
Is Thermoregulation Unimportant for Most Reptiles? An Example Using Water Pythons (*Liasis fuscus*) in Tropical Australia

Richard Shine

Thomas Madsen

School of Biological Sciences A08, University of Sydney, NSW 2006, Australia

Accepted 6/21/95

Abstract

*Studies on reptilian thermoregulation have been dominated by research on small diurnal lizards living in the temperate zone, in environments where thermoregulatory challenges are severe and the animals (i) consequently devote considerable time and effort to the maintenance of high stable body temperatures and (ii) are constrained in their times and places of activity by thermal factors. However, most reptiles live in the Tropics, in more thermally benign regions where the animal's ecology and behavior may be affected only trivially by thermoregulatory concerns. We present data on environmental temperatures and body temperatures of 26 radio-tracked water pythons (*Liasis fuscus*) in tropical Australia, to investigate the extent to which thermal considerations influence the day-to-day life of this species. Some effects are evident—for example, activity is reduced on cool nights, and gravid female pythons often bask in the few weeks prior to oviposition. Nonetheless, most pythons are able to maintain high and stable temperatures (approx. 30°C) throughout the year without overt thermoregulatory activities, because (i) ambient temperatures are generally high, (ii) microhabitats with distinctive thermal characteristics are easily accessible, and (iii) the large body sizes of adult pythons confer a high degree of thermal inertia. Overall, there are few features of the ecology of this species that appear to be substantially influenced by thermoregulation. Before we can place thermoregulatory biology in its proper perspective, we will need considerably more data on the thermal biology of tropical reptiles.*

Introduction

The notion that thermoregulation is of central importance in the daily life of most reptiles is a central tenet of modern herpetology, and it is heavily stressed in many general treatments of reptilian biology (e.g., Spellerberg

1982; Bradshaw 1986). Unfortunately, the statement may be untrue. Available data on reptilian thermoregulation are derived primarily from studies of temperate-zone reptiles, especially small diurnal lizards living in areas such as deserts, where the high diurnal range in ambient temperatures means that a lizard must devote considerable time and effort to thermoregulation if it is to maintain high and stable body temperatures (Cowles and Bogert 1944; Cogger 1974; Avery 1982). We do not dispute the importance of thermoregulatory activities for such animals or the significance of the local thermal environment for other aspects of the animal's ecology (e.g., temporal and spatial patterns of activity). However, we contend that most reptiles do not live in these kinds of environments. The vast majority of reptilian species live in the Tropics (see, e.g., Pianka and Schall 1981; Vitt 1987), where the thermal challenges to an ectotherm are very different (e.g., the major problem is to lose rather than gain heat) and, commonly, thermal challenges may be trivial. Especially for large ectotherms living in tropical environments, high and stable body temperatures may be attainable through thermoconformity, without any need for specifically thermoregulatory behaviors. Similarly, the consistently high environmental temperatures may place few (if any) thermal constraints on the times and places that activity can occur.

The conceptual basis for current interpretations of reptilian thermoregulation was profoundly influenced by the classic paper of Huey and Slatkin (1976), who proposed that maintenance of a particular body temperature by a reptile would generally involve both a benefit to the animal (e.g., enhanced physiological performance) and a cost (in time, energy, and risk, due to the behaviors needed to maintain that temperature). Thus, precise thermoregulation would be exhibited only when the benefits exceeded the costs. Benefits may well be ubiquitous, but costs are not. If "optimal" body temperatures are always easily attainable, without incurring significant costs, then thermoregulation per se may be virtually irrelevant to the day-to-day activities of a reptile. Under this view, body temperatures are still important to the animal's performance, but regulating temperature requires so little effort, or modification of other activities, that this regulation is unimportant. That is, the requisite resource is so readily available that it is not a limiting factor. Water falls into this category for most fishes. We suggest that "suitable body temperature" falls into the same category for most reptiles.

In order to explore this heresy further, we need detailed information on the thermal biology of tropical reptiles. Few such data are available, and most of these studies have been based on diurnal lizards (e.g., Inger 1959; Alcalá and Brown 1966; Shine and Lambeck 1989), the group for which behavioral thermoregulation is likely to be most important because of their generally small body sizes (and consequent low thermal inertia) combined

with high diurnal thermal heterogeneity. The other tropical taxa that have been studied extensively in this respect are lizards living in environments of low thermal heterogeneity (aquatic habitats and closed forests: e.g., Shine and Lambeck 1985; Rummery et al. 1995), where the opportunities for behavioral regulation of body temperatures are very limited. It is thus not surprising that many of these animals have proved to be thermoconformers, with little overt thermoregulatory behavior (e.g., Ruibal 1961; Huey and Webster 1976; Hertz, Huey, and Stevenson 1993). The present article is part of a long-term investigation of the ecology of water pythons in tropical Australia. In the course of this work we have measured body temperatures of radio-tracked pythons, and we now present these data in the context of the ideas discussed above.

