

Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*

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Summary

1. The interface between thermal biology and foraging mode has attracted little scientific attention, but may be crucially important to the biology of ectothermic predators. Slip & Shine (1988c) suggested that the ability of large heavy-bodied snakes to ambush nocturnally active mammals relied on the snakes' control of cooling rates through their thermal inertia (via body size and postural adjustments) and microhabitat selection.

2. We tested assumptions underlying this hypothesis, using Diamond Pythons (*Morelia s. spilota*) from southeastern New South Wales. Our laboratory studies confirmed that larger body sizes and coiled postures significantly retarded cooling rates, and that body temperature affected the snakes' ability to detect potential prey items.

3. The magnitude of these effects on cooling rates was great enough to extend the time period substantially over which an adult Diamond Python, lying in ambush in a suitable microhabitat, would be able to detect and capture nocturnally active prey. For example, the times taken for pythons to reach thermal equilibration under our experimental conditions (cooling from 33 to 12 °C) were < 1 h for hatchling pythons regardless of posture, 1 h for outstretched juveniles, 2 h for coiled juveniles and outstretched adults, and almost 8 h for coiled adults.

4. The high rates of cooling of juvenile pythons, even when they are tightly coiled, may force them to rely upon diurnally active prey rather than crepuscular or nocturnal species.

Key-words: Foraging mode, gigantothermy, Pythonidae, posture, thermoregulation

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Introduction

Although the interplay between foraging mode and thermoregulation has received less emphasis than the influence of foraging mode on life-history traits (e.g. Vitt & Congdon 1978; Huey & Pianka 1981), thermal biology may be an important determinant of foraging success for many animals (Avery, Bedford & Newcombe 1982). This may be especially true of terrestrial ectotherms such as most reptiles, that live in thermally heterogeneous environments and whose performance abilities are often very sensitive to temperature (e.g. Huey & Slatkin 1976). For example, the timing, place and duration of predatory bouts may be constrained by thermal factors if the predator must enter a thermally unfavourable environment to obtain its food, as is the case with Californian Gartersnakes capturing fishes in coldwater streams (Lind & Welsh

1994) and Giant Tortoises searching for edible vegetation in hot, unshaded areas of Aldabra Atoll (Swingland & Lessells 1979). The present paper examines another situation in which thermal biology may constrain foraging in important ways: ambush predation by snakes.

Large heavy-bodied snakes of diverse phylogenetic lineages have evolved a suite of morphological and behavioural characteristics that enable them to ambush prey successfully. Such 'sit-and-wait' predators include many species of the families Viperidae (e.g. Klauber 1956; Reinert, Cundall & Bushar 1984), boids (Pope 1975), Pythonidae (Slip & Shine 1988d), some Colubridae and a few Elapidae (Shine 1980). Typically, the ambushing snake lies partially coiled, in a microhabitat where it is well camouflaged, and strikes at prey from this concealed vantage point (Greene 1983; Reinert *et al.* 1984; Slip & Shine 1988a). Because ambush predators rely upon the approach of prey, they hence tend to feed on very active prey taxa (Huey & Pianka 1981). Specialization

on large prey may be favoured, because of the 'costs' (to subsequent prey-capture opportunities) of the predator revealing its presence (Pyke, Pulliam & Charnov 1977). Hence, ambush predation relies upon the availability of large prey that have high activity levels: characteristics are more often true of endotherms than of ectotherms (Pough 1980). Perhaps for this reason, many ambush-feeding snakes are specialists on mammalian prey (Shine 1980). Because the prolonged immobility needed for prey ambush is incompatible with 'shuttling' thermoregulation, ambush predators may be forced to accept non-optimal (and variable) body temperatures (Secor & Nagy 1994). In temperate-zone habitats where most medium-sized mammals are crepuscular or nocturnal (such as is true over much of Australia: Russell, Lee & Wilson 1989), ambient temperatures fall rapidly over the period of prey availability. If the snake's ability to detect and capture prey diminishes at lower temperatures, thermal factors may significantly constrain the success of ambush predators, or the geographical ranges (climatic conditions) over which such species occur.

