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Patterns of Body Temperature in Wild Freshwater Crocodiles, *Crocodylus johnstoni*: Thermoregulation versus Thermoconformity, Seasonal Acclimatization, and the Effect of Social Interactions

FRANK SEEBACHER AND GORDON C. GRIGG

We determined diurnal and seasonal patterns of body temperature (T_b) in *Crocodylus johnstoni* in the wild by monitoring T_b and behavior of 15 crocodiles, as well as measuring water, air and ground temperatures, and solar radiation. Two fundamentally different diurnal patterns of T_b occurred. One (pattern A) was similar to that described as typical for thermoregulating heliothermic reptiles, in that crocodiles shuttled between basking on land and cooling in water so that T_b formed a plateau elevated above water temperature (Tw) during the day. In the other (pattern B), crocodiles did not leave the water, and T_b equalled T_w throughout the day. Some crocodiles showed either pattern A or pattern B throughout the year, and some behaved differently at different seasons. The preferred body temperature range (PBTR) of those crocodiles that thermoregulated for all or most of the year changed seasonally, parallelling seasonal changes in T_w. The midpoint of the PBTR changed from approximately 29 C to 33 C, winter to summer. Intraspecific aggression prevented some crocodiles from thermoregulating effectively, and their PBTR was significantly lower when experiencing aggression from other crocodiles, compared with when undisturbed.

IN studies of crocodilian thermal relations, there has been a much greater focus on the elucidation of mechanism than on the determination of patterns that occur in the wild. Thus, we know that crocodilians show a whole range of behaviors including basking (Modha, 1968), shuttling between land and water (Spotila, 1974), and posturing in water (Smith, 1979; Fish and Cosgrove, 1987), which are known to be of thermoregulatory significance (Lang, 1987). We know also that, under laboratory conditions at least, they exhibit physiologically induced changes in thermal conductance, leading to heating and cooling hysteresis, caused by changes in peripheral blood flow (Grigg and Alchin, 1976; Smith et al., 1978; Robertson and Smith, 1978). Most of the behavioral studies and all of the physiological work have been undertaken on captive animals, often in conditions that restrict the animal from expressing its normal patterns of behavior (Vernberg and Vernberg, 1974; Gans, 1976). There are some data that describe natural patterns of body temperature (T_b) in some crocodilians (Diefenbach, 1975; Smith, 1975; Loveridge, 1984), but long-term descriptions of T_b patterns of undisturbed crocodilians in the wild are lacking. This study focuses on a determination of the pattern of body temperatures seen in *Crocodylus johnstoni* in the wild and will, we hope, lay a foundation for gaining a better understanding of the extent to which the behavioral and physiologi-

cal mechanisms known to occur in crocodilians are expressed in real situations.

Beyond straight description, diurnal patterns of T_b were analyzed with the aim of determining the extent to which *C. johnstoni* actually regulate their body temperature in the wild; the occurrence of thermoregulation is often accepted as a paradigm in reptilian thermal relations, but the alternative, thermoconformity, has rarely been examined. At the outset, we speculated that a crocodile's thermoregulatory behavior may be more conspicuous in the cold months when water temperatures are low, with less sign of it in the warmer months when water temperature (T_w) approaches the preferred T_b range (PBTR; Cowles and Bogert, 1944; Bartholomew, 1972).

We also examined the possibility of there being seasonal changes in the PBTR of freshwater crocodiles in the wild, correlating with seasonal changes in T_w. Further, by comparing observed values of T_b with calculated values of operative environmental temperatures (Bakken and Gates, 1975), we could determine whether any seasonal changes in PBTR were likely to be a consequence of limitations imposed by the thermal environment or an expression of regulation at a different level. It is important to realize that seasonal shifts in observed values of T_b do not necessarily reflect an expression of the animal's choice but may result from environmental limitations. For example, Van Damme et al. (1987)

COPEIA, 1997, NO. 3

showed that seasonal shifts in the T_b of the lizard *Lacerta vivipara* occurred because lizards were unable to warm to summer levels during winter. This must be a common pattern in cool temperate climates. However, Christian et al. (1983) demonstrated that Galapagos land iguanas actively choose lower T_b during winter, even though the thermal environment was such that summer T_bs were attainable.

