' would not only be considerably warmer (just under $31^\circ C$) compared with the 100 kg and even the 1000 kg animals, but its daily T_b variations would be minimal (less than $0.1^\circ C$) in both winter and summer. There were, however, seasonal differences in T_b : the 10 000 kg 'dinosaur' was warmer than smaller animals, but its T_b differed by nearly $5^\circ C$ between winter and

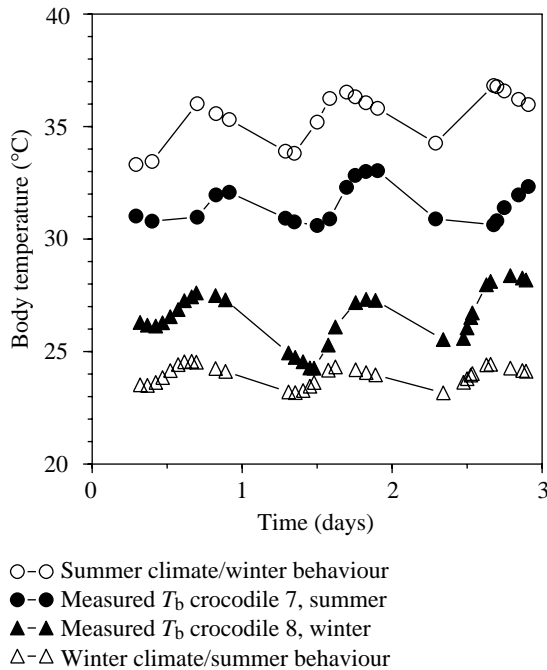


Fig. 9. Body temperature (T_b) measured (filled symbols) in two 520kg crocodiles in winter and in summer, and the corresponding mathematically predicted T_b (open symbols) when the behaviour observed in crocodiles is seasonally reversed, i.e. crocodiles behave as in winter in a summer climate, and show summer behaviour in a winter climate.

summer when it displayed behaviour similar to that observed in *C. porosus*.

Discussion

The thermal relationships of crocodylians have been the focus of scientific research since the 1940s. Colbert et al. (1946) had recognised that the effect of large mass and the resultant thermal inertia would act in dampening T_b fluctuations in the face of variable environmental temperatures, and the notion that T_b becomes more stable with mass is by no means a new concept. What has been lacking so far is an analysis of field data from large animals. Our demonstration that the observed decrease in the amplitude of the daily T_b cycle is predictable by relatively simple mathematics not only provides a definite corroboration of earlier speculations about mass homeothermy in ectotherms, but also indicates that the thermal relationships of crocodiles are driven primarily by physical relationships rather than by physiological mechanisms. The fact that both the daily and seasonal amplitudes of T_b cycles and 'average' values of T_b are predictable from entirely physical characteristics of the animals and their environment indicates that physiological mechanisms such as metabolic heat production and heating/cooling hysteresis are unimportant in the thermal relationships of crocodiles above 32 kg.

Behaviour, however, is clearly a very important component

in the thermal relationships of large crocodiles. Indeed, it is through their behaviour that crocodiles effected thermoregulation by seasonally changing patterns of movement between water and land and by behavioural posturing. It is now well known that small crocodiles can change their immediate thermal environment with a change in posture (Seebacher, 1999), but the response time of T_b to changes in the thermal environment is much longer in *C. porosus* compared with small crocodiles such as *C. johnstoni*. Accordingly, the *C. porosus* in our study 'shuttled' between thermally different microhabitats over a much longer seasonal time period than has previously been known from other reptiles. Seasonal behavioural thermoregulation enabled *C. porosus* to minimise annual fluctuations in T_b , which would have been considerably larger had the crocodiles behaved in the reverse pattern to that observed in the field. The fact that crocodiles as large as 1000 kg were able effectively to thermoregulate behaviourally would indicate that large dinosaurs, too, could have maintained a narrow range of T_b by behavioural means. It seems likely that dinosaurs would have altered their behaviour not only seasonally, but also with latitude: in the tropics, they must have been crepuscular or nocturnal to avoid overheating, while they probably sought sun in winter, but remained in shade during summer, in mid to high latitudes.

Overheating must have been a problem for medium- and large-sized dinosaurs in low latitudes. The previously unrecognised fact that T_b increases with mass in animals exposed to solar radiation probably means that large dinosaurs in the tropics had to avoid sun at any time of year. Our mathematical predictions showed that the T_b of a 10000 kg