The interplay between thermal biology and foraging mode may be very important for ectothermic species living under relatively cool climatic conditions. Thermal influences on foraging efficiency are particularly interesting in the case of ectotherms that are able to modify their rates of heat exchange with the environment. The degree of control that an organism can exert over its rate of heat transfer is likely to be maximized in animals with large body sizes (and the consequently high thermal inertia, combined with a greater ability to achieve hysteresis via physiological modifications: Grigg, Drane & Courtice 1979) and with behavioural control over their rate of heat transfer. The Diamond Python (*Morelia s. spilota*) of southeastern New South Wales is such a species. It is large (to 6 kg), lives in cooler conditions than does any other pythonid species (Cogger 1992) and, like all snakes, can significantly modify its surface area to volume ratio (and thus, rate of heat exchange) by postural modifications (Benedict 1932). This species uses tight coiling to reduce heat loss in a number of ecological contexts; for example, brooding females coil tightly around their eggs to maintain high and relatively constant incubation temperatures via shivering thermogenesis (Slip & Shine 1988b).

Slip & Shine (1988c) suggested that the ability of Diamond Pythons to ambush nocturnal mammals may be enhanced by the snake's ability to reduce its cooling rate through its large body size, and the adoption of a tightly coiled posture within a sheltered microhabitat. The consequent retardation in cooling rate may significantly extend the time period over which the python can detect and capture prey. Adult Diamond Pythons do indeed maintain high body temperatures late into the night, whereas conspecific hatchlings and juveniles do not (Slip & Shine 1988c;

Ayers 1992) but the mechanism by which adult snakes maintain high temperatures remains unclear. Hence, the relative thermal importance of body size and posture, vs other possible influences (e.g. microhabitat selection) remains speculative. Like all hypotheses, Slip & Shine's (1988c) idea rests upon a variety of assumptions. The most important are that cooling rates are reduced by large body size and a coiled posture, and that body temperature affects the snake's ability to perceive, capture and/or handle prey. To evaluate these ideas, we quantified cooling rates and performance capacities of Diamond Pythons over a range of body sizes, at various temperatures.

Materials and methods

COOLING RATES

Thirty-two pythons from central coastal NSW (within 100 km of Sydney) were divided into hatchlings (< 12 months of age, < 80 cm snout-vent length [SVL]), 15.4–25.2 g, juveniles (80–150 cm SVL, 65.9–879.9 g) and adults (> 150 cm SVL, 962.6–2323.6 g) and randomly assigned to one of two postural categories (outstretched or coiled) such that each of the six treatments contained an equal number of animals. The sequence of trials was determined with a random numbers table, and all snakes were more than 7 days post-absorptive when tested. Each snake was anaesthetized (intramuscular injection of 200 mg kg⁻¹ Ketamine HCl) to ensure that it maintained its treatment posture for the duration of the trial. Snake body temperature was recorded using a thermocouple inserted 2 cm into the cloaca.

Each snake in the 'outstretched' treatment was placed within a plastic open mesh tube (Handymesh, grid size 1 × 1 cm²) to maintain its posture. The tubes (diameter 8 cm, length 218 cm for juveniles and adults; diameter 2 cm, length 32 cm for hatchlings) rested on small styrofoam supports (≈ 2-cm high) inside a styrofoam box (for juvenile and adult snakes, total length 2.25 m; for hatchlings, 57 × 38 × 26 cm³) inside a growth cabinet maintained at 12 °C. In the 'coiled' treatment, each snake was arranged into a flat coil with its tail at the centre. Adjacent coils were held together by adhesive tape, attached ventrally. The snake was placed into a plastic mesh box (23 × 23 × 7 cm³ for adults and juveniles; 6 × 6 × 3 cm³ for hatchlings) on foam supports within a 57 × 38 × 26 cm³ styrofoam box.