Material and Methods

Water pythons (*Liasis fuscus* [= *Liasis mackloti* of some authors]) are large (to 3 m total length, 5 kg) terrestrial snakes that are widely distributed in tropical Australia. They are generally found close to water bodies (thus their common name) and swim readily but spend most of their time in terrestrial habitats (Shine 1993). The snakes are usually located in dry savannah woodland, in soil cracks or reed beds on the open floodplain, or among reed beds in standing water. During the 3-mo wet season, when much of the floodplain is inundated, some snakes live in these aquatic habitats for weeks at a time (Madsen and Shine 1996). In our study area, the pythons feed almost exclusively on small mammals, mostly rats (Shine 1993).

We studied water pythons in Fogg Dam and its adjacent floodplain, 70 km east of the city of Darwin in the Northern Territory of Australia. Weather data have been recorded twice daily for the last 15 yr at the Coastal Plains Research Station, less than 3 km from Fogg Dam. The area lies within the Wet-Dry Tropics, and rainfall is highly seasonal. Approximately 75% of the 1,300-mm annual precipitation falls in monsoonal storms during the annual wet season (December–February). The thermal environment also shows significant seasonal variation. Temperatures are high year-round, with maximum air temperatures relatively consistent (monthly mean maximum air temperatures range from 31° to 36°C) but minima more variable (15°–24°C). Nighttime temperatures are lower in the dry season, owing to the lack of cloud cover. Water temperatures in Fogg Dam show relatively little diurnal variation, especially in shaded areas, but show a gradual seasonal shift from approximately 25°C in the dry season to 30°C in the wet season (see Shine and Lambeck [1989] for data on water temperatures from a nearby

area). Solar irradiation is intense, especially while skies are cloudless for several months during the dry season.

In order to characterize the ambient thermal environment, we monitored temperatures in a variety of microhabitats (at the ground surface, in shaded air, in water, in soil cracks in the black soil of the floodplain, and in varanid burrows in the red soil of the higher, drier surrounding countryside) as well as in physical models of snakes painted to match water pythons in shape and reflectance. Such models provide estimates of the body temperatures that snakes would attain if they remained in the same site for long enough to attain thermal equilibrium (e.g., Peterson, Gibson, and Dorcas 1993). Our models were constructed of hollow copper pipes 25 cm long and 6 cm in diameter; pilot studies showed that length of the model had little effect on its internal temperature (see also Peterson et al. 1993). Reflectance of the paint covering the models (as measured in a Beckman DK-2A spectrophotometer) averaged 10.9%, similar to that of dark-colored snakes (Peterson et al. 1993). The models were placed in an area that received full sunlight, and their internal temperatures (and surrounding ambient temperatures) were monitored and recorded every 10 min for a 5-d period with portable data loggers (Hobo-temps). Thermal data were taken in this way during the late dry season (September 1994), at a time of year that is intermediate between the extremes reached during the annual cycle.

Temperature-sensitive radio transmitters (Holohil model no. SI-2T, 45 × 15 mm, 35 g) were calibrated in the laboratory against a certified thermometer, at increments of 2°C over the range of 10°–40°C. The transmitters were then surgically inserted into the peritoneal cavities of 26 adult water pythons under halothane anesthesia, after which these snakes were released at the site of original capture and monitored frequently over the next 30–442 d (\bar{X} = 168 d). Snakes were generally located daily (and their body temperatures then determined) during the dry season. We also recorded shaded air temperature at the same time, 1 m above the ground and as close as possible to the snake. Many areas became impassable to us with the onset of wet-season flooding, so that monitoring frequency declined at this time, but several snakes remained accessible for monitoring throughout this period. Thus, we have large data sets from all months from July to March (we were absent on other fieldwork from April to June each year).

As part of a capture-mark-recapture program, we also obtained information on the numbers of active pythons each night by searching the dam wall for approximately 60 min shortly after sunset. Snakes caught at this time are engaged primarily in foraging activities: the pythons remain inactive during the day (usually in soil cracks or in dense vegetation) and move at dusk to feeding sites (usually on the floodplain). Because we carried out these

searches in the same area each time, and recorded the duration of the search and the numbers of people involved, we are able to calculate the numbers of pythons collected per person per hour. This figure can thus be compared to climatic data, to examine any possible influences of weather conditions on activity levels of the snakes.

Finally, we measured body temperatures of water pythons in the laboratory, to compare with field data. Selected temperatures were assessed in May 1995 by placing six unfed captive pythons in large thermal gradients (1–2 m long) so that the snakes could select temperatures within the range from 21.5° to more than 45°C. At least 6 h after the snake was introduced to the gradient, the body temperature of the coiled snake was measured with an infrared thermometer focused on the lateral surface of the body. Five readings were taken for each snake, with an average of approximately 1 h between successive readings. Cooling rates of adult pythons were also measured under controlled conditions, to assess the degree to which large body size influenced thermal inertia. Three adult pythons (masses of 1.6–2.1 kg) were placed in separate cloth bags and had thermistor probes inserted 3 cm into the cloaca and held in place with adhesive tape on the tail. Another probe was placed inside an empty bag. The probes were connected to Hobo-temp data loggers that recorded temperatures every 4 min. Experiments commenced when the snakes had body temperatures of 28°–29°C. Their cooling rates were measured under two conditions: (i) when the bags were transferred to an air-conditioned room (22°C), where they were suspended in midair so that cooling was primarily by convection into the surrounding air, and (ii) when the bags were placed on the ground surface at sunset (1900 hours), to mimic cooling rates of pythons in ambush positions on the floodplain at night. In this latter test situation, most heat loss will be by conduction to the ground, rather than by convection (Peterson et al. 1993). The former test situation allows us to estimate thermal time constants (because ambient temperatures were constant), for comparison with data on other species. The latter test situation provides a closer approximation to field conditions.