Furthermore, we frequently observed that crocodiles engaged in aggressive interactions which often culminated in subordinate animals being chased from their basking sites, and we speculated that these encounters may have an effect on T_b of the subordinate crocodiles. The behavior of crocodilians is complex and quite unlike that of other reptiles (Lang, 1987). Crocodilians are known to have intricate social systems (Garrick, et al. 1978), which are usually characterized by a dominance hierarchy (Lang, 1987) within which animals communicate using an array of signalling systems (Lang, 1989; Vliet, 1989). Given the social nature of crocodilians, behavioral displays obviously can be of an interactive nature involving more than one animal. However, the effect of social interactions on the physiology of individual animals has not been documented. We describe the effect that aggressive behavior can have in preventing subordinate animals from raising their T_b to their PBTR.

MATERIALS AND METHODS

We measured body temperatures over a 2.5-yr period by surgically implanting temperature-sensitive radio transmitters (Sirtrack, Austec) into the peritoneal cavity of 15 *C. johnstoni* in the wild. The study was carried out on a population of crocodiles in a rocky waterhole (approximately 100 m × 30 m in size) connected to the Lynd River, Queensland, Australia (17°07′S, 144°03′E), which flows permanently at this point. The waterhole supports a relatively large natural population of *C. johnstoni* which, during the dry season, may number 50 individuals. The sexes and masses of the study animals are summarized in Table 1; the crocodiles ranged from juveniles (2.5 kg) to small and medium-sized adults (10–20 kg). A large adult of this species would weigh around 50 kg (Webb and Manolis, 1989).

Transmitters had a projected life of approximately 2 yr. However, we lost many prematurely, either through emigration of the individual or transmitter failure, resulting in unequal sample sizes. The transmitter/battery package was coated in an inert, impermeable wax made from par-

TABLE 1. OCCURRENCE OF T_b PATTERNS (NUMBER OF DAYS OBSERVED; PAT. A = PATTERN A, PAT. B = PATTERN B, INTERM. = INTERMEDIATE PATTERN), SEX AND MASS (KG) OF THE STUDY ANIMALS, AND THE MONTHS EACH CROCODILE WAS SAMPLED (1 = JANUARY, 2 = FEBRUARY, ETC.)

Croc	Sex	Mass	Pat A	Pat B	Interm.	Month
1	M	3.90	35	11	6	5, 6, 7, 10, 11
2	F	3.15	1	25	4	7, 10, 11
3	M	2.57	13	3	1	7, 8
4	M	4.70	18	9	2	9, 10, 11
5	F	7.25	38	8	2	1, 7, 8, 9, 10, 11
6	M	8.75	26	11	6	1, 9, 10, 11
7	M	2.60	18	0	0	7, 8
8	M	20.50	4	1	2	11
9	F	3.75	7	0	0	7, 8
10	F	5.50	0	12	0	7
11	M	3.10	6	29	3	7, 10, 11
12	F	6.35	31	4	3	1, 9, 10, 11
13	F	12.27	8	13	11	3, 5, 11
14	F	9.54	52	15	12	2, 3, 5, 6, 7, 10, 11
15	M	10.86	4	1	2	11
Total			261	142	54	

affin and polyvinyl beads (Elvax) in the ratio 80:20 by mass. The coated packages weighed approximately 30 g, only 1.15% of the body mass of the smallest individual studied. Transmitters were calibrated in a temperature-controlled water bath (range of calibration temperatures 2–40 C) against a certified mercury thermometer. Calibration runs were carried out at least twice on each transmitter prior to implantation, with 1–2 months between runs, to confirm stability. There was no drift over that time period in any of the transmitters used. We derived a fifth-order polynomial calibration equation for each transmitter, relating pulse interval and calibration temperature, allowing pulse intervals measured in the field to be converted to temperature with an accuracy of 0.3 C. We implanted transmitters in the field using sterile techniques and a local anaesthetic (Xylocaine), and crocodiles were released within 24 h of capture. All surgical and handling procedures had the approval of the University of Queensland's Animal Experimentation Ethics Committee. Signals could be received up to 0.5 km from a crocodile on land, 100–200 m from an individual at the surface of the water, and less when an animal was submerged. We received signals from the top of a rocky outcrop bordering the waterhole, using a Telonics TR-2 scanner-receiver and either a hand held unidirectional twin element antenna (Telonics) or a permanently installed twin yagi null-peak antenna. Body tem-

