Behavioural Postures and the Rate of Body Temperature Change in Wild Freshwater Crocodiles, *Crocodylus johnstoni*

Frank Seebacher[*]

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

ABSTRACT

I recorded body temperature and behaviour of eight *Crocodylus johnstoni* in the wild over a 2-yr period in order to quantify the effect of posturing on body temperature and to provide a mechanistic explanation of how behaviour affects body temperature. Behaviour was categorised according to the proportion of a crocodile's surface area exposed from the water (0% exposed [=diving] to 100% exposed [=basking]). Crocodiles did not simply shuttle between the extremes of 100% exposed and diving but showed an array of intermediate postures. Rates of body temperature change were negative for exposures less than 40% and positive for 60%–100% exposed. This was due to the difference between operative temperature and body temperature, which was negative during diving but increased with the percentage of exposure, up to 25°–30°C during basking. For any particular posture, the rate of body temperature change decreased with increasing mass. Thermal time constants were shortest during diving and longest during basking. A heat-transfer equation predicted the rate of body temperature change well, except that it underestimated the rate of body temperature change during 80% and 100% exposed. Exposing only a small part of their body when in water (20%) slowed heat loss considerably, allowing crocodiles to spend more time in the water while maintaining body temperature within their preferred body temperature range.

Introduction

Freshwater crocodiles (*Crocodylus johnstoni*) show a pattern of thermoregulation similar to that seen in terrestrial lizards (Christian and Weavers 1996; Seebacher and Grigg 1997): a warming period in the morning followed by shuttling between heat source (basking in sun) and heat sink (water) during the day, when body temperature (T_b) forms a plateau elevated from water temperature. This T_b plateau is demarcated by the upper and lower boundaries of the preferred T_b range. After sundown crocodiles remain in the water, and during the night T_b decreases to water temperature levels in crocodiles with a mass of 2.5–20 kg (Seebacher and Grigg 1997). This pattern of T_b conforms to the accepted paradigm of reptilian thermal physiology, which postulates that many reptiles regulate their T_b and that regulation implies costs and benefits for the animal (Huey and Slatkin 1975; Christian and Weavers 1996; but see also Shine and Madsen [1996] for an example contrary to this paradigm).

Behaviour performed primarily for the purpose of T_b regulation can be seen as a cost of thermoregulation, while time spent within a preferred T_b range represents a benefit. Basking, that is, the exposure of the body to sun on land resulting in an increase in T_b, has been credited with particular significance in thermoregulation of reptiles (Modha 1968; Hammond et al. 1988; Carrascal et al. 1992). Assuming that the main purpose of basking behaviour is raising T_b, it could be viewed as a "cost" of thermoregulation, and minimizing time spent basking would be desirable. Basking is a cost only insofar as an animal cannot spend the time devoted to basking on performing other behaviours, but it is not a cost in terms of physiological rate functions, which also proceed during basking. It would, however, be advantageous, both behaviourally and physiologically, to increase rates of heating and decrease rates of cooling so that the time during which T_b is within the preferred T_b range is maximized.

Behaviours performed between basking episodes might be of thermal significance if they allowed reptiles to slow cooling rates and reduce basking frequency. Hence, for crocodiles, different behavioural postures performed at the water surface may each have a distinct effect on rates of T_b change and thus play an important role in thermoregulation.

The effect of behavioural postures on T_b depends on processes of heat transfer. With a change in behavioural posture, crocodiles change their immediate microhabitat and consequently the operative environmental temperature (Bakken and Gates 1975; O'Connor and Spotila 1992) they experience, so that each posture is thermally distinct. Theoretically, the rate of T_b change during any particular posture can be predicted by the mass and the thermal time constant of the crocodile, the physical properties of the surrounding medium (convection coefficients in air and water), and the temperature difference

between operative temperature and T_b. The thermal time constant itself is independent of the difference between operative temperature and T_b but dependent on body mass, the convective environment, and the total conductance of the body (Grigg et al. 1979; Robertson and Smith 1981; Monteith and Unsworth 1990).