Statistical analysis of radiotelemetry data is rendered difficult by the lack of independence between successive data points gathered from the same animal, thus precluding a simple “lumping” procedure (e.g., Leger and Didrichson 1994). To avoid this problem, most of our analyses use only a single mean value for each individual snake. In cases where we have pooled data from different individuals, we have used two-factor ANOVAs incorporating individual snake number as a factor, so that the relative magnitude of differences among versus within individuals (the prime determinant of

statistical artifacts arising from pooling: Leger and Didrichson 1994) can be evaluated.

Results

Environmental Temperatures

The most striking result from our thermal measurements is the wide range of body temperatures potentially available to the pythons (fig. 1). Physical models of snakes in full sunlight exceeded 40°C for most of the day, which indicates that snakes would have no difficulty in attaining very high tem-

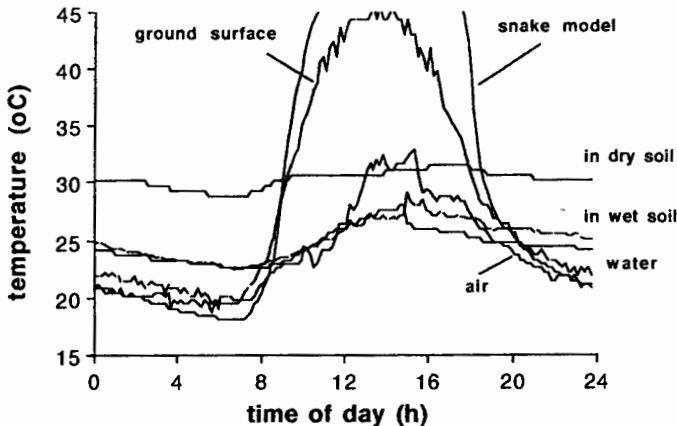


Fig. 1. Mean temperatures measured in water python models and in a variety of microhabitats in the Fogg Dam study area, late in the dry season (September 1994). "Snake model" indicates the internal temperature of a thin metal tube painted to match the reflectance of the snakes and placed in full sunlight; "water" indicates the temperature measured in shaded water, 20 cm deep, in Fogg Dam; "in wet soil" indicates the temperature taken 30 cm down a crack in black floodplain soil; "in dry soil" indicates the temperature taken 30 cm down a varanid burrow in a higher, dry area surrounding the floodplain; "air" indicates the temperature of shaded air, 10 cm above ground; "ground surface" indicates the temperature of bare soil in full sunlight. The graph shows only temperatures less than 45°C; models attained greater than 60°C on cloudless days. Data are based on mean values for four replicates of each habitat type, measured over 4 d. Day-to-day and site-to-site variation over this period was negligible (range < 2°C) for most habitats, so only mean values are shown.

peratures if they chose to do so. The habitats occupied by water pythons are very open, so most snakes would have to move less than 1 m to be fully exposed to solar irradiation. Similarly, diurnal temperatures close to 30°C were available on the ground surface, in shaded microhabitats, or in subterranean retreats for all of the year. The nocturnal fall in ambient temperatures was minor in the wet season and did not significantly reduce the range of potential body temperatures available to the pythons (fig. 2). However, nocturnal minima in the dry season were low enough that snakes might be unable to maintain body temperatures greater than 28°C during