Heating tape attached to the inner surface of the lid of each styrofoam box maintained temperatures within the closed boxes at > 35 °C. Thermocouples attached to a data-logger monitored internal temperatures of boxes and snakes once per minute. Prior to each trial the boxes (with snakes inside) were closed and heated until snake body temperatures stabilized at 33 °C, after which the heating tape was switched off and the box lids removed. Snake body temperatures

were monitored until they equilibrated at 12 °C. The thermal equilibration times and thermal time constants (time constants of the exponential rate of cooling, τ) were calculated for each snake. τ is defined as the time required for the body temperature to change by 63% of the differential between body temperature and ambient temperature (see Bakken & Gates 1975 for method of calculation).

To assess ontogenetic shifts in the surface area to volume ratio, mass was used as an index of volume (i.e. we assumed that the density of pythons did not vary significantly with size). The surface areas of outstretched pythons were calculated using the relationship $S = K.M^{0.67}$, where S = surface area and M = mass. The surface area of coiled snakes could not be accurately estimated. A value of 12.54 was used for the constant K , from the mean of five values (range 12.0–13.2) empirically determined for boid snakes by Benedict (1932).

TONGUE-FLICK CYCLE RATES

We chose tongue-flick cycle rate (TFCR) as a performance measure, based on the central role of chemoreception in prey detection by squamates (Peterson, Gibson & Dorcas 1993). Thirty-six pythons were grouped into size classes, as above, and randomly assigned to one of three temperature treatments (10, 20 or 30 °C) such that there were equal numbers of animals for each treatment. The temperature treatments were chosen to cover the range of body temperatures recorded for Diamond Pythons in the field (Slip & Shine 1988b,c; Ayers 1992). A random treatment sequence was used, and snakes had not been fed for at least 3 days prior to trialing. All trials were conducted within a temperature-controlled growth cabinet, under constant light levels. The test arena was a glass aquarium (90 × 34.5 × 39 cm³) divided into halves by fly-screen mesh. The left-hand end of the tank contained a shallow water-filled tray on which was placed a glass dish. A pulley system enabled a weighted, bottomless opaque plastic bottle to be raised or lowered over the glass dish. When the bottle was lowered, water in the tray (2-cm deep) formed a complete seal around its base, to prevent any rodent odours reaching the snake.

The trialing procedure was as follows. The cabinet was set to the required temperature and a snake placed in the right-hand end of the aquarium. After thermal equilibration (2 h for hatchlings; 4 h for juveniles; 10 h for adults), a stimulus object (a live mouse) was placed in the glass dish and the bottle lowered over it. Thirty minutes later, the plastic bottle was lifted to reveal the mouse, and the python was filmed with a video camera for 2 min. The video was replayed frame-by-frame to score the number of tongue-flick cycles per second. A tongue-flick cycle was defined as an extension of the tongue vertically upwards, and then downwards (i.e. as per the definition of Stevenson, Peterson & Tsuji 1985).

Results

COOLING RATES

We discarded results for eight pythons that did not maintain their treatment posture throughout the trial. Thus, data were available for four snakes for each of the six treatments. Variances in cooling rates were heterogeneous (Cochran's $C = 0.76$, $\nu = 3$, $k = 6$, $P < 0.05$), but log-transformation removed this heterogeneity ($C = 0.53$, $\nu = 3$, $k = 6$, $P > 0.05$). A two-factor ANOVA on the transformed data indicated that cooling rates were affected by body size ($F_{2,18} = 0.01$, $P = 0.0001$) and posture ($F_{1,18} = 18.76$, $P = 0.0001$), but the interaction between size and posture was not significant ($F_{2,18} = 0.95$, $P = 0.40$). Figure 1 illustrates the influence of both size and posture on cooling rates in terms of τ and thermal equilibration time. SNK tests indicated that cooling rates were significantly different among all size classes, and both postures, at the 5% level of significance. Ratios of surface area to mass calculated for 18 outstretched pythons were about fourfold lower for adults (mean = 1.06 ± 0.07 , range 0.96–1.17, $n = 6$) than for hatchlings (mean = 4.18 ± 0.31 , range 4.35–5.25, $n = 7$; rank test, $P < 0.001$).