Despite the widely accepted paradigm of behavioural thermoregulation in reptiles, the effect of posturing on T_b has rarely been quantified, particularly in wild animals, and my aim in this study was to quantify the effect of behavioural posturing and shuttling on T_b and to analyse the cost and benefit of thermoregulation in thermodynamic terms.

Material and Methods

Study Site and Sampling Methods

Observations were made in a water hole (approximately 100 m × 30 m) connected to the Lynd River in North Queensland, Australia (17°07′ S, 144°03′ E), that supports a natural population of *Crocodylus johnstoni* (approximately 50 animals). I caught the four male and four female crocodiles (2.60–8.75 kg) used in this study with set nets and implanted temperature-sensitive radio transmitters into each individual's peritoneal cavity. The surgery was performed in the field using sterile techniques and a local anaesthetic (Xylocaine) and procedures approved by the University of Queensland's Animal Experimentation Ethics Committee. I released the animals at their point of capture within 24 h of capture and allowed them to recover for at least 4 d before collecting data. Before release, I marked crocodiles on their backs with different coloured spray paint so that individuals could be identified easily from up to 100 m away with binoculars. I made observations from the top of a rocky outcrop adjacent to the water hole, which was ideal for the purpose because I was 20–30 m above the crocodiles and thus unnoticed.

I monitored T_b and behaviour of each crocodile for 6–10-d periods during a number of field trips over a 2-yr period (between July and October in 1991 and 1992); the total sample size was 18 d of data per crocodile, except for two crocodiles that were sampled for 10 d only and a third animal that was sampled for 14 d. Sample sizes for each behaviour and crocodile are not equal because each crocodile behaved differently, and I was not always able to watch each marked animal every day during fieldwork.

During each trip, I measured T_b every 5–15 min and also at the onset of any "new" posture using a Telonics TR-2 scanner/receiver system and a handheld unidirectional antenna (Telonics, Pasadena, Calif.). The length of the interval between two transmitter signals is temperature dependent, and transmitters were calibrated in a temperature-controlled water bath against a certified thermometer. In the field, temperature-dependent time intervals between transmitter signals were measured with a stopwatch and were later converted into temperature using

the previously determined calibration curves (with an accuracy of ±0.3°C).

The behaviour of the marked animals was sampled continuously whenever possible (Altman 1974), concurrently with T_b and environmental measurements from the first emergence of the animals in the morning until dusk (typically 0830–1730 hours). I recorded the sequence of behaviours and the duration of each type of behaviour for each animal. Shaded areas were rare in and around the water hole, so I used data from crocodiles in the sun only. Crocodiles are primarily aquatic, only leaving the water to bask and for nesting, so I defined types of behavioural postures by estimates of the proportion of a crocodile's dorsal and lateral surface area exposed from the water: 0% exposed (=diving), 20%, 40%, 60%, 80%, and 100% exposed (=basking). Smith (1979) described some putative "thermoregulatory" postures (without giving T_b data) of alligators with respect to the water surface, and his "high float" category would be similar to 40% exposed, "common float" is similar to 20% exposed, and "complete submergence" is equivalent to diving as used here.

Seebacher and Grigg (1997) reported two patterns of T_b in *C. johnstoni*, thermoregulation and thermoconformity. I used data from thermoregulating crocodiles only, from the first emergence in the morning, when T_b rose above water temperature, until retreat at dusk.

I measured water temperatures with temperature-sensitive radio transmitters placed at depths of 0.15 m and 1.5 m and following the same sampling protocol as for T_b. Solar radiation, shaded air temperature, and ground temperature were recorded every 30 min by a tube solarimeter (Irricrop Technologies, Narrabri, Australia) and calibrated temperature sensors (accurate to ±0.3°C) connected to a data logger (Data Electronics, Melbourne). The air temperature sensor was placed in the shade on the bank of the water hole, and the sensor measuring ground temperature was in a crevice just large enough to accommodate it on a rock similar to those used by crocodiles for basking. The tube solarimeter was on an exposed rock next to the water hole, where it was unlikely to be interfered with by crocodiles.