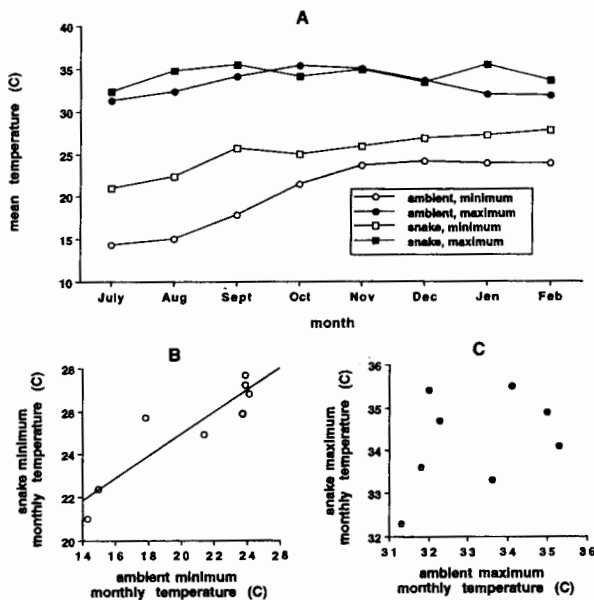


Fig. 2. Monthly variation in ambient temperatures and snake body temperatures. Climatic data are from Middle Point Village, based on 15 yr of data. Snake temperatures are from radio-tracked water pythons. Minimum and maximum temperatures are calculated as mean values of annual climatic data (so each figure is based on $n = 15$ yr) or means of data from each snake (one reading from each snake, so $n = 26$). The upper graph (A) shows that maximum temperatures of the air and the snakes vary little over the year, whereas minima for both are higher in the late dry season and the wet season (November–February). The lower graphs (B and C) plot ambient temperatures against snake temperatures, with one data point for each month. Minimum ambient temperatures are correlated with minimum snake body temperatures (B; $P < 0.02$), but maximum ambient temperatures and maximum snake body temperatures are not significantly correlated (C; $P > 0.40$).

some part of the night (fig. 2). Apart from these brief periods, there seems to be no reason why water pythons could not easily maintain body temperatures close to 30°C (the mean temperature selected in the laboratory thermal gradient) at all hours of day or night, throughout the year, with minimal overt thermoregulatory behavior. For example, a snake that simply remained within a red-soil burrow would experience this regime (fig. 1). Similarly, a snake that remained in shaded areas throughout the day, moved around on the soil surface for a few hours after sunset, and then retired to a subterranean habitat for the night (as is usually the pattern) would only occasionally experience body temperatures far from 30°C (fig. 1).

Thermoregulatory Behavior of Snakes

We rarely observed overt basking in water pythons, except for gravid females in August–September, a few weeks prior to oviposition (T. Madsen and R. Shine, unpublished manuscript). If basking was common, even in relatively subtle form (such as a sun-shade mosaic or deep within reed beds), we should have observed it because we have spent many hours in the area during the day, and we recorded the behaviors of our radio-tracked snakes whenever we located them. The radio-tracked pythons rarely moved during daylight hours, regardless of whether they were in full shade or partial sun.

Spatial Patterns of Activity

The patterns of habitat use in our telemetered pythons gave little suggestion of temperature-mediated microhabitat selection. The radio-tracked snakes used a wide variety of thermally distinctive habitats throughout the year, and we often recorded adjacent snakes (< 10 m apart) in very different habitats. For example, on the open floodplain, it was common to find some radio-tracked snakes deep within soil cracks while others remained on the soil surface under dry grass. The body temperatures of these snakes reflected their microhabitats (snakes in soil cracks were cooler: see fig. 1) but the ready availability of adjacent, cooler retreat sites apparently did not influence habitat selection by the animals in hotter places. The same was true of snakes sheltering within sedge clumps growing in the open water of the dam: they could have selected cooler temperatures simply by submerging but rarely did so.

Temporal Patterns of Activity

The times of activity similarly bore little obvious relationship to thermal conditions in the environment. Most python activity occurred shortly after

dusk, but snakes were occasionally seen active at all hours of the day and night. For example, we recorded several long forays by radio-tracked pythons during daylight hours—sometimes across the open floodplain where the snakes were exposed to the full force of solar irradiation for hours at a time.

Effect of Ambient Temperatures on Snake Activity Levels

Cool nights during the dry season (minimum < 20°C) depressed snake activity. Figure 3 shows that the numbers of pythons we captured during our regular surveys on the dam wall were reduced on cooler nights (minimum air temperature vs. number of pythons captured: July: $n = 31$ nights, $r = 0.52$, $P < 0.003$; August: $n = 24$ nights, $r = 0.44$, $P < 0.03$; September: $n = 22$ nights, $r = 0.59$, $P < 0.004$; October: $n = 18$ nights, $r = 0.65$, $P < 0.003$). However, nights were always warm enough for high activity levels during the wet season, and no correlation between air temperatures and snake activity was evident at this time of year (fig. 3; for all months with $n > 10$ nights, $r < 0.20$, $P > 0.30$).

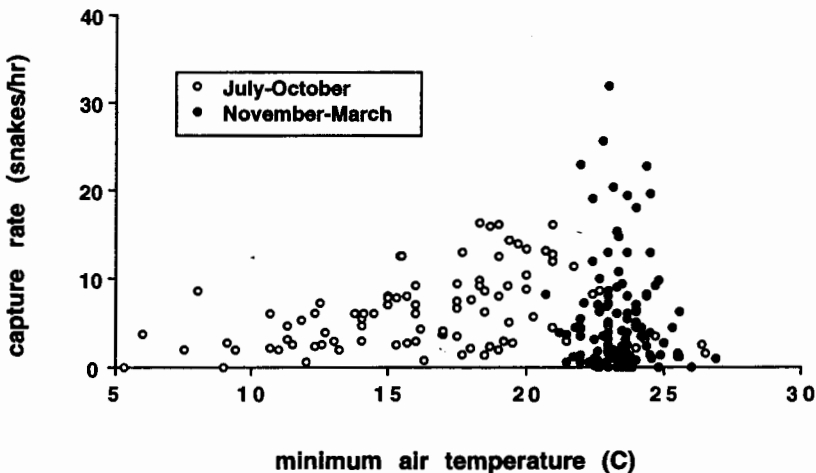


Fig. 3. Capture rates of water pythons (snakes per person per hour) after sunset on the wall of Fogg Dam, as a function of minimum air temperature that night. Each point represents data from one night's captures. Climatic data are from the weather station at Middle Point. Circles show dry-season data (July–October) and dots show wet-season data (November–March). Low minimum ambient temperatures apparently constrain snake activity in the cooler months but not in warmer times of year. See text for statistical analyses of these data.