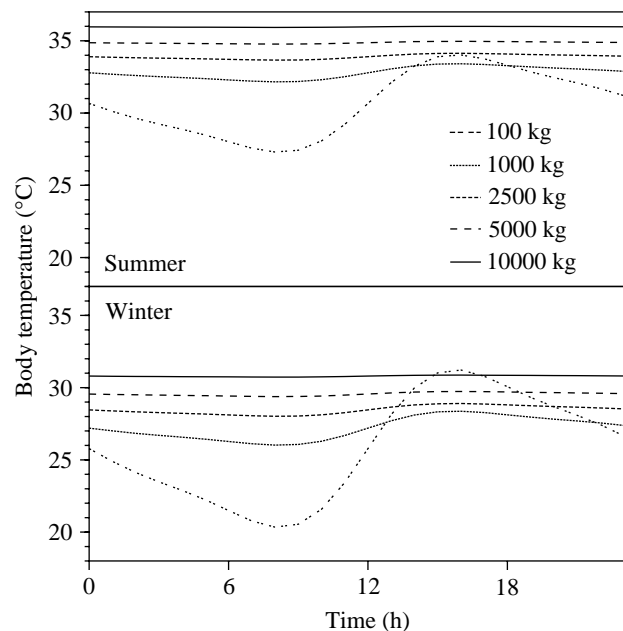


Fig. 10. Predicted body temperature (T_b) of 'crocodiles' ranging in mass from 100 to 10000 kg in summer and in winter. With increasing mass, T_b becomes high and stable.

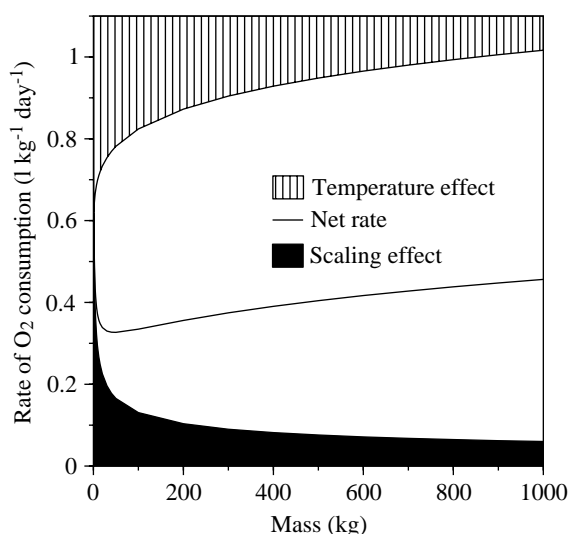


Fig. 11. Speculations about the metabolic rate of large crocodiles: the 'temperature effect' shows the increase in metabolic rate due to the increase in body temperature (T_b) with mass and the associated Q_{10} effect, and the 'scaling effect' shows the allometric decrease in metabolic rate with increasing mass. The 'net rate' shows the sum of the two, which decreases initially, but then increases again in crocodiles over 50 kg when the Q_{10} effect is greater than the scaling effect.

'dinosaur' at our study site would have fluctuated annually between 31 and 36 °C, which is within a normal reptilian range. Few reptiles, however, would tolerate a constant T_b of much more than 36 °C, except for some desert lizards. If dinosaur physiology was essentially reptilian, we would predict that dumping, rather than gaining, heat would have been of much more concern for dinosaurs at low latitudes. It must be added to our speculations about dinosaurs that most dinosaurs were terrestrial and had a more or less upright posture, or their bodies were at least raised off the ground. This would most certainly affect their thermal relationships, but in a way that supports our speculations rather than contradicts them: the heat exchange of a terrestrial animal with minimal surface area in contact with the ground would be almost entirely determined by convection in air, by solar radiation and by the relative importance of the two. This would mean that, in this case, T_e would be higher and the increase with mass would be more pronounced than if animals were in contact with the ground and/or thermally tied to the very high convection coefficients in water. Also, dinosaurs were a hugely diverse group and we are not implying that all dinosaurs had the same thermal strategies. What we are suggesting is that large dinosaurs could well have been ectothermic homeotherms over much of their range.

The fact that T_b increases with mass allows some interesting energetic speculations. Metabolic rate in reptiles decreases allometrically with mass according to well-documented scaling laws (Bennett and Dawson, 1976). However, as T_b increases with mass, and assuming a metabolic Q_{10} effect typical for crocodylians ($Q_{10}=2-3$; Grigg, 1978), the metabolic scaling effect may be counteracted by the Q_{10} effect, and metabolic

rate per unit mass may actually increase with body mass. We used published data on *Alligator mississippiensis* metabolic rates (Coulson and Hernandez, 1983: Figs 2.1, 2.2; Table 2.1) to investigate the contrary effects of increased temperature and scaling on metabolism (Fig. 11). Using a 1 kg alligator as the starting point, we calculated the increase in mass-specific rate of O_2 consumption with mass due to the increase in daily T_b and the scaling decrease in the rate of O_2 consumption with mass (Fig. 11). The different shapes of the temperature and scaling curves mean that the rate of O_2 consumption decreases initially due to the greater effect of scaling at lower mass, but the increase in T_b with increasing mass counteracts the scaling effect to such an extent that the rate of O_2 consumption increases again in animals larger than 50 kg, a pattern quite contrary to that traditionally expected from allometric scaling of metabolic rate. This hypothetical increase in aerobic metabolic rate would result in greater and more sustainable levels of activity, and it has been proposed that dinosaurs may have had metabolic rates greater than those typical for most modern reptiles (for a review, see Reid, 1996). However, rather than invoking physiological mechanisms, we have shown that physical attributes of large size combined with behavioural thermoregulation may, by themselves, have promoted higher metabolic rates in larger animals.

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