Mathematical Description of T_b Change

I present T_b in its differential form, as a rate of change (dT_b/dt), and I predicted rates of T_b change by modifying Robertson and Smith's (1981) differential equation (4). I partitioned convection in air and water and converted mean T_b change to core T_b change, thus accounting for thermal gradients within the body as suggested in that article. The resulting equation was:

$$dT_b/dt = \frac{\{[(Kah_w/K + h_w)\Delta T_w + (Kbh_a/K + h_a)\Delta T_e]A/Mc\}}{\{1 + [(\lambda - 1)(h/K + h)]\}},$$

where K is the overall conductance (J m^{-2} °C^{-1} s^{-1}), a is the proportion of the crocodile in water, h_w is the convection co-

efficient in water (J m^{-2} °C^{-1} s^{-1}), ΔT_w is the difference between water temperature and T_b (°C), b is the proportion of the crocodile out of water, h_a is the convection coefficient in air (J m^{-2} °C^{-1} s^{-1}), ΔT_e is the difference between operative temperature on land and T_b (°C), A is the total surface area of the crocodile (m^2), M is the crocodile's mass (kg), and c is the specific heat of crocodiles; on the basis of dissections and morphometric measurements of 200 *Crocodylus porosus* (F. See-bacher, unpublished data), I estimated the body to be composed of 4 parts muscle, 2 parts water, and 1 part fat (J kg^{-1} °C^{-1}), λ is a parameter characterising the difference between mean and core T_b (dimensionless), and h is the combined convection coefficient. Thermal time constants are incorporated into the conductance term $K = \lambda M c / A \tau$, where τ is the thermal time constant. For a detailed explanation of parameters, particularly conductance and the difference between mean and core T_b, consult Robertson and Smith (1981). I calculated convection coefficients using methods given by Mitchell (1976). Operative temperatures were calculated by solving a steady state energy budget equation for T_b (Tracy 1982; Seebacher and Grigg 1997).

Thermal time constants were calculated by methods given by Robertson and Smith (1981), assuming that crocodiles experienced a step function change in operative temperature when changing postures. I verified this assumption by graphically examining T_b and operative temperature data for every bout, rejecting bouts during which operative temperature varied by more than 2.5°C, and using median operative temperature during the bout as the step temperature for the remainder. I took care not to include the thermal relaxation period, a period of complex thermal "reorganisation" before the exponential change of T_b (Robertson and Smith 1981), when calculating thermal time constants. Mean sample sizes (range, SE) for each body mass (crocodile) were 10.3 bouts (7–18, 1.76) for basking, 7.8 bouts (2–11, 1.59) for 80% exposed, 3.8 bouts (2–6, 0.60) for 60% exposed, 2.2 bouts (1–6, 0.79) for 20% exposed, and 4.4 bouts (3–8, 0.93) for diving. Crocodiles did not always remain in one posture long enough for me to calculate thermal time constants, especially after excluding the thermal relaxation period, and sample sizes were too small to calculate time constants for the 40% exposed category.