Relationship between Ambient Temperature and Snake Body Temperature

Seasonal Effects. Maximum air temperatures varied only slightly throughout the year and were not significantly correlated with maximum snake temperatures measured in the same month ($n = 8$ mo, $r = 0.37$, $P = 0.37$; fig. 2). In contrast, monthly minima varied over a greater range, and air temperatures and snake body temperatures were significantly correlated in a comparison of monthly minimum values ($n = 8$ mo, $r = 0.91$, $P < 0.002$; fig. 2). Mean body temperatures of the radio-tracked water pythons also showed significant monthly variation. Two-factor ANOVAs, with month and snake identification number as the factors, were carried out separately for each sex (because we expected that reproductive activities might affect thermal characteristics more in females than in males). Differences among individual males were not significant ($F_{7,284} = 1.86$, $P = 0.08$), but there were strong differences among monthly means (effect of month: $F_{7,284} = 10.90$, $P < 0.0001$). For females, differences among individuals were significant ($F_{17,981} = 9.51$, $P < 0.001$) and similar in magnitude to differences among months ($F_{8,981} = 13.61$, $P < 0.0001$). Data pooling in these analyses should thus have little effect on the results (Leger and Didrichson 1994). Although these analyses document seasonal variation in body temperatures, the range of monthly means was low. For months with more than 50 readings, the range in monthly mean body temperatures was less than 2°C —from 28.8°C (August and November) to 30.4°C (January). The general pattern was for maximum temperatures of both the snakes and the air to remain high and relatively constant throughout the year, whereas minimum temperatures of both the snakes and the air showed a small but significant annual cycle (figs. 2 and 4). Thus, the seasonal changes in mean temperatures (above) result primarily from changes in the minima rather than the maxima.

Daily Effects. Because seasonal shifts in temperatures were minor (see *Seasonal Effects* above), we combined data from throughout the year to analyze changes in temperatures over the course of the day. If mean hourly values from each monitored snake are used, the data reveal considerable differences among individual snakes (fig. 5A). Nonetheless, a compilation of all data shows a clear pattern of overnight minima, with a gradual increase throughout the day until late afternoon and then a gradual decline in the evening (fig. 5B). A one-factor ANOVA, with hour as the factor, confirmed that these temporal shifts are highly significant ($F_{16,287} = 7.44$, $P < 0.0001$). As for the seasonal pattern (above), however, perhaps the most striking aspect of the data is not the existence of a diel

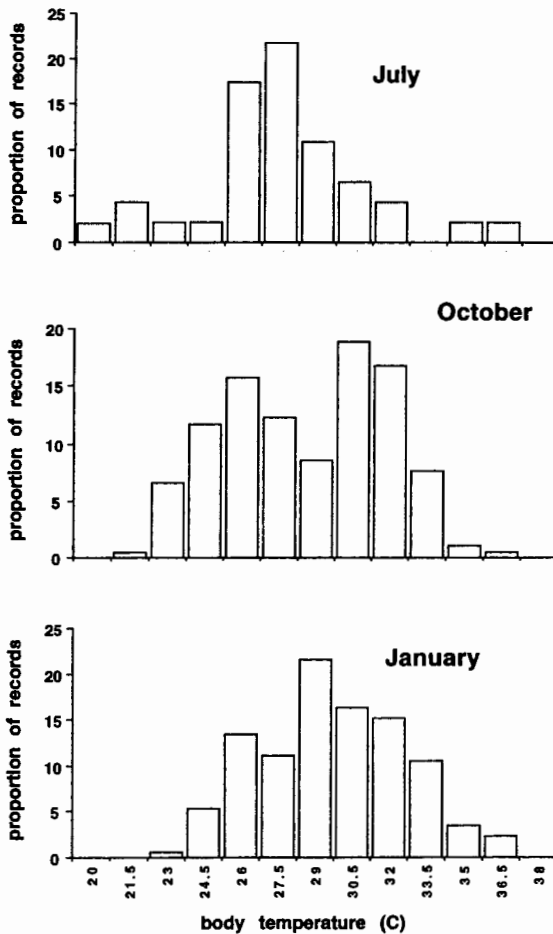


Fig. 4. Frequency distributions of body temperatures of radio-tracked water pythons during July (upper graph), October (middle graph), and January (lower graph). Maximum body temperatures remain constant through the year, but minima are lowest during the early to middle part of the dry season (July). The horizontal axis shows the midpoint of each temperature interval.

cycle but the relatively small range of body temperatures over which it occurs. Mean body temperatures stayed within the range of 28°–33°C throughout the day (fig. 5). The low variances associated with these hourly means are also notable, which suggests that there was little variation among individuals in the body temperatures that they exhibited. Variances were highest for the overnight minimum temperatures (fig. 5), because of the significant seasonal variation in this parameter (see *Seasonal Effects* above).