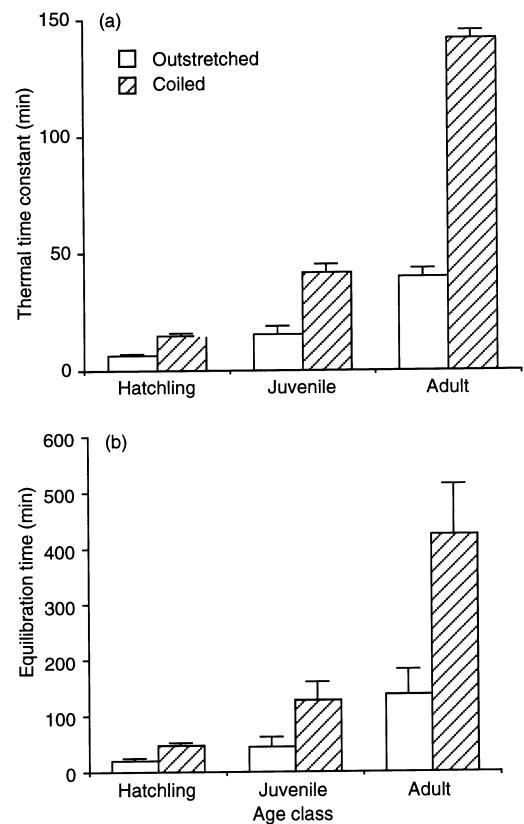


Fig. 1. Cooling rates of Diamond Pythons as a function of body size (age class) and posture: (a) the thermal time constant (τ); (b) the time to thermal equilibrium (from 33 to 12 °C) under our experimental conditions. Both graphs show mean \pm 1 SE. See text for explanation and statistical tests.

TONGUE-FLICK CYCLE RATE

Data for 27 snakes (three per treatment) were used in the analyses; videos of the other nine snakes were discarded because of poor film quality or lack of response by the snake. In each of the successful trials it was clear (from the snake's orientation, and the sudden increase in TFCR when the bottle was lifted) that tongue-flicking commenced in response to movement of either the bottle or the mouse. A two-factor ANOVA (with body size category and temperature as the factors, and tongue-flick cycle rate as the dependent variable) showed that TFCRs were not affected by body size ($F_{2,18} = 0.11$; $P = 0.90$) or the interaction between body size and temperature ($F_{4,18} = 0.22$, $P = 0.99$), but TFCR increased rapidly at higher temperatures ($F_{2,18} = 144.16$, $P = 0.0001$). The differences among all three temperatures were significant (SNK tests: $P < 0.05$: see Fig. 2).

Incidental observations made during these trials, and from field observations (Ayers 1992), indicate that the locomotor ability of Diamond Pythons is also reduced at lower temperatures. Snakes moved more slowly at 10 °C than when warmer, and were more alert at higher temperatures (responding to the experimental stimulus almost immediately at 20 and 30 °C, whereas some snakes at 10 °C did not respond at all). General coordination (balance and strike aim) was also superior at higher temperatures. Pythons at 30 °C struck rapidly and accurately, and recoiled quickly. In contrast, those at 10 °C struck slowly and inaccurately, often losing their balance and toppling forwards after striking.

