

Short notes

Temperature preferences of *Xenodon dorbignyi*: field and experimental observations

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We examined substrate temperature preferences of the South American hognose snake (*Xenodon dorbignyi*) in the field and in the laboratory. Individuals captured in the field were placed in a thermal gradient chamber, where they preferred temperatures averaging 32.8°C and avoided substrate temperatures below 10.5°C and above 37.5°C. The mean body temperatures of snakes exposed to the thermal gradient was 23.4°C, which was similar to field measurements. Gravid females had higher temperatures than males. In the experimental chamber, *X. dorbignyi* remained above ground even when exposed to extremely high or low temperatures. Our results corroborate the hypothesis that *X. dorbignyi* is a thermal generalist that uses a broad range of substrate temperatures, representing an adaptation to the large variation in daily temperatures in sand dunes with few shelters above ground.

Key words: snakes, substrate selection, thermoregulation

Thermoregulation is a central component of habitat use and activity patterns in ectothermic animals (Huey et al., 1989; Peterson et al., 1993), and probably the most important proximate factor influencing habitat selection by terrestrial squamates (Reinert, 1993). Knowledge of the mechanisms that affect both habitat selection and activity patterns have provided a framework for developing hypotheses and theories about evolution, community structure and maintenance of species diversity (Gibbons & Semlitsch, 1987; Reinert, 1993). Maintaining an appropriate operational body temperature enhances prey detection and capture (Shine et al., 2002), and is important for reproduction (Graves & Durvall, 1993; Lewelyn et al., 2005; Shine, 2006) as well as locomotor performance and physiological processes such as digestion (Toledo et al., 2003). The maintenance of body temperature within an optimal range requires active regulatory processes involving behavioural and/or physiological adjustments (Huey et al., 1989; Huey, 1991; Reinert, 1993). The understand-

ing of how reptiles regulate their body temperatures is fundamental to many ecological issues (Dunson & Travis, 1991; Peterson et al., 1993). Unfortunately, limited information is available concerning the thermal aspects of neotropical species compared with their temperate counterparts. A common assumption states that in the tropics, low fluctuations in temperature between seasons facilitate the maintenance of relatively stable body temperatures (Shine, 2006). However, considerable heterogeneities in climatic conditions in the neotropics suggest that studying species that occur over wide geographic areas would generate useful information regarding the thermal affinities of neotropical reptiles. Currently, very few studies provide such information (Rocha et al., 2009).

The South American hognose (*Xenodon dorbignyi*) is a small, semi-fossorial xenodontine snake (Cadle, 1984), formerly classified as *Lystrophis dorbignyi* (Zaher et al., 2009), with a wide geographic distribution including southern Brazil, Paraguay, Uruguay and Argentina (Lema, 1994). A large distribution may reflect a high degree of thermal plasticity, but field data on the ecology of *X. dorbignyi* are scarce (Oliveira et al., 2001; Maciel et al., 2003; Tozetti et al., 2009a). *Xenodon dorbignyi* is diurnal, exhibiting above-ground activity throughout the year (peaking from October to March, i.e. spring–summer; see Oliveira et al., 2001), with a diet predominantly composed of anurans and occasionally lizards (Oliveira et al., 2001). This species forages actively on the surface, but avoids above-ground activity during the hottest part of the day (unpublished observations), possibly due to high substrate temperatures. As the secretive behaviour of this snake makes field observations difficult, controlled experiments can help to determine preferred body temperatures (Hertz et al., 1993). In this study we examine whether *X. dorbignyi* shows thermal affinities, and whether it chooses substrates based on thermal cues. Sand dunes, the habitat upon which *X. dorbignyi* relies, are currently being lost at alarming rates, and ecological studies of species associated with this habitat will further our understanding of whether they will be able to survive in the future (Seeliger et al., 2000; Seeliger, 2003).