peratures were usually recorded every 15 min during the day and every 30 min at night. During the day, measurements were made by timing pulse intervals with a stopwatch and matched with observations of behavior whenever possible. At night, we recorded signals on a remote sampling system described by Grigg et al. (1992). Sample sizes are shown in Table 1 (see Results). It should be noted that the logistics involved in a study like this are very challenging not only because of the remote location of the study site (several hours drive to the nearest town) but also because the success of telemetrically recording T_b of wild animals is very much dependent on the "cooperation" of the animals. It is beyond the control of the researcher when a crocodile decides to move several kilometres downstream from the study site or spends the afternoon underneath a large rock that blocks the signals.

Some transmittered crocodiles were paint marked on their backs for behavioral observations made ad libitum concurrently with T_b measurements. We made behavioral observations from the same rocky outcrop from which we measured T_b, which was ideal for the purpose because the observer was 20–30 m above the crocodile and thus unnoticed. Observations included aggressive encounters whose effect on T_b was evaluated by comparing the T_b value measured each time a crocodile was chased into the water with those in which the same crocodile voluntarily retreated into the water after basking at a similar time of day (within 2 h) on the preceding or following day. Comparison of T_b values between days were unlikely to be confounded by environmental conditions, which were such that crocodiles were not prevented from attaining their preferred T_b levels at any time during the study (see Results).

We measured water temperatures at two depths, shallow (10–15 cm) and deep (1.5 m), with calibrated temperature sensors (National Semiconductor LM 335, accurate to 0.3 C) suspended in the water column and connected to a data logger (Data Electronics). A radio transmitter, placed in 1.5 m of water, at a different location from the other sensors, also reported deep water temperature. There was good agreement between temperatures taken at different places using different techniques. We recorded measurements every 30 min for the duration of each field trip, but some measurements using the data logger were lost in equipment failures. Mean monthly deep T_w were the average of all measurements taken between day 10 and day 20 of each month. When samples were taken across two months, we averaged measurements between day 20 of the first month and day 10 of the sec-

ond month. We calculated mean daily extremes by averaging daily minima and maxima for all the days sampled per month which were used to calculate the mean monthly water temperatures. In addition to T_w, we also monitored air (T_a) and ground temperatures (T_g) and solar radiation by sensors (National Semiconductors LM335 and a tube solarimeter [Irricrop Technologies], respectively) connected to a data logger and following the same protocol as for T_w. The T_a sensor was in the shade on the bank of the water hole, and the sensor measuring T_g 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 waterhole where it was unlikely to be interfered with by crocodiles.

Operative environmental temperature (T_e) was defined by Bakken and Gates (1975) as "the temperature of an inanimate object of zero heat capacity with the same size, shape and radiative properties as an animal and exposed to the same microclimate." As such, T_e is useful for predictions of the T_b an ectotherm could attain under a particular set of environmental conditions, and possible environmental limitations on the achievement of a desirable T_b can be evaluated (Christian et al., 1983). We calculated T_e by solving a steady state energy budget equation for body temperature (Tracy, 1982) and using heat transfer relations for conduction and solar radiation given in that paper. Convective heat transfer was calculated by methods given in Mitchell (1976).