Discussion

Slip & Shine (1988c,d) proposed (i) that the foraging success of adult Diamond Pythons depends on their ability to detect and capture fast-moving mammalian

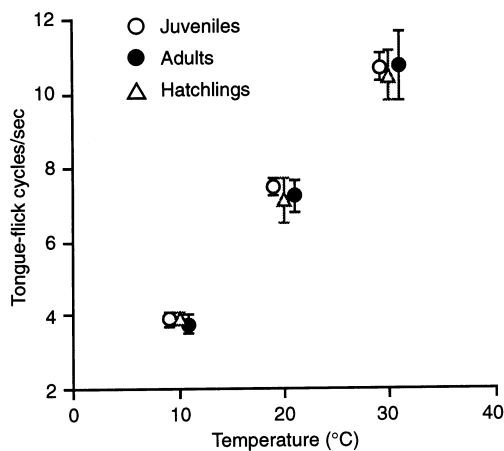


Fig. 2. Tongue-flick cycle rates of Diamond Pythons exposed to a potential prey item (a live mouse) as a function of body size (age class) and temperature. Means \pm 1 SE are shown, with symbols displaced slightly on the horizontal axis to avoid overlap. See text for explanation and statistical tests.

prey at low ambient temperatures, and (ii) that this ability in turn depends on the capacity of large pythons to retard cooling rates by virtue of their large body size, microhabitat selection, low frequency of movements and adoption of coiled postures. The results of our investigations strongly support some of the basic assumptions underlying this hypothesis, specifically the ideas that a large body size and adoption of a coiled posture reduce rates of heat loss and that higher body temperatures enhance the snakes' ability to detect and capture active prey items. We now look at these results in more detail, to evaluate the degree to which Slip & Shine's hypothesis is supported by our data.

INFLUENCES ON THE RATE OF COOLING

First, we consider a methodological issue involved with our experimental design. Because our study used anaesthetized animals, our results may underestimate the influence of physiological mechanisms (such as the redirection of blood flow: Benedict 1932; Grigg *et al.* 1979) on rates of heat exchange. However, the possible omission of such physiological mechanisms from our study should strengthen rather than weaken our conclusions. Any hysteresis induced by physiological mechanisms would act to retard cooling, and would do so to a greater extent in large than in small animals (Grigg *et al.* 1979). Thus, cooling rates would be even slower than we have measured (and hence likely to be more significant biologically) in unanaesthetized snakes, especially larger ones.

The lower cooling rates exhibited by larger pythons (Fig. 1) are consistent with previous studies on the effects of body size on rates of cooling in other reptiles (Peters 1983). The sixfold increase in equilibration time caused by a 100-fold increase in average body mass approximates the magnitude of effects observed in other taxa (Peters 1983). Rates of heat loss also depended on posture, with outstretched pythons cooling about three times faster than coiled pythons of the same body mass. This difference was greatest for the largest animals (Fig. 1), perhaps because of differences in the relative surface areas of outstretched and coiled snakes of different sizes.

INFLUENCE OF TEMPERATURE ON PREY DETECTION

The rate of tongue-flicking by Diamond Pythons was highly sensitive to body temperature, with TFCR increasing markedly between 10 and 30 °C (Fig. 2). TFCRs were thus highest at temperatures close to those recorded for active Diamond Pythons in the field (mean daily maximum body temperature = 29.2 °C: Slip & Shine 1988a,c). Our incidental observations suggest that other aspects of performance (e.g. perception, coordination and motor ability) are reduced in Diamond Pythons at low body temperatures, as is the case for many other reptile species

(Greenwald 1974; Greenwald & Kanter 1979; Avery *et al.* 1982). Thus, it seems likely that a python's ability to capture prey, as well as to detect it, may increase at higher body temperatures.

EXTRAPOLATION TO THE FIELD

Our data are based entirely on laboratory studies, and hence are difficult to extrapolate to field conditions where the thermal environment is vastly more complex than in our experiments. For example, rates of heat transfer can be affected by the snake's selection of microhabitats, its movements, wind speed and conductive as well as convective heat loss (e.g. Peterson *et al.* 1993). Some aspects of our cooling experiments in the laboratory are likely to overestimate rates of cooling in the field, because anaesthesia may have reduced the importance of physiologically controlled responses to cooling (e.g. redirection of blood flow away from the periphery), and the snakes could not be formed into coils as tight (and three-dimensional, with considerable heaping on one coil upon another) as has often been observed in the field. This tighter coiling would be expected to reduce surface area, and hence the rate of heat loss (Benedict 1932). On the other hand, our experimental system minimized the possibilities for conductive cooling, which may result in greater rates of heat transfer than convection (Grigg *et al.* 1979).