Fieldwork was carried out in an area of coastal sand dunes (sampling area was approximately 333 ha; 30°22'37"S; 50°17'38"W; at sea level) in the municipality of Balneário Pinhal on the northern coast of Rio Grande do Sul State, Brazil. The area is characterized by sparse vegetation, including shrubs and plants associated with temporary lagoon systems (Waechter, 1985). The climate is humid subtropical (Vieira & Rangel, 1998), with average annual temperatures of 20°C (15.4°C in winter and 24.8°C in summer) and a uniform annual precipitation averaging 1322.9 mm (Hasenack & Ferraro, 1989). Individual *X. dorbignyi* were found by visual searches between November and December 2007, a period that includes the breeding season (pers. obs.). Searches were carried out between 0700 and 1800, which includes the daily activity peak of this species (Oliveira et al., 2001). Captured individuals were measured (size and body mass) and marked

Table 1. Substrate and body temperatures (in °C) recorded for male and female *Xenodon dorbignyi* during above-ground activity in the field and in a thermal gradient in the laboratory.

	Thermal gradient chamber temperatures (°C)				Field temperatures (°C)			
	mean ± SD (range)				mean ± SD (range)			
	Males (n=15)	Non gravid females (n=8)	Gravid females (n=5)	All snakes (n=28)	Males (n=11)	Non gravid females (n=8)	Gravid females (n=2)	All snakes (n=21)
Used substrate temperature	23.1±7.6 (10.5–37.5) 57 samples	26.1±7.4 (11.0–34.5) 32 samples	23.4±5.9 (15.3–34.3) 19 samples	24.1±7.35 (10.5–37.5) 108 samples	22.6±4.5 (17.5–31.0) 11 samples	19.4±2.9 (14.5–24) 7 samples	26.3±0.4 (26.0–26.5) 2 samples	22.4±4.8 (14.5–33.5) 21 samples
Body temperature	21.5±5.8 (10.5–32.0) 56 samples	26.4±6.32 (10.5–39.0) 32 samples	24.1±4.1 (17.5–32.5) 19 samples	23.4±6.0 (10.5–39.0) 106 samples	24.1±5.2 (17.5–35.0) 10 samples	22.5±8.4 (5.0–30.0) 7 samples	27.5±0.7 (27–28.0) 2 samples	24.3±6.3 (5.0–35) 21 samples
Available substrate temperature	24.1±7.4 (7.0–41.5) 106 samples				24.3±5.0 (14.0–38.5) 21 samples			

using permanent tattoos on ventral scales (Di-Bernardo et al., 2007). Sex was determined by everting the hemipenis and/or cloacal probing. The belly of females was palpated to determine reproductive state (e.g. the presence of eggs or large follicles; Fitch, 1987).

At capture, each snake's surface body temperature was recorded with a non-contact infrared thermometer (Raytek model RAYMT4U – accuracy of ±2 °C) positioned 5 cm from the snake's body (Tozetti et al., 2009b). We also recorded substrate temperatures immediately beneath the snake using the same method, except for snakes that were found moving.

After capture, snakes were taken to the laboratory and kept unfed in plastic boxes (20 × 30 cm) for a four-day acclimation period. They were subjected to a 12h:12h L:D photoperiod (provided by a fluorescent light) at constant temperature of 25 °C and air humidity of 40%, before being transferred to the thermal gradient chamber. The chamber consisted of a rectangular box (150 × 75 × 60 cm) with glass walls, mounted on a sheet of galvanized steel (0.5 mm thick). An electric resistance heater was attached under one end of the sheet and a cooling coil at the other end, producing a gradient ranging from 7.0 to 41.5 °C. A layer of sand (5 cm) collected from the snake's capture site was provided as substrate.

