

## Refuge Use in a Patagonian Nocturnal Lizard, *Homonota darwini*: The Role of Temperature

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**ABSTRACT.**—The thermal quality of diurnal refuges is important to the performance and survival of nocturnal reptiles. We studied refuge use on both slopes of an east–west-oriented hill by the thigmothermic gecko *Homonota darwini*, the southernmost-distributed nocturnal lizard in the world, in the vicinity of Bariloche, Río Negro, in the Patagonia of Argentina. Because of the harsh climatic conditions in Patagonia, suitable refuges are limited, and retreat-site use is important for these geckos. *Homonota darwini* used refuges significantly more frequently on the warmer western slope in our study site. Geckos on the western slope used those refuges with higher temperatures regardless of size and thickness of rocks that acted as retreats. We tested whether refuge temperature affected locomotor performance of these lizards. Performance experiments showed that maximum sprint speed was affected by the temperature of the refuges. Refuges at 22.5°C allowed lizards to achieve their fastest sprint performance. Unexpectedly, sprint performance of lizards that used refuges with temperatures >32°C was the lowest among all tested refuge temperatures (18°, 22.5°, 27.5°, and 33°C). Our data illustrate the importance of the thermal quality of refuges for reptiles living in extreme environments.

Nocturnal ectotherms depend on diurnal refuges for shelter and as sites for thermoregulation (Kerney and Predavec, 2000; Webb and Shine, 2000). Such retreats may be key to survival. For example, in Australia, removal of diurnal shelters caused a decline of nocturnal reptiles (Webb and Shine, 2000). Although physiological mechanisms can be important for some thermoregulating reptiles (Bartholomew, 1982; Autumn and DeNardo, 1995; Dzialowski and O'Connor, 2001), behavior seems to be the most common way that small reptiles cope with variable thermal environments (Hill, 1980; Hertz et al., 1993; Huey et al., 2003). To achieve body temperature, a direct or indirect source of heat must be available. Interestingly, many nocturnal lizards thermoregulate during daytime (Bustard, 1967; Autumn, 1999; Kearney, 2001). Consequently, nocturnal lizards often have higher body temperatures during the day than during the night (Gil et al., 1994; Autumn and DeNardo, 1995; Autumn, 1999; Cruz et al., 2004). The availability of thermally suitable microhabitats allows nocturnal reptiles to elevate performance and metabolic processes and, thus, is critical for lizards to maintain their physiology within their acceptable range (Adolph, 1990). Therefore, diurnal refuges may

constitute the only microhabitats where nocturnal lizards can achieve adequate body temperatures for such processes.

We studied the nocturnal lizard *Homonota darwini* from Patagonian steppe habitat of southern Argentina (Ceí, 1986; Abdala, 1997; Piantoni et al., 2006), where the availability of adequate thermal microhabitats is restricted. *Homonota darwini* are small Patagonian geckos (approximate mean adult snout–vent length 43 mm; mass 2–4 g) that use rocks as diurnal refuges (Cruz et al., 2004; Ibargüengoytia et al., 2007). If these geckos use daytime refugia for thermoregulation, as other gecko species do, then we predicted that they would use warmer over cooler available potential refuge locations. If so, this may be a benefit for digestion during daytime and may contribute to a better performance to acquire food during nighttime. Finally, we tested nighttime locomotor ability capabilities after establishing refuges with different thermal characteristics during daytime, as a proxy of the effect of temperature of refuges used during daytime.

### MATERIALS AND METHODS

Fieldwork was conducted at El Cóndor ranch in the vicinity of San Carlos de Bariloche, Río Negro province, Argentina (41°06'S, 71°08'W; 900 m). The habitat has rocky promontories surrounded by rubble of different sizes on

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sandy soils. The vegetation is typical Patagonian shrub steppe (Correa, 1998). Field measurements were recorded February through March 2004 and 2005, during which period geckos are not reproductively active (Ibargüengoytia and Casalins, 2007).

Our study is composed of two parts: first, determining refuge use and body temperatures in the field; and second, sprint performance experiments and thermal preferenda in the lab. Lizards used for the field and lab components were captured at two different rock promontories 150 m apart from each other.