Results

Behaviour

Typically, crocodiles shuttled between land and water during the day and T_b remained above water temperature (Fig. 1). Crocodiles showed a suite of behavioural postures at the water surface (Fig. 1) rather than always shuttling between diving and basking, as seen during the afternoon in Figure 1*A*. The T_b of a crocodile moving between basking and partial exposure (60%) remained stable during that period but rose fairly sharply with a longer period of basking in the late afternoon (Fig. 1*B*). T_b of the individual illustrated in Figure 1*C* gradually decreased
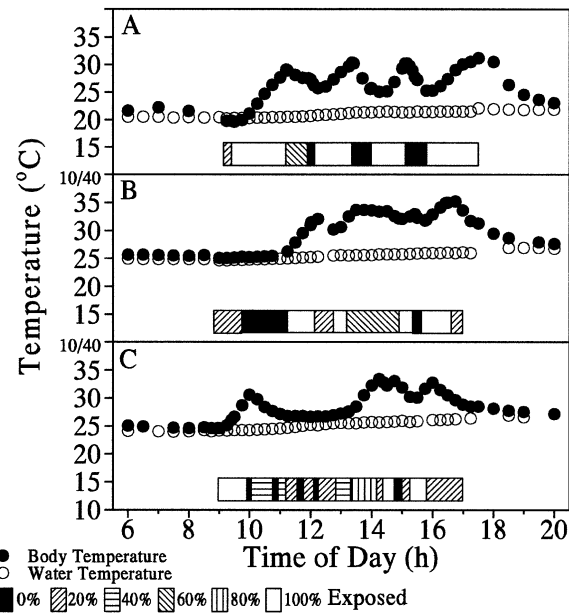

Figure 1. Three representative examples of diurnal T_b patterns and underlying behavioural sequences. Crocodiles always heated in the morning, and T_b was generally above water temperature until sundown. Data are from crocodiles weighing 3.9 kg (*A*), 8.75 kg (*B*), and 4.7 kg (*C*).

to near water temperature over a 2–3-h period while the crocodile shuttled between diving and 40% exposure, after an initial basking bout in the morning. This was followed by a period of shuttling between 0%–20% exposure and basking in the later afternoon, during which T_b rose again to well above water temperature.

Shuttling between basking and 0%–20% exposure was the behavioural sequence observed most commonly (Fig. 2). After basking, crocodiles either dived or remained at the water surface with a small part of their body exposed (20%), but other behaviours were displayed rarely after basking (Fig. 2). After diving, crocodiles either basked or stayed at the water surface 20% exposed. After 20%–40% exposure, crocodiles performed every other behaviour with similar frequency, while they were most likely to bask or retreat further into the water (20% exposed) after 60% exposure. There was no clear pattern in the behaviours following 80% exposure except that crocodiles were least likely to bask.

T_b

The rate of T_b change increased with an increase in the difference between T_b and operative temperature (Fig. 3*A*). The increase in rate of T_b change stabilised at differences between operative temperature and T_b exceeding 10°C. This is presumably because of resistance to heat transfer occurring primarily
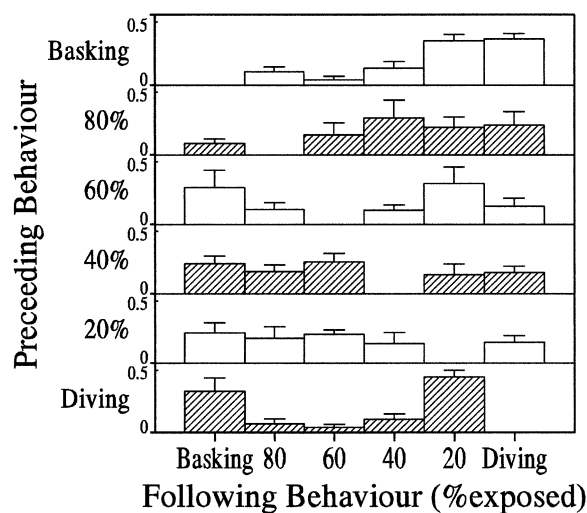
Figure 2. The frequency with which each posture (*vertical axis*) was followed by any other posture (*horizontal axis*) between the first heating episode in the morning and retreat into the water in the evening (means + SE).

within the body (i.e., the Biot number is very high; Incropera and DeWitt 1996), and further increase in the difference between operative temperature and T_b does not affect the rate of T_b change. The greatest rates of heating and cooling occurred during basking and diving, respectively. Crocodiles cooled at exposures of less than 40% when the difference between operative temperature and T_b was negative, and they heated at exposures greater than 40% when operative temperature was higher than T_b (Fig. 3B). Operative temperature during 0% exposure was well below T_b but increased with exposure until 100%, when operative temperature exceeded T_b by more than 20°C, on average (Fig. 3B).