Despite these difficulties, field data on the thermal biology of Diamond Pythons (Slip & Shine 1988a,b,c; Ayers 1992) enable us to draw some tentative conclusions. We know that large Diamond Pythons typically form tight coils and remain virtually immobile in sheltered habitats, that nocturnal mammals are the most frequent prey, and that the snakes maintain relatively high body temperatures late into the night (Slip & Shine 1988c). Smaller conspecifics do not rest in tight coils in ambush postures: instead, they tend to be diurnally active, and spend much of their time outstretched or loosely coiled in thick vegetation or up trees (Ayers 1992). The smaller snakes feed mostly on diurnally active prey (lizards), heat rapidly in the morning, and cool rapidly in the evening (Slip & Shine 1988b; Ayers 1992). In tropical areas, by contrast, juvenile as well as adult pythons are active nocturnally rather than diurnally, and ambient temperatures may have little influence on activity levels of pythons of any size (Shine & Madsen 1996).

Is the ability of large Diamond Pythons to remain warm late into the evening due to body size, control over posture, an interaction between these two factors, or some entirely different phenomenon such as the selection of thermally favourable microhabitats? Our results suggest that the retardation of cooling rates achieved through large size and tight coiling is crucial to the ability of large snakes to remain warm at night. Field studies have not found any microhabitats that remained as warm as the large pythons; and, if such

habitats were available, we might expect the smaller pythons to use them as well (and hence remain warm). Postural changes may be particularly significant for large pythons. Whereas coiling enabled hatchlings to extend their equilibration time by < 30 min under our experimental conditions, adults could delay equilibration by > 4 h. Although hatchlings may gain little by remaining above ambient temperatures for an additional 30 min each day, maintenance of a higher body temperatures by adults for an additional 4 h may significantly enhance their ability to detect and capture nocturnally active prey.

Thus, our data suggest that large Diamond Pythons can indeed cool so slowly (because of their large size and ability to coil) that they are capable of efficiently detecting and capturing prey even late into the evening, when ambient temperatures have fallen to low levels. These results provide support for Slip & Shine's (1988c) hypothesis in this respect, although further data are needed before confident conclusions can be drawn about the relative importance of the various factors influencing nocturnal temperatures in these pythons. For example, it would be instructive to monitor body temperatures of coiled anaesthetized pythons placed in typical ambush positions in the field, to compare to available data on the thermal characteristics of free-ranging snakes. Although many snakes that are ambush predators live in tropical regions where overnight cooling is unlikely to have much biological significance, there may nonetheless be many taxa for which control of cooling rates has significant implications for foraging biology. At the very least, the prolonged immobility required by a camouflaged ambush predator may preclude shuttling between thermally 'optimal' habitats, and hence force it to be a thermoconformer (e.g. Secor & Nagy 1994; Rummery *et al.* 1995). The interplay between thermal ecology and foraging biology is likely to be important for taxa that forage in other ways as well. It is interesting to note that the thermal inertia provided by large body size has been identified as an important influence on foraging tactics of reptiles as diverse as Gartersnakes in coldwater streams of northern California (Lind & Welsh 1994), Giant Terrestrial Tortoises on Aldabra Atoll (Swingland & Lessells 1979) and pythons in eastern Australia (present study). Size-related ontogenetic shifts in foraging biology (involving prey size, prey type, foraging modes and foraging microhabitats) are widespread in reptiles (e.g. Taylor 1986; Shine 1986, 1991), and the possible role of size-mediated shifts in thermal biology in this phenomenon may have been underestimated. Hence, further studies on the ways in which thermal biology interacts with foraging mode would be of great value.

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