At site 1, we collected refuge measurements, presence or absence of geckos under rocks, and field temperatures of lizards and refuges. We sampled both sides of a hill with slopes oriented east–west along this study area. The sampling effort was the same for both slopes, allowing us to compare the presence of geckos on the sunnier and, thus, warmer west face of the hill to the colder east face. We obtained field body temperatures ( $T_b$ ) of geckos encountered in their diurnal refuges (1,000–1,700), by introducing a type K ( $\pm 0.1^\circ\text{C}$ ) thermocouple (Extech 421502, Waltham, MA) into the cloacae within 20 sec of capture (Schwarzkopf and Shine, 1991). At the moment of capture, soil (inserting thermocouple tip 0.01 m into the substratum) and internal roof (contacting thermocouple tip to the rock surface) temperatures were recorded as well. We compared temperatures and measurements (length, width, and thickness) of actual used rocks by geckos and potential rocks (not used or random rock) during the first two of the four samplings (because the area studied was the same across the entire study, and we marked the used rocks). Immediately after collecting a lizard in a refuge, we recorded the data, and then we collected the same data from a nearby randomly selected rock that was chosen among five similar rocks at  $\approx 1\text{--}2$  m distance. The random choice was conducted by numbering the five nearby rocks, chosen from among those with similar characteristics of the used rock (we excluded those rocks that were too small or too deeply imbedded in ground) and then rolling a die to choose the random rock (Goldsbrough et al., 2005).

We also compared temperatures between potential refuges on each side of the hill (west and east). Outdoor/industrial HOBO (Pocasset, MA) data logger probes ( $\pm 0.1^\circ\text{C}$ ) were attached to the internal surface of six potential refuges (three on the west and three on the east slope of the hill). Thus, we acquired temperatures every hour for 10 days from 6 to 15 March 2005. From these data, we analyzed the daytime hours (0800–2000) when geckos were confirmed to be in their refuges.

At site 2, we collected eighty-four lizards, later transferred to the lab for experimental trials in cloth bags on the same day of capture. Only adults with intact tails were used for these purposes; sex was not determined because no evident sexual dimorphism is present in these lizards. To avoid using the same individuals in different experiments ( $T_{\text{sel}}$  trials, nonacclimation performance trials and acclimation trials), geckos were claw clipped when released at the original point of capture.

We measured preferred body temperature ( $T_{\text{sel}}$ ) of 12 adult individuals in two thermal gradients that consisted of six lanes each (lanes were  $1.20 \times 0.12$  m). Each track was separated from the next by a 0.4-m high opaque wall. For the hot side, we used a 1,000-W infrared stove with a potentiometer that was suspended 0.50 m above one end of the gradient. The cool side was maintained at approximately  $18^\circ\text{C}$ . The thermal gradient provided a temperature range from  $18\text{--}44^\circ\text{C}$ . Small flat rocks ( $\sim 0.07 \times 0.07 \times 0.02$  m) were placed every 0.15 m and separated from one another by 0.05 m along each track of the gradient (Cruz et al., 2009). We recorded geckos  $T_{\text{sel}}$  by inserting an ultra-fine thermocouple into the cloacae and grabbing the specimens from their shoulders to avoid heat transfer when handling; then lizards were released in the middle section of the track ( $\approx 0.60$  m from each extreme) to allow them to choose their retreats. Data were acquired every hour during photophase (0900–1900) for two consecutive days (18  $T_b$  data from each one of the 12 geckos). Thermal gradient temperatures, taken every 15 cm along the lanes, fitted significantly on a linear function ( $r^2 = 0.61$ ,  $P = 0.02$ ). Because these trials took place over a short period (two days), lizards were not fed during these experiments. Water was sprayed two times a day across the tracks. Set-point temperatures were estimated from  $T_{\text{sel}}$ . For each lizard the bounding interquartile range (middle 50% of observations) was used to represent the upper and lower limits of set point temperature range (Hertz et al., 1993).

Because one of our interests was to test whether locomotor performance was better for specimens collected on the west slope of the hill, we measured speed performance for four geckos captured on the eastern slope of the hill and for 22 individuals collected on the western slope. This was set after transporting the lizards immediately to the lab; trials were carried out on the same night of capture (i.e., no acclimation).