The magnitude of the effect of behavioural postures on T_b decreased with increasing mass (Fig. 3C). The mean rates of cooling and heating during 0%–40% and 60%–100% exposure, respectively, decreased with increasing mass, except for 80% and 60% exposure, where this trend was not pronounced. Logarithmic curves were drawn for 100% ($Y = 0.1871 - 0.04771$ $\ln(X)$; $R^2 = 0.59$) and 0% ($Y = -0.2192 + 0.08289 \ln(X)$; $R^2 = 0.67$) exposed.

Thermal time constants express the relationship between mass and T_b change, but they also depend on the convective environment of the crocodile. The effect of high convection coefficient in water, compared to air, is shown most clearly in the short time constants for diving compared to the relatively long time constants for basking, and also in the gradual increase of time constants with exposure and decreasing surface area in water (Fig. 4). There was a logarithmic increase of thermal time constants (τ) with mass for all exposures with the following equations: $\tau(0\%) = -27.56 +$

$48.35 \ln(\text{Mass})$ ($R^2 = 0.92$), $\tau(20\%) = -73.06 + 71.31$ $\ln(\text{Mass})$ ($R^2 = 0.69$), $\tau(60\%) = 56.30 + 32.92 \ln(\text{Mass})$ ($R^2 = 0.053$), $\tau(80\%) = -123.82 + 171.46 \ln(\text{Mass})$ ($R^2 = 0.67$), $\tau(100\%) = -6.05 + 108.97 \ln(\text{Mass})$ ($R^2 = 0.86$). The logarithmic curves fit the time constants well for all exposures, except for 60% exposed, where the very low R^2 indicates that time constants did not increase logarithmically with mass. The effect of mass on T_b change shown in Figure 3 is an expression of the increase in time constants with mass (Fig. 4).

I used the equation for rate of change in T_b to predict the field data, providing a direct comparison of how well thermodynamic theory represented the thermal relations of live animals (Fig. 5). I used thermal time constants determined in this study (Fig. 4) in the calculations. This may compromise the independence of predicted values from measured values somewhat. However, there are no comparable published data on time constants for different behavioural postures, and the comparison will still give an indication of how well heat-transfer theory predicts the transient response of T_b to changes in posture. Predicted values were not significantly different from measured values (Mann-Whitney test, all $U < 2.60$, $P > 0.05$) for
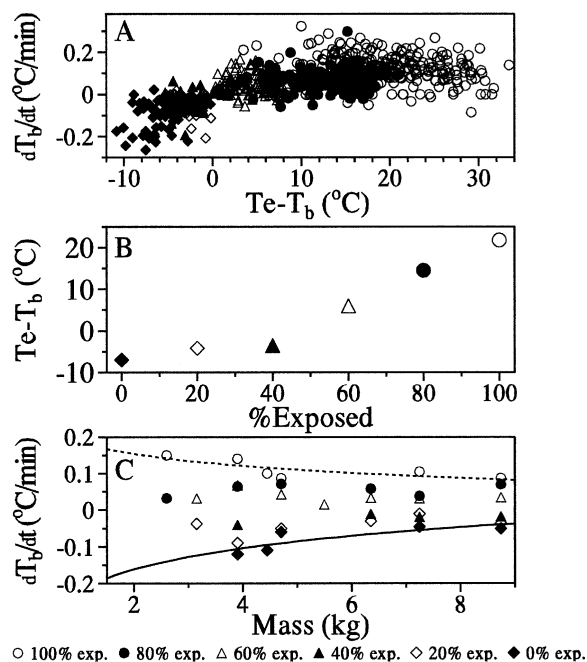