RESULTS

Diurnal patterns of body temperature.—Two fundamentally different diurnal patterns of T_b were observed depending upon whether crocodiles emerged to bask or remained in the water. One (pattern A) was similar to that described by Heatwole (1976) as typical for a thermoregulating heliothermic reptile, and the other (pattern B) showed T_b equal to T_w for the entire day. The frequency of occurrence of each pattern, as well as the sex and mass of the study animals and the months of sampling, are shown in Table 1. Typically, T_b rose in the morning to a plateau "range" during the day and then decreased in the evening to equilibrate with T_w overnight (Fig. 1). The plateau phase resulted from a crocodile shuttling between the land (heat source) and water (heat sink). Basking was defined as a crocodile having 75% or more of its body on land and in the sun. In more detail, T_b rose during an initial basking phase in the morning until it reached a local maximum (T_{bmax}) at which point
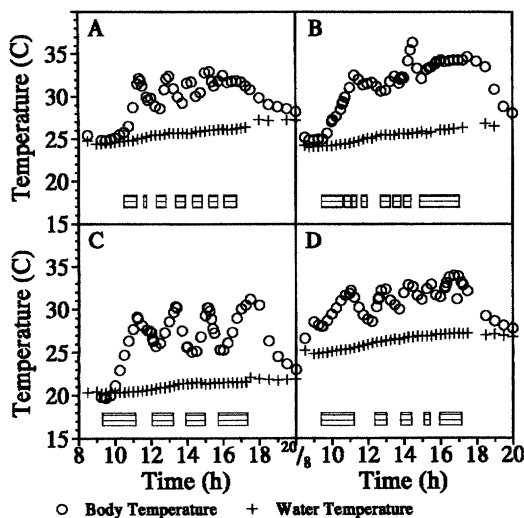
Fig. 1. Representative examples of thermoregulatory diurnal T_b pattern (pattern A) (A: crocodile #4, September; B: crocodile #5, September; C: crocodile #1, July; D: crocodile #6, October). The crocodiles emerged to bask in the morning until T_b reached a local maximum (T_{bmax}) when the animals reentered the water, emerging to bask again when T_b reached a local minimum (T_{bmin}). This sequence of behavior was repeated until evening resulting in a plateau of T_b during the day, but T_b equilibrated with T_w overnight. Basking periods are indicated by the hatched boxes above the x-axis. Difference between T_{bmin} and T_{bmax} defines the PBTR.
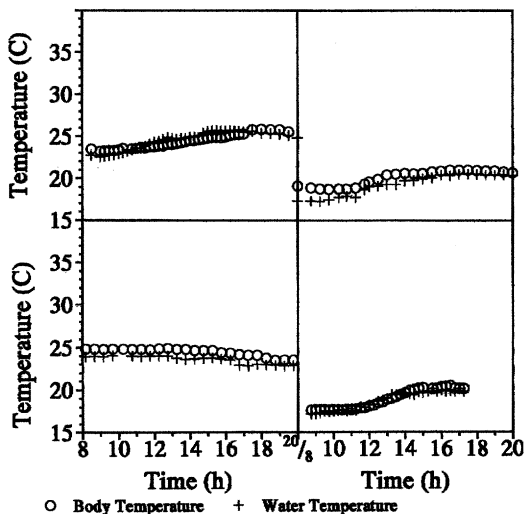

Fig. 2. Representative examples of the thermoconforming diurnal T_b pattern (pattern B) (A: crocodile #5; B: crocodile #11; C: crocodile #13; D: crocodile #3). The crocodiles stayed in the water for the entire day, and T_b was not different from T_w.

the crocodile retreated into the water where it stayed until T_b reached a local minimum (T_{bmin}) when the crocodile reemerged to bask. This sequence of behavior was repeated until evening, resulting in a number of T_{bmin} and T_{bmax} during the day; T_b fell to within 1–2 C of T_w overnight in all crocodiles studied.

During the second pattern (pattern B), T_b was not different from water temperature in any of the study animals (Fig. 2). The T_b was significantly lower than shallow T_w in all crocodiles (Mann-Whitney test, $P < 0.0001$ for all crocodiles) and significantly higher than deep T_w in all crocodiles (Mann-Whitney test, $P < 0.01$ for all crocodiles) except for crocodiles #1 ($P = 0.57$) and #5 ($P = 0.69$) where T_b was not different from deep T_w. Pattern B resulted from crocodiles spending all day at the water surface or under water (data not shown). Although we could not see crocodiles under water, their whereabouts were known from their transmitter signals received with a unidirectional antenna, and it is unlikely that they were at the water surface or on land without being seen.

Apart from patterns A and B, we also ob-

served a pattern of T_b that was intermediate between the two when crocodiles basked once resulting in one T_{bmax}, but otherwise T_b was not different from T_w during the day. We rarely observed this pattern compared with patterns A and B (Table 1) and considered it to be an attempt at achieving pattern A, disrupted by disturbance such as intraspecific aggression (see below).