Because of few captures of lizards on the eastern slope, we were not able to compare how lizards perform in the field between sites; thus, we used another experiment to test the role of

temperature acclimation as a proxy of refuge choice, on locomotor performance. We created artificial refuges in glass terraria. Each refuge consisted of small flat andesitic stones (approximately  $10 \times 10$  cm). For each trial, we used 100-W infrared bulbs suspended at different elevations over the refuges to make possible each one of the following four temperatures: 18.5°, 22.5°, 27.5°, or 33°C. Temperature was maintained with a thermostat attached to the interior roof of the retreat. Lizards were acclimated in these refuges for three consecutive days prior to locomotor trials. Forty-six lizards collected on the west slope of the hill were used in these experiments: 11 in the 18.5°C refuge (group A), 12 in the 22.5°C refuge (group B), 12 in the 27.5°C refuge (group C), and 11 in the 33°C refuge (group D). Lizards often refused to feed in captivity. Therefore, we did not feed any of the lizards and conducted the races after three days to avoid weakness as a consequence of starvation. On the evening of the third day of acclimation, each lizard was sprinted three times in a  $2.0 \times 0.08$ -m horizontal racetrack. The sides of the racetrack were marked every 0.01 m to facilitate recording sprint rates and total distances. Lizards were placed on one end of the racetrack and prompted to run with a light tap on the base of their tails. Races were conducted at night to coincide with the natural activity period of these geckos (from 2200–0030 h). Lizard  $T_b$  during trials ranged from 22.1–26.1°C ( $\pm 2^\circ\text{C}$  of maximal speed performance of 24°C; Ibargüengoytia et al., 2007). Lizard sprints were filmed with a digital camera (Panasonic SV200). Each time the gecko stopped along the track, we recorded the distance run. Films were digitally captured with Windows Media Player V 11.0 (Microsoft, Redmond, WA). To calculate sprint speed, a chronometer window was inserted using the program Premier-pro (Adobe systems, San Jose, CA).

We considered the maximum speed as the fastest sprint recorded from the three trials. Maximum distance was the longest sprint distance made by a gecko across the three trials. We used the fastest run or longest distance run as an estimate of maximal sprint capacity (Bonine and Garland, 1999; Vanhooydonck and Van Damme, 2001). Four lizards showed evidence of submaximal performance (one at the 18.5°C acclimation group and three from the 33°C group), and, therefore, were not included in analyses (Losos et al., 2002).

We tested for normality and homogeneity of variance prior to using data in ANOVA or *t*-tests. When these assumptions were not met, we used Kruskal-Wallis or Mann-Whitney non-parametric tests. Means are given  $\pm 1$  SD.

## RESULTS

We searched for geckos on both slopes of the hill; sampling effort measured in person hours was similar for both slopes of the hill (approximately 24 h/person). The distribution of rocks in the field was similar on both slopes, too. Thus, the distribution of potential refuges apparently did not affect our observations.

*Homonota darwini* were more abundant on the west slope of the hill than on the east slope at site 1. We collected significantly more geckos on the west side (87) than on the east side of the hill (4), after the same effort on each side ( $X^2 = 70.74$ ;  $df = 3$ ;  $P < 0.001$ , pooled data from four sampling events). Both sides had andesitic igneous rocks. No geckos were found in refuges where ant colonies were present ( $N = 12$ , six on each slope of the hill).

We observed a positive relationship between the difference in temperatures of the exposed and underneath surfaces of the rocks and rock thickness ( $r = 0.38$ ,  $P = 0.006$ ,  $N = 54$ ), indicating that thicker rocks are poorer at transferring heat. On the west slope of the hill, mean temperature of refuges actually used by geckos was higher than the mean temperature of potential refuges (not used) by geckos from 0900–1730 h ( $21.4 \pm 8.3^\circ\text{C}$  and  $18.9 \pm 9.4^\circ\text{C}$ , respectively; Mann-Whitney  $U = 7,022$ ;  $P = 0.047$ ;  $N = 160$ ). Mean temperature of potential refuges on the west side of the hill, from 0730–2000 h, were significantly higher than those on the east side ( $15.7 \pm 0.75^\circ\text{C}$  and  $12.8 \pm 6.9^\circ\text{C}$ , respectively; Mann-Whitney rank test  $U = 13,385.5$ ;  $P = 0.001$ ,  $N = 366$ ). Differences between west and east sides were more pronounced during evening hours (Fig. 1).

The mean thickness of rocks actually used as refuges was 10.3 cm ( $\pm 5.1$ ,  $N = 46$ ), the mean longest diameter was 38.3 cm ( $\pm 11.8$ ,  $N = 46$ ), and the mean shortest diameter was 21.9 cm ( $\pm 8.1$ ,  $N = 46$ ). In the case of unused rocks (potential refuges), mean thickness was 10.3 cm ( $\pm 3.8$ ,  $N = 46$ ), mean rock major diameter 34.2 cm ( $\pm 9.3$ ,  $N = 46$ ), and finally rock minor diameter 20.7 cm ( $\pm 8.2$ ,  $N = 46$ ). Thus, unused (potential) refuges were not significantly different in size or thickness from actually used refuges (Mann-Whitney rank test  $P > 0.13$  in all cases).