Snakes were individually placed into the chamber and allowed to acclimatize for 12h. A virtual grid of 18 sectors (each one measuring 25 × 25 cm; identified by letters a to r) was created over the arena substrate to help record the position of the snake. Records were made over a period of 9 h through systematic observations at 0800, 1100, 1400 and 1700, corresponding to the species' activity peaks in the field (Oliveira et al., 2001). The following data were recorded: 1) snake position along the gradient (grid); 2) superficial snake body temperature (in °C) taken in the middle of the body; 3) substrate temperature (as close as possible to the snake); and 4) substrate temperature in the centre of each quadrant in the virtual grid. When animals used more than one quadrant, we measured the temperature of the quadrant nearest the snake's mid-body. Temperature measurements were obtained using the same non-contact infrared thermometer as in the

field. Each snake was exposed to the gradient only once, and released at the site of capture after the experiment. After each test, the sand was replaced to remove chemical cues left by previously tested animals. Each observation was considered a sample, totalling four samples for each snake. Measurements were obtained for superficial snake body temperature (*T_b*), used substrate temperature (*T_{us}*), available temperature (*T_{av}*, used in gradient chambers) and set-point temperature range (*T_{st}*, representing the central 68% of all *T_b*'s registered in the laboratory; see Hertz et al., 1993). The measurements of a set-point range (preferred body temperature) provide a starting point for understanding species' thermal affinities (Webb & Shine, 1998; Blouin-Demers & Weatherhead, 2001a,b).

Body and substrate temperature differences among males, non-gravid females and gravid females were compared using one-way analysis of variance (ANOVA) (Zar, 1999). A *t*-test was used to compare used and available substrate temperatures. Differences were considered significant at *P*<0.05 (Zar, 1999) in all tests.

Twenty-eight *Xenodon dorbignyi* individuals (15 males, average body size = 399.2 mm, range 138.0–494.0 mm; 13 females, average body size = 381 mm, range 265.0–481.0 mm, including five gravid females) were captured. Four males and three females were captured by local collectors and thus lacked field temperature information; temperatures from an additional female and three males that were moving during capture could also not be measured. The average *T_{us}* by snakes above ground was 22.4±4.8 °C (range 14.5–33.5 °C), with no significant differences between the field and experimental conditions (*t* = -1.07; *df*=48; *P*=0.29, Table 1). No significant difference was observed in average *T_{us}* among males (22.6±4.5 °C; range 17.5–31.0 °C), non-gravid females (19.4±2.9 °C; range 14.5–24.0 °C), and gravid females (26.3±0.4 °C; range 26.0–26.5 °C) in the field (*F*=0.92; *df*=20; *P*=0.42). Average *T_b* recorded in the field (24.3±6.3 °C; range 5.0–35 °C) was not significantly different from temperatures recorded under experimental conditions (*t*=0.73; *df*=48; *P*=0.47; *n*=29). There was no significant difference in the average *T_b* of males (24.1±5.2 °C; range 17.5–35.0 °C), non-gravid (22.5±8.4 °C; range 5.0–30.0 °C) and gravid

females in the field ($27.5 \pm 0.7^\circ\text{C}$; range $27.0\text{--}28.0^\circ\text{C}$; Table 1) ($F=0.27$; $df=2$; $P=0.76$).

In the thermal gradient chamber the mean temperature of all substrates used (*Tus*) was $24.1 \pm 7.35^\circ\text{C}$ (range $10.5\text{--}37.5^\circ\text{C}$, Table 1). Snakes most frequently used quadrants that had an average *Tus* of 32.8°C (range $29.0\text{--}36.5^\circ\text{C}$; $t=-17$; $df=215$; $P=0.002$; Fig. 1), avoiding substrate temperatures below 10.5°C and above 37.5°C (Fig. 1). Average *Tus* in the thermal gradient did not differ significantly among males ($23.1 \pm 7.6^\circ\text{C}$; range $10.5\text{--}37.5^\circ\text{C}$), non-gravid females ($26.1 \pm 7.4^\circ\text{C}$; range $11.0\text{--}34.5^\circ\text{C}$) and gravid females ($23.4 \pm 5.9^\circ\text{C}$; range $15.3\text{--}34.3^\circ\text{C}$) ($F=0.96$; $df=27$; $P=0.39$) (Table 1).