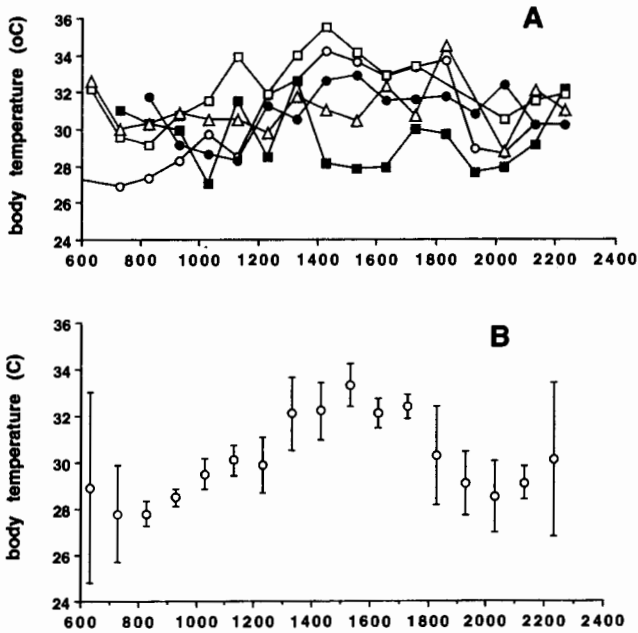


Fig. 5. Body temperatures of radio-tracked water pythons as a function of the time of day at which readings were taken. The upper graph (A) shows the mean hourly values for selected individual snakes, whereas the lower graph (B) shows overall hourly mean values ± 1 SE. Data are combined for all months of the year.

Individual Differences

A two-factor ANOVA (with month and snake identification number as the factors) revealed no significant differences among male snakes in mean monthly body temperatures, whereas female pythons showed significant interindividual differences (see above, under *Seasonal Effects*). Nonetheless, the range of mean temperatures among all of our telemetered snakes was very low (for cases where $n > 10$, means of 26.8°–32.9°C). We calculated an overall mean body temperature for each snake (the grand mean of all hourly means) and found that this value was significantly correlated with the body size of the snake: larger snakes had lower average temperatures ($n = 26$, $r = -0.48$, $P < 0.013$).

Selected Temperatures in the Laboratory

Captive pythons selected temperatures over a wide range (extremes from 22.9° to 38.6°C), but mean selected temperatures were similar among the

six snakes (means from 28.2° to 31.5°C). A one-factor ANOVA, with snake identity number as the factor, revealed no significant differences among snakes in their mean selected temperatures in the thermal gradient ($F_{5,29} = 1.17$, $P = 0.35$).

Cooling Rates in the Laboratory

Captive pythons cooled only slowly when exposed to either a rapid drop in air temperature (experiment 1) or a gradual cooling at sunset (experiment 2). In the first experiment, six pythons with body temperatures of 28°C, moved to an air temperature of 23°C, did not attain equilibrium within the 2 h of the experiment. Thermal time constants (t) of these snakes averaged 177.8 (SD = 120.6, range = 100.0–340.1, $n = 6$). In the second experiment, pythons with initial body temperatures of 29°C maintained temperatures greater than 25°C throughout the 10 h of the experiment, by which time soil temperatures were less than 23°C.

Discussion

In general, our data support the proposition that thermoregulation is a relatively unimportant component of the day-to-day lives of water pythons. The following attributes of the thermal biology of *Liasis fuscus* suggest that the ambient thermal environment of these pythons is so benign that the snakes do not need to expend much time, energy, or risk to modify their body temperature levels behaviorally: (i) scarcity of overt basking (except in gravid females), (ii) apparent lack of thermally mediated microhabitat selection, (iii) year-round activity (although activity levels may be depressed by low ambient temperatures for part of the year; fig. 3), (iv) similarity between temperatures selected in a thermal gradient and those exhibited in the field, (v) low degree of variation in body temperatures through time, either daily or seasonally, and (vi) low degree of variation in body temperatures of different individuals, despite considerable differences in the habitats they occupy. The trend for larger snakes to have lower average temperatures is consistent with the hypothesis that the primary thermoregulatory challenge is to lose heat, rather than to gain it, because the higher thermal inertia of large snakes may enable them to remain cooler in hot environments.

What characteristics of the environment and the study animal make it so easy for the pythons to maintain high and stable body temperatures without overt thermoregulatory activities? First, the climate is warm year-round, with

mean air and soil temperatures close to the body temperature levels selected by many reptilian species (approx. 30°C: Avery 1982), including water pythons in the laboratory. Second, a range of thermally distinctive microhabitats (e.g., water, grass clumps, soil cracks) is easily accessible within the study area (fig. 1). Third, the large body size of the snakes confers a high degree of thermal inertia ("gigantothermy"), enabling the animals to tolerate sub-optimal environmental conditions (especially, high solar irradiation during the day and cool soil surfaces at night) for long periods of time without rapid changes in body temperature. Water pythons are not atypical in this respect: the thermal time constants of *L. fuscus* are similar to those of other large pythons (Grigg, Drane, and Courtice 1979; Ayers 1992).