Seasonal changes in PBTR and occurrence of diurnal body temperature patterns.—We tested the hypothesis that the occurrence of the patterns was dependent on season by fitting log-linear models (Fienberg, 1970) to the discrete count data of the number of days each pattern was observed per month in each crocodile. In this analysis, we used only those crocodiles that were sampled for at least three months during which a gradient in environmental conditions existed (crocodiles #1, 2, 4, 5, 6, 11, 12, 13, 14). The relative occurrence of patterns A and B was independent of month in five crocodiles (crocodiles #1, 2, 5, 13, 14; $P > 0.2$ for all crocodiles). Of these, #1, 5, and 14 mainly showed pattern A regardless of month, whereas pattern B was predominant in crocodile #2 at any month sampled. Crocodile #13 showed both patterns in similar proportions, but there was no trend with month sampled. In the remainder of the crocodiles (#4, 6, 11, 12), the occurrence of the patterns was not independent from month ($P < 0.03$ for all crocodiles). We dropped some months from

(A) a Croc #1   b Croc #4   c Croc #5
    d Croc #6   e Croc #12   f Croc #14
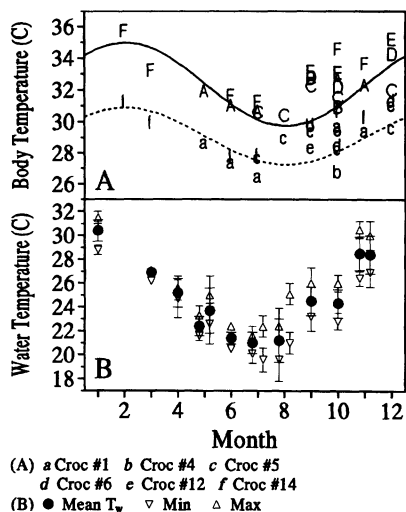(B) ● Mean T_w ▽ Min   △ Max

Fig. 3. (A) Seasonal cycles of mean monthly T_{bmin} (lower case letters) and T_{bmax} (upper case letters). Data are shown for each crocodile separately, and 95% confidence intervals were less than 1 C for all means shown. The fitted curves show simple harmonic oscillations and the equations are given in the text. (B) Mean monthly T_w and mean daily minima and maxima of T_w per month ($\pm$ 95% confidence intervals).

the analysis to explore similarities between months. A significant fit on the reduced dataset identified the months that were similar to each other but different from those that have been dropped. Trends in the raw data were used to decide which months to drop from the analysis, and a number of combinations were tried until the best fit was determined (Fienberg, 1970). We found that pattern A occurred mainly in the cooler months and pattern B in the hotter months in crocodiles #4, 6, and 12, whereas the reverse was true for crocodile #11, which showed pattern A in the hotter months only.

The T_{bmin} and T_{bmax} changed cyclically with season in all study animals that showed this pattern over several months, being highest in summer (December–January) and lowest in winter (June–August; Fig. 3). The midpoint of the range changed by 4 C from approximately 29 C in winter to approximately 33 C in summer. The seasonal changes in T_{bmin} and T_{bmax} could be described by harmonic oscillations with the following equations:

$$T_{bmin} = 29.06 + 1.82\sin[(2\pi x/12) + 0.8],$$
$$R^2 = 0.40 \qquad (1)$$
$$T_{bmax} = 32.37 + 2.60\sin[(2\pi x/12) + 0.5],$$
$$R^2 = 0.71 \qquad (2)$$

We compared monthly T_{bmin} and T_{bmax} separate-

ly by one-way analyses of variance for individual crocodiles. We used sample sizes of no less than three days (six observations) and up to 10 days (21 observations) per crocodile per month. T_{bmin} and T_{bmax} each differed significantly between months in all crocodiles ($P < 0.01$ in all cases) except crocodile #5 in which T_{bmax} did not vary between months ($P = 0.12$). Given their aquatic habit, the best indicator of changing seasonal conditions in the crocodiles' environment was water temperature; changes in the T_{bmax} and T_{bmin} parallelled seasonal changes in T_w and mean monthly T_w (Fig. 3). We sampled T_w in July and August 1992 during the day only, and means for these months are thus not shown in Figure 3. However, it was possible to determine daily minima and maxima in these months because those occurred in early morning and late afternoon. There was a 7–9 C difference in mean T_w between the hottest (November–January) and coldest months (June–August).