Average *Tb* of snakes was $23.4 \pm 6.0^\circ\text{C}$ (range $10.5\text{--}39.0^\circ\text{C}$; Table 1) with no significant differences among males, non-gravid females and gravid females ($F=2.86$; $df=27$; $P=0.076$). The *Tb* of males was lowest ($21.5 \pm 5.8^\circ\text{C}$; range $10.5\text{--}32.0^\circ\text{C}$), followed by gravid females ($24.1 \pm 4.1^\circ\text{C}$; range $17.5\text{--}32.5^\circ\text{C}$; Table 1). Non-gravid females had the highest average *Tb* ($26.4 \pm 6.32^\circ\text{C}$; range $10.5\text{--}39.0^\circ\text{C}$). *Tset* varied from 18 to 30°C (Fig. 1). However, due to the small number of gravid females, the power of the statistical tests used for comparisons between these and other snakes was below the desired threshold of 0.80 , and negative results should be interpreted with caution.

Our results indicate that *Xenodon dorbignyi* shows a wide range of body temperatures in both the field and under controlled laboratory conditions. These results do not confirm that active foragers are “thermal specialists” (Secor & Nagy, 1994), but reinforce that *X. dorbignyi* is a thermal generalist. We believe that the relatively wide range and the low minimum temperature recorded (10.5°C) reflects an adaptation to sand dune habitats characterized by constant changes in substrate temperatures

throughout the day, combined with a lack of surface shelter sites.

Gravid females have been shown to have higher preferred temperature values in association with increased metabolic demands (Graves & Durvall, 1993; Hailey & Coulson, 1996; Akani et al., 2002; Shine, 2006). Indirect evidence suggests that some tropical snakes are active thermoregulators when pregnant and when fed (Luiselli & Akani, 2002; Luiselli, 2006). In our case, temperatures recorded for gravid females were higher than those of other individuals, and the lower body temperatures for males could reflect low thermal selectivity during the mating season when they search for females.

Considering the characteristics of the study habitat and local winters with temperatures close to zero, it is possible that surface temperatures reach lethal levels during the day, causing the South American hognose snake to avoid above-ground activity. This is supported by low rates of capture during the hottest and coolest parts of the day (pers. obs.). However, in the experimental gradient *X. dorbignyi* remained above ground across the entire temperature range, suggesting thermal plasticity.

Lillywhite (1987) reviewed the literature on the preferred body temperature of snakes and summarized data for 55 species from five families. The mean preferred body temperature ranged from 28 to 34°C and was often close to 30°C . *Xenodon dorbignyi* has a relatively wide temperature range, overlapping with species from temperate climates (Blouin-Demers & Weatherhead, 2001b). In our study area, daily air temperatures in the cold season varied between 0°C and 30°C , making above-ground activity possible. Further studies are needed of the thermal regimes experienced by animals in retreat sites, which might differ from those experienced by surface-active animals (Huey et al., 1989).

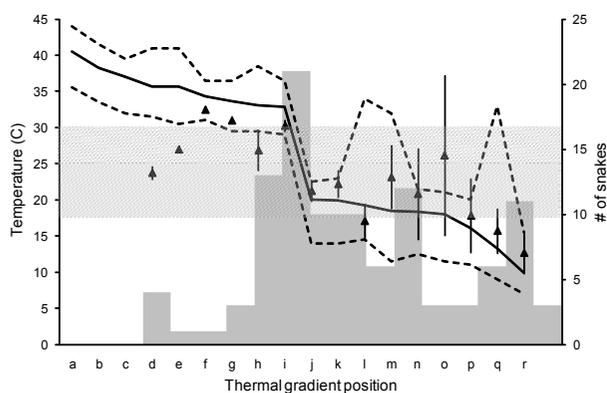


Fig. 1. Average substrate temperatures (in $^\circ\text{C}$) in each sector (a–r) of the thermal gradient chamber (see methods for details), snake body temperatures, and number of snakes recorded per sector. Hatched area = range of preferred body temperature (set-point temperature or *Tset*) that represents the central 68% of all body temperatures recorded in the laboratory (*Tset* = 18.0°C – 30.0°C). Bars = number of snakes. Solid line = average substrate temperature; Dashed line = maximum and minimum substrate temperatures; \blacktriangle = average body temperatures of snakes per quadrant; vertical lines = range of body temperatures of snakes.

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