What aspects of the biology of *L. fuscus* are significantly affected by the snake's thermal relations? Clearly, basking behavior by gravid females falls into this category, as does the reduction in foraging activity of pythons on cool dry-season nights (fig. 3). We do not see any other obvious effects of thermal relations on our pythons. In particular, thermal constraints on the times and places of activity seem to be minor. Some shallow-water areas of the floodplain become excessively hot (> 40°C) during afternoons in the wet season, but we see little python activity at this time anyway. The nocturnal behavior of the pythons could be interpreted as a thermally forced trait, because the high temperatures reached by our physical models exposed to direct sunlight (fig. 1) suggest that pythons would not be able to remain in full sunshine for long periods. Three observations argue against this hypothesis: (i) Occasionally, pythons are seen active during the day, and gravid females often bask in full sun for hours. Their large body size reduces heating rates to the point that prolonged exposure to full irradiation is apparently not a problem. (ii) The pythons are nocturnal throughout the year, rather than reverting to diurnal activity in cooler months. (iii) Other Australian pythons are primarily nocturnal also, even in much cooler (southern Australian) habitats (Cogger 1992). Similarly, the other main feature of activity patterns in water pythons—a concentration of movements in the hours immediately after sunset—might be interpreted as thermally forced (because soil surface temperatures fall to low levels overnight; fig. 1), but this argument is weakened by the facts that (i) the pythons show the same pattern even during the wet season, when the nocturnal drop in soil temperatures is minimal; (ii) the pattern is shown by large as well as small pythons, despite their considerable differences in thermal time constants and, thus, ability to maintain high body temperatures in cool ambient conditions (Ayers 1992); and (iii) the pattern is more easily explained by foraging tactics (i.e., stop moving after a suitable ambush site is located) without the need to invoke a more subtle thermoregulatory argument.

The high and stable soil temperatures in our study area have another important effect on the biology of water pythons, in a way that reduces costs of thermoregulatory activities. Python eggs require high, relatively constant temperatures for successful incubation, and females of most python species provide these incubation conditions by wrapping themselves around the clutch and producing heat by muscular contractions (Grigg and Harlow 1984). This shivering thermogenesis imposes a large energy cost on reproducing females (Slip and Shine 1988). In contrast to all other pythons studied to date, many of the female water pythons in our study area desert their eggs within a few days of laying and can thereby obtain enough food in the succeeding months to be able to reproduce again the following year (T. Madsen and R. Shine, unpublished manuscript).

How do water pythons fit within the spectrum of thermoregulatory "strategies" usually recognized in reptiles? They are relatively stenothermic (fig. 5), but the scarcity of overt thermoregulatory behavior and the general correlation between ambient temperatures and snake temperatures (fig. 2) might lead one to classify them as "thermoconformers" (Huey and Slatkin 1976). Any such category, however, depends on a comparison between the thermal profiles of the organism and those available in the environment, and most attempts to apply these models implicitly assume that the primary aim of thermoregulatory behavior is for the animal to attain body temperatures that are higher than those experienced in the absence of thermoregulatory behavior (Hertz et al. 1993). The problem with applying these models to water pythons is that the environment of these snakes enables them to select from among a wide range of thermally distinctive microhabitats with little or no cost; and the temperatures selected by the pythons are lower than those that would be experienced in many microhabitats (fig. 1). Thus, the most significant problem for a water python—if, indeed, a problem exists at all—lies in how to keep cool, not in how to get warm. Under the cost-benefit model of thermal biology, thermoconformity is expected primarily in circumstances where thermoregulatory behavior would impose such high costs to the organism that precise thermoregulation is not worthwhile (Huey 1974; Huey and Slatkin 1976). For water pythons, however, the costs of thermoregulation are likely to be trivial in terms of time and energy (the entire range of thermal microclimates is readily available within a short distance) as well as risk (adult pythons have few if any natural predators). Rather than attempting to force water pythons into any particular category of thermoregulatory strategy, it seems more sensible to conclude that these issues simply have little relevance to the biology of our study animals. Previous studies on other reptiles in the Wet-Dry Tropics of Australia have also found relatively high and stable body temperatures, and little

overt thermoregulatory behavior, in diurnal terrestrial lizards as well as nocturnal aquatic snakes (Shine and Lambeck 1985, 1989; Christian and Bedford 1995). Thermoregulation undoubtedly occurs in all of these species, but it seems to be accomplished with little effort and little impact on other aspects of the animal's ecology.