Mean diurnal body temperature ( $T_b$ ) of geckos in the field was  $21.5^\circ\text{C}$  (range 8.6–40.2 S.D. = 7.84,  $N = 91$ ) and increased from morning to evening on the study site ( $r^2 = 0.73$ ;  $P < 0.001$ ;  $N = 91$ ). Gecko body temperature also showed a positive relationship with refuge temperature (multiple regression  $F_{2,90} = 423.6$ ,  $P < 0.001$ ). Both internal roof surface and substrate temperatures were good predictors of

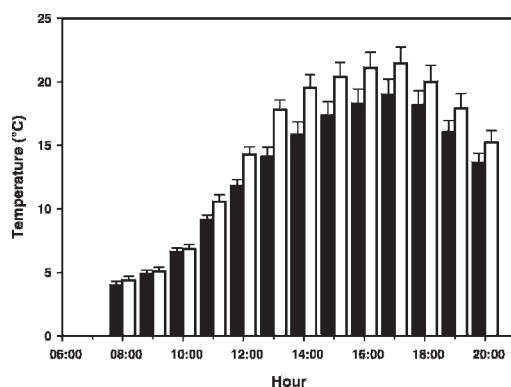


FIG. 1. Hourly variation in refuge mean temperatures ( $\pm$ SD,  $N = 366$ ) from western (white bars) and eastern (black bars) slope of the hill in the study site.

gecko  $T_b$  (multiple regression;  $r^2 = 0.91$  and  $0.84$ , respectively;  $N = 91$  and  $P < 0.001$  for both).

Preferred mean body temperature obtained during the photophase in the thermal gradient was  $27.4^\circ\text{C}$  (range  $21.6$ – $40.5^\circ\text{C}$ ;  $SD = 3.7$ ,  $N = 12$ ). At our study site, 54% of  $T_b$ s obtained in the field fell below and 16% above the thermal interquartile range ( $25$ – $75\%$ ,  $23.5 \pm 1.1^\circ\text{C}$ ;  $29.5 \pm 3.8^\circ\text{C}$ , respectively) for  $T_{sel}$  obtained in the lab. Only 23% of field  $T_b$ s fell between upper and lower limits of the set point.

For the trials of lizards acclimated to refuges under controlled temperatures, we detected significant differences among acclimation groups in maximum speed (ANOVA:  $F_{3,39} = 3.11$ ,  $P = 0.038$ ). Lizards in the acclimated at  $22.5^\circ\text{C}$  running at  $0.26$  m/sec were the fastest; groups A and D were the slowest (Fig. 2). It is interesting that sprint performance peaked with intermediate refuge temperatures. No significant differences were observed in the maximum distance run between acclimation groups (Kruskal-Wallis  $H = 3.04$ ,  $df = 3$ ,  $P = 0.386$ ). Neither maximum sprint speed ( $P = 0.897$ ,  $N = 40$ ) nor the distance sprinted ( $P = 0.971$ ,  $N = 40$ ) were correlated with lizard body temperature at the moment of running, probably because of the narrow range of  $T_b$ s used in the trials ( $22.4$ – $26.1^\circ\text{C}$ ).

## DISCUSSION

Refuge temperature is an important aspect for ectotherms, also (Webb and Shine, 2000; Converse and Savidge, 2003; Goldsbrough et al., 2005). For example, spiders from eastern Australia grow faster in warmer refuges (Goldsbrough et al., 2005). *Homonota darwini* used diurnal retreats almost exclusively on the warmer west slope of the hill (95.6%) compared

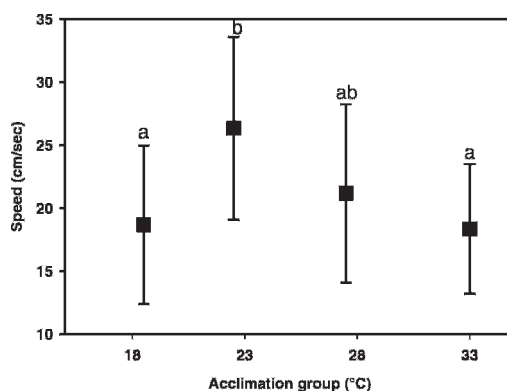


FIG. 2. Mean values ( $\pm$ SD) for maximum speed per acclimation group (group 18  $N = 11$ ; group 23 = 12; group 27 = 12; group 33 = 11). Letters denote groups identified by Tukey post hoc test ( $\alpha 0.05$ ).

to the cooler eastern slope at our study site and used the warmer refuges among the available. Thus, it may be possible that *H. darwini* uses these refuges to thermoregulate during photophase as has been observed for other geckos (Kearney and Predavec, 2000; Kearney, 2001).