Figure 3. Rate of T_b change increased nonlinearly with the difference between operative temperature and T_b (*A*). The mean difference between operative temperature and T_b increased from −7°C during 0% exposure to over 20°C during 100% exposure (*B*; SE < 0.7°C for all means). The magnitude of the mean rate of T_b change decreased with mass, except for 80% and 60% exposed, where this trend was not pronounced (*C*; all SE < 0.035°C). Logarithmic curves were fitted to the data for basking (*dotted line*) and diving (*solid line*).
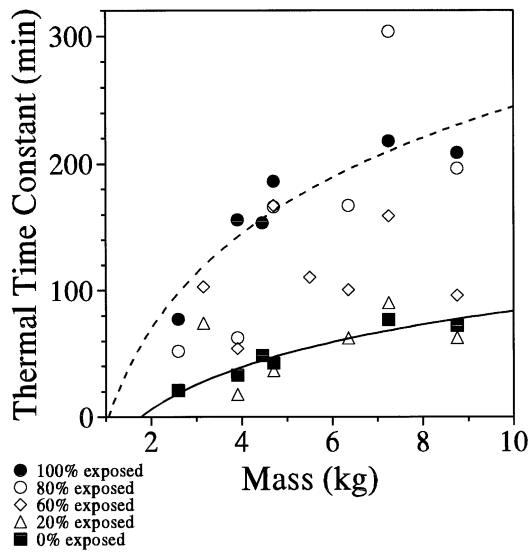
Figure 4. Thermal time constants calculated for each exposure category except for 40% exposed, where the sample sizes were too small. Time constants increased logarithmically with mass, although, for clarity, only the curves for diving and basking were plotted.

exposures between 0% and 60%, but the equation significantly underestimated rate of T_b change for 80% and 100% exposures (Mann-Whitney test, all $U > 7.20$, $P < 0.0001$).

Discussion

Crocodiles in the wild employed behavioural posturing and shuttling as an effective tool for altering rates of T_b change. Basking is the most conspicuous behaviour of crocodiles, and it has long been suspected to play a role in thermoregulation (Cott 1961; Modha 1968). However, my data showed that crocodiles did not simply shuttle between extremes of basking and diving but performed an array of intermediate postures whose thermal effect was clearly visible in the diurnal patterns of T_b.

Rates of T_b change during different behavioural postures depended on the temperature difference between the environment and the body, and on the mass of the animals. The relative importance of convection in air and water, absorption of solar radiation and conduction to the ground in the overall heat transfer between crocodile surface and the environment changed with a change in behavioural posture, so that each posture represented a distinct thermal microhabitat. The difference between the operative temperature of these "microhabitats" and T_b determined whether crocodiles heated or cooled. However, heating and cooling rates were dependent on body mass as well, so that the magnitudes of rates of T_b change decreased with mass for any given posture. Thermal time constants characterise the change in T_b in response to a change in posture. Using operative temperatures as the step temperature,

rather than simply air or water temperature as in many laboratory trials (e.g., Grigg et al. 1979), I was able to determine thermal time constants for different behavioural postures, which allowed me to use heat-transfer theory to predict T_b.