In summary, our data show that tropical pythons can maintain high and relatively stable temperatures throughout the year, with little overt thermoregulatory behavior. Thermal constraints may influence the snakes in minor ways—for example, some microhabitats may be too hot for long-term residence during daylight hours, and air and ground temperatures at night may sometimes be low enough to reduce python activity. Nonetheless, the general picture that emerges from our data is that pythons can easily attain suitable body temperatures throughout the year, without the need for costly thermoregulatory behaviors and without imposing significant constraints on spatial or temporal patterns of activity. This conclusion stands in contrast to the prevailing paradigm that thermoregulatory “problems” are of central importance in reptilian biology. We believe that the popularity of this paradigm reflects the general allopatry of herpetologists (mostly temperate-zone organisms) and reptiles (mostly tropical organisms). If we are to place the thermoregulatory biology of reptiles in its proper perspective, we need more information on the thermal relations of reptiles in the places where most reptiles live—that is, the Tropics.

Acknowledgments

We thank B. Cattle, P. Harlow, R. Lambeck, and D. Slip for field assistance, C. Dollison and L. Huth for climatic data, and P. Doughty for comments on the manuscript. We are especially grateful to G. Bedford for gathering information on thermal biology of captive pythons on our behalf. The Australian Research Council and the National Geographic Society provided financial support for this study.

Literature Cited

- ALCALA, A. C., and W. C. BROWN. 1966. Thermal relations of two tropical lizards on Negros Island, Philippine Islands. *Copeia* 1966:593–594.
- AVERY, R. A. 1982. Field studies of body temperatures and thermoregulation. Pages 93–166 in C. GANS and F. H. POUGH, eds. *Biology of the Reptilia*. Vol. 12. Academic Press, New York.

- AYERS, D. Y. 1992. Effect of body size and posture on the thermal biology of diamond pythons, *Morelia spilota spilota* (Serpentes: Boidae). Honours thesis. University of Sydney.
- BRADSHAW, S. D. 1986. Ecophysiology of desert reptiles. Academic Press, Sydney.
- CHRISTIAN, K. A., and G. S. BEDFORD. 1995. Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii*, in northern Australia. *Ecology* 76: 124–132.
- COGGER, H. G. 1974. Thermal relations of the mallee dragon, *Amphibolurus fordii* (Lacertilia: Agamidae). *Aust. J. Zool.* 22:319–339.
- . 1992. Reptiles and amphibians of Australia. 4th ed. Reed, Sydney.
- COWLES, R. B., and C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Museum Nat. Hist.* 83:261–296.
- GRIGG, G. G., C. R. DRANE, and G. P. COURTICE. 1979. Time constants of heating and cooling in the eastern water dragon, *Physignathus leseuerii* and some generalisations about heating and cooling in reptiles. *J. Therm. Biol.* 4:95–103.
- GRIGG, G., and P. S. HARLOW. 1984. Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. *Copeia* 1984:959–965.
- HERTZ, P. E., R. B. HUEY, and R. D. STEVENSON. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142: 796–818.
- HUEY, R. B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001–1003.
- HUEY, R. B., and M. SLATKIN. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51:363–384.
- HUEY, R. B., and T. P. WEBSTER. 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *crisatellus* group on Puerto Rico. *Ecology* 57:985–994.
- INGER, R. F. 1959. Temperature responses and ecological relations of two Bornean lizards. *Ecology* 40:127–136.
- LEGER, D. W., and I. A. DIDRICHSON. 1994. An assessment of data pooling and some alternatives. *Anim. Behav.* 48:823–832.
- MADSEN, T., and R. SHINE. 1996. Seasonal migration of predators and prey: pythons and rats in tropical Australia. *Ecology* (in press).
- PETERSON, C. R., A. R. GIBSON, and M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pages 241–314 in R. A. SEIGEL and J. T. COLLINS, eds. *Snakes: ecology and behavior*. McGraw-Hill, New York.
- PIANKA, E. R., and J. J. SCHALL. 1981. Species densities of Australian vertebrates. Pages 1676–1694 in A. KEAST, ed. *Ecological biogeography of Australia*. Junk, The Hague.
- RUIBAL, R. 1961. Thermal relations of five species of tropical lizards. *Evolution* 15: 98–111.
- RUMMERY, C., R. SHINE, D. L. HOUSTON, and M. B. THOMPSON. 1995. Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). *Copeia* 1995: 818–827.
- SHINE, R. 1993. Ecological studies on Australian pythons. Pages 29–40 in M. URICHECK, ed. *Proceedings of the Fifteenth International Herpetological Symposium*, Seattle.

- SHINE, R., and R. LAMBECK. 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes, Acrochordidae). *Herpetologica* 41:351-361.
- . 1989. Ecology of frillneck lizards *Cblamydosaurus kingii* (Agamidae) in tropical Australia. *Aust. Wildl. Res.* 16:491-500.
- SLIP, D. J., and R. SHINE. 1988. Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *J. Zool. Lond.* 216:367-378.
- SPELLERBERG, I. F. 1982. *Biology of reptiles*. Blackie, London.
- VITT, L. J. 1987. Communities. Pages 335-365 in R. A. SEIGEL, J. T. COLLINS, and S. S. NOVAK, eds. *Snakes: ecology and evolutionary biology*. Macmillan, New York.