The positive relationship between  $T_b$  and refuge temperature suggests that *H. darwini* is thigmothermic as are other Neotropical geckos (Marquet et al., 1990; Aun and Martori, 1994; Colli et al., 2003). However, body temperature during diurnal inactivity within refuges of *H. darwini* is lower than other *Homonota* species, such as *Homonota fasciata* ( $27.15^\circ\text{C}$ ; Aun and Martori, 1994) and *Homonota underwoodi* ( $23.9^\circ\text{C}$ ; Werner et al., 1996). These latter studies come from warmer localities in northern Argentina, but even the same species may show differences at different periods: *H. darwini*  $T_b$  in our study was nearly  $2^\circ\text{C}$  lower than those obtained by Ibarquengoytia et al. (2007), who included data for a greater number of years (more important, they also included  $T_b$  data from warmer months, November and December). This may explain the difference between these studies.

In general terms, nocturnal lizards show a lower  $T_b$  than diurnal lizards when active (Vitt, 1986; Autumn, 1999). Nevertheless, the lower  $T_b$  of geckos must be adequate for capturing prey and avoiding predators, which may be possible because of the low cost of locomotion associated with low temperatures (Autumn et al., 1994). This seems to be true for nocturnal lizards other than geckos as well (Hare et al., 2007). *Homonota darwini* occurs in the harsh Patagonian climate, which may influence the observed low  $T_b$  related to lowest set point for  $T_{sel}$  (more than 50% of the  $T_b$  data fell below it). This was observed in other nocturnal geckos (Angilletta and Werner, 1998). Indeed, Patagonian lizards,



in general, have lower  $T_b$ s than species of the same genus from other localities (Ibargüengoytia, 2005).

The importance of diurnal refuge temperature may stem from the necessity of reaching high enough  $T_b$  to complete digestive and physiological processes related to the previous night's activity (Kearney and Predavec, 2000). Besides, temperature of diurnal refuge may affect growth and food intake in Eublepharid nocturnal geckos (Autumn and DeNardo, 1995). Autumn et al. (1999) suggested that nocturnal lizards may have evolved an alternative physiology, where performance and physical activity are not exclusively related to  $T_b$  at the moment of nocturnal activity. Our performance experiments under controlled temperature of refuges showed that acclimation temperatures affected maximum sprint speed. However, while geckos acclimated to the lowest temperature were expected to have the lowest performance values, we found that those acclimated at the highest temperature showed a performance significantly lower than for lizards acclimated at 23°C. Refuge temperatures above 32°C were negatively correlated with performance. Refuges with high temperatures may cause overheating (Arad, 1995; Pough et al., 1998), which may explain the low performance found in trials above 32°C in our study. For example, the minimum panting temperature for this species was 35.9°C (Aguilar, 2006). Geckos performed best when they were acclimated at 22.5°C, similar to those temperatures of the refuge selected by geckos at our study site.

Vitt (1986) suggested that geckos do not reach high latitudes because of thermal limitations linked to their nocturnal activity. Although the diversity of geckos at high latitudes is low, *H. darwini* is very abundant along the Patagonian steppe (Daciuk and Miranda, 1980; Cruz, 1994), suggesting it is well adapted to these conditions or has few other nocturnal lizard species. Our results suggest the importance of thermally "good" refuges as they may allow animals to fulfill their physiological requirements during the day, such as digestion, and may help them achieve higher sprint speeds at night.

**Acknowledgments.**—We thank D. Añon Suarez, R. Espinoza, A. Herrel, T. Hibbits, N. Ibargüengoytia, M. Perotti, C. Ubeda, and two anonymous reviewers for their comments on early versions of the manuscript. I. Cerda and L. Silberberg helped with the lab experiments, M. C. Leonczyk and A. Aguilar helped in the field. Estancia El Cóndor allowed us to work on their property. Grants from CONICET (PIP 6287 and 2467) to FBC partially supported this study.

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Accepted: 6 October 2009.