Effect of aggressive behavior on the PBTR.—We observed many instances of intraspecific aggression in the form of one crocodile chasing another. Typically, an aggressor swam up to a basking crocodile and chased it from its basking site, occasionally then claiming the site for itself. Four crocodiles (#4, 6, 7, 12) were frequently displaced from basking sites by such encounters (on 12, 3, 4, and 7 occasions, respectively), and could be assumed to be subordinates. There did not appear to be any pattern with respect to the sex or mass of the subordinate crocodiles.

These aggressive encounters prevented subordinate crocodiles from raising their T_b to the levels typical for undisturbed crocodiles (Fig. 4). The most severe example of intraspecific aggression on the PBTR we observed was when crocodile #4 was chased from its basking site whenever it emerged to bask, resulting in T_b staying close to T_w for most of the day (Fig. 4A,D). In contrast, the least severe effect was when crocodile #7 was chased into the water on its first attempt to bask in the morning but reemerged shortly afterward to proceed undisturbed with the typical shuttling behavior for the remainder of the day (Fig. 4C).

The mean T_b at which each study animal was chased into the water was significantly lower (t-test) than the mean T_b when they voluntarily retreated in three study animals (crocodiles #4 [$P < 0.001$, df = 11], #7 [$P < 0.001$, df = 7] and #12 [$P < 0.05$, df = 3]), but there was no significant difference between the means in crocodile #6 ($P = 0.057$, df = 2; Fig. 5). Note that T_bs of crocodiles chased from their basking
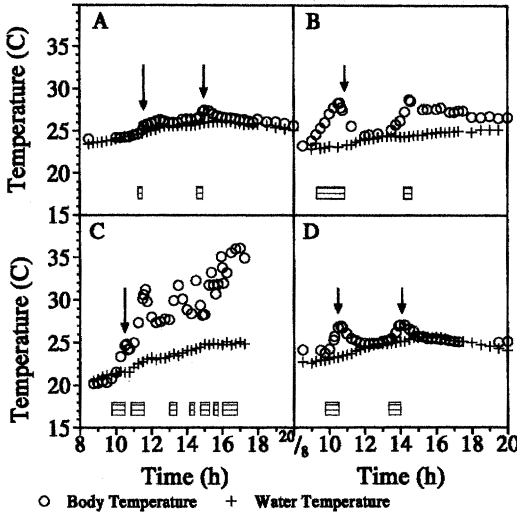
Fig. 4. Representative examples of the effect of intraspecific aggression on T_b when crocodiles were chased from their basking sites (arrows) (A: crocodile #4; B: crocodile #12, C: crocodile #7; D: crocodile #4). Basking periods are indicated by the hatched boxes above the x-axis.

sites were not used in the above analysis of T_{bmin} and T_{bmax}.

DISCUSSION

Freshwater crocodiles in the wild were capable of regulating their T_b during the day in a manner similar to that seen in terrestrial lizards. The local extrema observed during pattern A (T_{bmin} and T_{bmax}) were the result of crocodiles choosing to leave the water to bask or to retreat into the water after basking. It was thus warranted to conclude that crocodiles regulated their T_b in these instances, and we interpreted the T_{bmin} and T_{bmax} as the lower and upper boundaries, respectively, of a preferred T_b range. In contrast, the second and somewhat less common pattern (pattern B) was fundamentally different, in that crocodiles showing this pattern exercised no control over T_b, which followed fluctuations in T_w and was usually much lower than during pattern A (Figs. 2–3). Pough (1980) argued that the main advantage of ectothermy lies in its conferring a lower energy lifestyle than endothermy. Given the relatively high metabolic Q_{10} of crocodilians (Smith, 1975; Coulson and Hernandez, 1983), energy conservation during pattern B could be considerable. On the other hand, most physiological processes in reptiles are temperature dependent so that thermoregulation would most probably facilitate a more active lifestyle. There
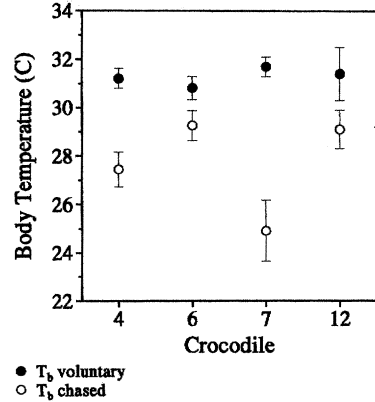