The effect of behavioural postures on T_b was predictable from heat-transfer theory, except when crocodiles were 80% exposed or basking. In thermoregulation, basking and 80% exposure maybe similar in that a crocodile aims at raising its T_b when performing those behaviours. It may be that the theoretical model did not predict rate of T_b change reliably during those behaviours because crocodiles attempt to increase rates of heating by increasing blood-flow rates and thermal conduction during basking. Some reptiles, including *Crocodylus johnstoni* (Grigg and Alchin 1976), are able to alter their blood-flow rates, resulting in heating/cooling hysteresis, which is believed to be of thermoregulatory advantage in that it decreases basking time and increases the time an animal can spend at a high T_b (Bartholomew 1982). The mass of the study animals fell in the range within which changes in blood flow could be effective in altering rates of heating and cooling (Turner and Tracy 1984). It is unknown, however, whether animals in the wild actually use physiological means to alter conduction. Changes in blood flow may be negligible in altering rates of T_b change in the light of, for example, high convection coefficients of water or the great difference between operative temperature and T_b during basking, which might override any physiological adjustment.
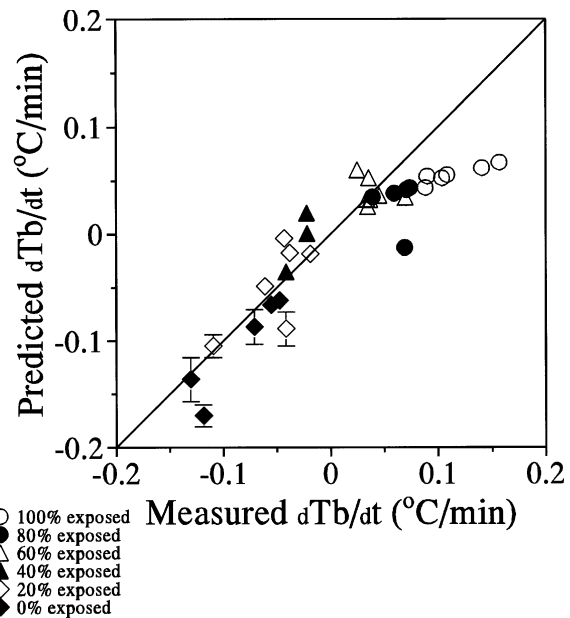

Figure 5. Predicted change in T_b (dT_b/dt) for each exposure category and crocodile (means $\pm$ SE) plotted against mean measured change of T_b. There were no significant differences between predicted and measured values from 0% to 60% exposed, but measured values were significantly higher for 80% and 100% exposure.

An investigation into these phenomena in wild animals would be of paramount importance for the understanding of thermoregulation in reptiles.

Given their aquatic habit, it may be advantageous for crocodiles to decrease time spent on land basking, and if the aim of thermoregulation is spending as much time as possible within the preferred T_b, then it is certainly advantageous to decrease cooling rates in the water. Decreasing cooling rates in water may be achieved behaviourally as well as physiologically. I used the heat-transfer equation to predict the time it takes crocodiles of different mass to cool from the upper boundary of their preferred T_b range ($\overline{X} = 32°C$; Seebacher and Grigg 1997), when they enter the water after basking, to the lower boundary of their preferred T_b range ($\overline{X} = 28.5°C$; Seebacher and Grigg 1997), when they reemerge to bask (Fig. 6). Exposure of 20% noticeably increased the time a crocodile can spend in the water at a T_b within its preferred T_b range (Fig. 6). An interesting point emerging from analysis of Figure 6 is the steep decline of time in water at high T_b with decreasing mass. A 100-g hatchling entering the water with T_b of 32°C would cool to 28.5°C within 1 min or less at either 20% or 0% exposure. It seems that high convection coefficients in water combined with small mass (100 g, however, is still much larger than the mass of most extant reptiles; Pough 1980) set a minimum effective size for thermoregulation in semiaquatic reptiles. It has been shown that thermoconformity is part of *C. johnstoni*'s thermal repertoire (Seebacher and Grigg 1997), and it seems likely that small crocodiles, up to perhaps 1–2 kg, are thermoconformers.
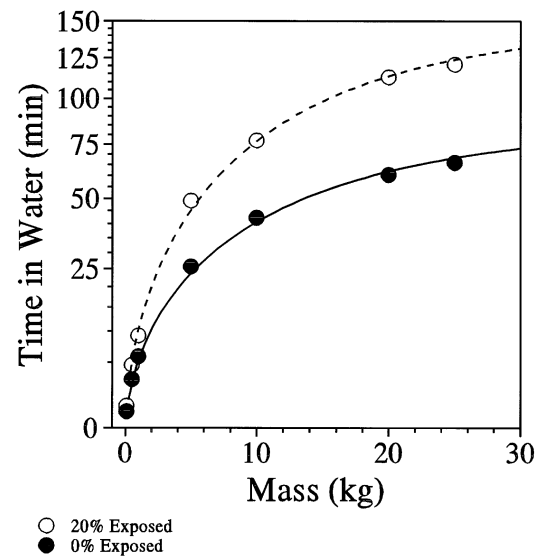
Acknowledgments