Fig. 5. Mean T_b values ($\pm$ 95% confidence intervals) at which crocodiles retreated voluntarily into the water after basking (T_b voluntary) and when they were chased into the water by another crocodile (T_b chased). The means were significantly different from each other in all crocodiles except #6 ($_t$-test).

may be good reasons for breeding crocodiles, or crocodiles intending to breed, to thermoregulate and maintain a high T_b. High levels of activity (Christian and Tracy, 1981; Huey, 1983) as well as testicular and ovarian development (Dawson, 1975) are facilitated by high temperatures, and maximum performances have been reported to occur within the preferred T_b range in some lizards (Licht, 1965; Dawson, 1975). Hence, thermoregulation could increase breeding success, because more active individuals may have an advantage during intraspecific struggles, which are common especially during the early (June–July) breeding season (FS, pers. obs.). Also, gonad development would have been facilitated in individuals with a history of higher T_bs. Although reproductive correlates might explain the thermal behavior of the larger, mature crocodiles (> 7–10 kg, Webb and Manolis, 1989), they do not account for the variation in thermal behavior observed in smaller, immature crocodiles. We feel that it is most appropriate to interpret the observed variation in thermal behavior in a broadly energetic context including reproductive considerations. Each crocodile would have to "perform a cost-benefit analysis" between thermoregulation and its advantages in levels of activity, reproduction, and growth rate on the one hand and the energy savings of thermoconformity on the other.

In those crocodiles that thermoregulated at different seasons, preferred body temperatures showed a clear seasonal cycle, correlating with changes in water temperature. The possibility that the lower PBTR in winter is the result of thermal limitations of the environment can be
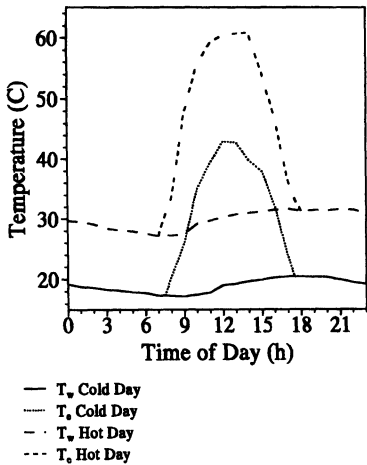
- — T_w Cold Day
- ······ T_e Cold Day
- — · T_w Hot Day
- --- T_e Hot Day

Fig. 6. Operative environmental temperatures, T_e, calculated for a very hot day and a very cold day, as well as deep T_ws for the same days. The T_e exceeded the PBTR for 5–6 h on the cold day and for 7–8 h on the hot day. Deep T_ws represent the minimum attainable T_bs for those days.

rejected, because operative environmental temperatures were well above the PBTR for prolonged periods during the day in all seasons. We calculated T_e for a 5 kg crocodile on a rock exposed fully to the sun for a very cold day (3 August 1990) and for a very hot day (14 January 1992) (Fig. 6). Results for all other days sampled would fall between these two extremes. Although T_e is mass dependent, it does not vary by more than 1 C between 1 kg and 20 kg body mass, and the T_e calculated for a 5-kg crocodile is therefore sufficiently representative for all study animals. The T_e equalled or exceeded the T_{bmax} for 5–6 h on the cold day and for 7–8 h on the hot day (Figs. 1,6). The T_w was well below the T_{bmin} on the cold day but approached it on the hot day. The thermal inertia of heating crocodiles has to be taken into account in this consideration, because it would cause a lag in body temperature rise compared with T_e. However, measured rates of heating of a 5-kg crocodile (the same mass as was used to calculate T_e) basking in winter are in the vicinity of 0.1 C/min (Grigg and Alchin, 1976) and allow some predictions to be made. Thus, assuming a crocodile's T_b equals T_w in the early morning on a cold day, say 20 C, T_b will rise to be within the PBTR after 1.5–2 h of basking. Also, the relatively large thermal time constant of 50–60 min for a 5-kg lizard-shaped reptile cooling in air (Grigg et al., 1979) will allow T_b to stay well above T_e for a considerable period of time while still on land in the late afternoon when ambient temperatures are falling. Hence, it can be as-

sumed that the lower PBTR observed in winter is a consequence of choice by the crocodile, not an environmental limitation, and that there is an acclimatization of PBTR.