Figure 6. The time crocodiles can spend in the water between basking bouts before they cool from the upper to the lower boundaries of their preferred T_b range. Predictions for crocodiles of different mass (0.1 kg, 0.5 kg, 1–25 kg) and different behaviors (0% exposed and 20% exposed) are shown.

Literature Cited

Altman J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Bakken G.S. and D.M. Gates. 1975. Heat transfer analysis of animals: some implications on field ecology, physiology and evolution. Pp. 255–290 in D.M. Gates and R.B. Schmerl, eds. Perspectives of Biophysical Ecology. Springer, New York.

Bartholomew G.A. 1982. Physiological control of body temperature. Pp. 167–211 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 12. Academic Press, London.

Carrascal L.M., P. Lopez, J. Martin, and A. Salvador. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. Ethology 92:143–154.

Christian K.A. and B.W. Weavers. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol Monogr 66:139–157.

Cott H.B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Trans Zool Soc Lond 29:211–356.

Grigg G.C. and J. Alchin. 1976. The role of the cardiovascular system in thermoregulation of *Crocodylus johnstoni*. Physiol Zool 49:24–36.

Grigg G.C., C.R. Drane, and G.P. Courtice. 1979. Time constants of heating and cooling in the eastern water dragon, *Physignathus lesueurii*, and some generalisations about heating and cooling in reptiles. J Therm Biol 4:95–103.

Hammond K.A., J.R. Spotila, and E.A. Standora. 1988. Basking behaviour of the turtle *Pseudemys scripta*: effects of digestive state, acclimation temperature, sex, and season. Physiol Zool 61:69–77.

Huey R.B. and M. Slatkin. 1975. Costs and benefits of lizard thermoregulation. Q Rev Biol 51:363–384.

Incropera F.P. and D.P. DeWitt. 1996. Fundamentals of Heat and Mass Transfer. Wiley, New York.

Mitchell J.W. 1976. Heat transfer from spheres and other animal forms. Biophys J 16:561–569.

Modha M.L. 1968. Basking behavior of the Nile crocodile on Central Island, Lake Rudolph. East Afr Wildl J 6:81–88.

Monteith J.L. and M.H. Unsworth. 1990. Principles of Environmental Physics. 2d ed. Edward Arnold, London.

O'Connor M.P. and J.R. Spotila. 1992. Consider a spherical lizard: animals, models and approximations. Am Zool 32: 179–193.

Pough F.H. 1980. The advantages of ectothermy for tetrapods. Am Nat 115: 92–112.

Robertson S.L. and E.N. Smith. 1981. Thermal conductance and its relation to thermal time constants. J Therm Biol 6: 129–143.

Seebacher F. and G.C. Grigg. 1997. Patterns of body temperature in wild freshwater crocodiles, *Crocodylus johnstoni*: thermoregulation vs. thermoconformity, seasonal acclimatization and the effect of social interactions. Copeia 1997: 549–557.

Shine R. and T. Madsen. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons (*Liasis fuscus*) in tropical Australia. Physiol Zool 69: 252–269.

Smith E.N. 1979. Behavioral and physiological thermoregulation of crocodilians. Am Zool 19:239–247.

Tracy C.R. 1982. Biophysical modeling in reptilian physiology and ecology. Pp. 275–321 in C. Gans and F.H. Pough, eds. Biology of the Reptilia. Vol. 12. Academic Press, London.

Turner J.S. and C.R. Tracy. 1984. Body size and the control of heat exchange in alligators. J Therm Biol 10:9–11.