Seasonal changes in the physical environment often elicit a seasonal compensatory response in ectothermic vertebrates (Fry, 1958; Hutchison and Maness, 1979), and many ectotherms acclimatize to changes in environmental temperature by adjusting metabolic rate functions in a way that minimizes the effects of temperature over the temperature range they experience (Hazel and Prosser, 1974; Dawson 1975). Metabolic acclimatization has been shown to involve changes in rates of biochemical functions (Rao, 1967; Hazel and Prosser, 1974) and the activity of metabolic enzymes (Licht, 1967; Olson, 1987) and is often measured in terms of changed rates of oxygen consumption at a particular temperature (Patterson and Davies, 1978; Blem et al., 1986; Blem and Blem, 1990). Fish, particularly, undertake metabolic acclimation in response to seasonally changing temperature regimes (Hazel and Prosser, 1974) perhaps because the aquatic habitat restricts their scope for behavioral thermoregulation. Aquatic and semiaquatic reptiles too are restricted in this way, and some are known to show metabolic acclimatization (turtles; Olson, 1987; Olson and Crawford 1989) or acclimation (aquatic snakes; Blem and Blem, 1990). As in fish, the ability of crocodiles to thermoregulate is limited by their lifestyle, so that seasonal metabolic acclimatization in response to different temperature regimes, particularly water temperature, could be of selective advantage. *Crocodylus johnstoni* spend most of their time in the water, perhaps 16 h a day, with T_b near T_w. Thus, abilities to compensate metabolically for seasonally changing T_w would not be surprising. We suggest that the striking seasonal cycle in PBTR, parallelling T_w, might reflect metabolic acclimatization.

Aggressive behavior could override physiological and physical aspects of thermoregulation and might make a physically benign habitat quite inhabitable for some crocodiles. Considering the thermal dependence of most physiological processes in reptiles (Dawson, 1975), this intraspecific aggression could have a detrimental effect on the fitness of some individuals, especially when they are prevented regularly from raising their T_b to the preferred T_b range. The stimulus for aggressive behavior could originate from the strong social hierarchy observed in many species of crocodilians. The sample size of marked crocodiles in this study was too small to allow examination of the social structure of the whole population in the waterhole. Howev-

er, even within the small marked population, certain features emerged which are consistent with existing knowledge on crocodilian social hierarchies and interactions (Lang, 1989). Crocodile #5, a mature female (C. Limpus, pers. comm.), was never subordinate in aggressive encounters. On the contrary, she was the aggressor in many encounters involving marked (crocodiles #4 and 6) and unmarked crocodiles. In those encounters, she either left her basking site, chased another crocodile from its basking site and then returned to her original site, or she emerged from the water and chased another crocodile from its basking site and then claimed that site herself; aggressive encounters were rarely observed when both crocodiles were in the water. These observations indicate that crocodile #5 was dominant at least with respect to the animals she chased, and she might have acted in demarcating her territory; on the other hand, chasing crocodiles to claim their basking site herself might indicate competition for basking sites. We observed that crocodiles rarely basked on the sandy shores of the waterhole but preferred rocky islands. Even when they were chased from their basking site on a rock, crocodiles remained in the water rather than basking on the sandy shore even though it was vacant. This preference for rocky islands could have created a shortage of basking sites, because most islands had crocodiles basking on them at any time of the day. Thermally appropriate microhabitats can be viewed as an ecological resource over which individuals within a population compete (Magnuson et al., 1979). This speculation agrees with Tracy and Christian (1986) who argued that animals exploit and compete for their physical environment, in particular the thermal environment, in a similar manner as for their biotic environment.

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