VARIATION IN BODY TEMPERATURE AND THERMOREGULATORY BEHAVIOR BETWEEN TWO POPULATIONS OF THE LESSER EARLESS LIZARD, *HOLBROOKIA MACULATA*

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Abstract. Body temperatures and thermoregulatory behavior of field-active *Holbrookia maculata* were evaluated for two sites at approximately equal elevation (approximately1200 m) in southern New Mexico: 1) a population at White Sands National Monument, and 2) a population at the Jornada Long-term Ecological Research site. *H. maculata* at WS had significantly lower body temperatures (mean = 36.3°C) than those measured at the Jornada Long-term Ecological Research site (mean = 39.5°C). The slope of a regression of body temperature on air temperature was significantly different between populations (White Sands National Monument; 0.65, the Jornada Long-term Ecological Research site; 0.36). The microhabitats in which individuals were first observed correlated with body temperatures at White Sands National Monument, but not at the Jornada Long-term Ecological Research site. These data suggest that environmental temperature differences between sites influenced body temperatures and thermoregulation in behavior *H. maculata*.

INTRODUCTION

Since the seminal work of Cowles and Bogert (1944) a large body of reptilian research has been devoted toward understanding how lizards interact with their thermal environments. The contention that all species maintain a narrow range of body temperatures through physiological (Heath 1964) and behavioral (Cowles and Bogert 1944) adjustments has been modified by research showing that this range can be broad when species are examined across seasons and populations (Huey et al. 1977; Grant and Dunham 1990; Smith and Ballinger 1994; Van Damme et al. 1989, 1990). For example, Bashey and Dunham (1997) have recently shown that microhabitat use and activity patterns differed between high elevation and low elevation populations of *Cophosaurus texanus*. These studies suggest that the thermal environment has the potential to influence the behavior and physiology of lizards.

The lesser earless lizard, *Holbrookia maculata*, is a medium-sized, semi-arenicolous phrynosomatid found across much of the Great Plains of the United States, including southern New Mexico (Degenhardt et al. 1996).   It is associated with sandy blowouts (disturbed sites with sparse vegetation; Ballinger and Jones 1985). Within the range of this species is a population that inhabits gypsum ($CaSO_4$-nH_2O) sand dunes at White Sands National Monument (WS), New Mexico (Ruthven 1907). The thermal environment at WS is generally "cooler" than non-gypsum environs outside of the dunes (Dixon 1967). This difference arises because of the physical properties of gypsum (V. Gutschick, pers. comm.), which include high reflectivity (Wheeler et al. 1994), low thermal capacity for heat exchange (Weast 1986), and evaporation from shallow subterranean water (Houk and Collier 1994). Sufficiently low environmental temperatures could influence body temperatures of this lizard and, therefore, its ability to thermoregulate, forage, grow, mate, and escape predation.

Few studies have examined thermoregulation in *Holbrookia maculata*.   Sena (1978) reported a mean body temperature of 34.3 °C (N = 174) for a population in eastern New Mexico.   Brattstrom (1965) collected body temperatures from three individuals (locations not reported) and calculated a mean body temperature of 37.8 °C. Individuals housed within semi-natural enclosures had a mean preferred body temperature of 35.7 °C (N = 41) (Clarke 1965).   Dixon (1967) recorded body temperatures of *H. maculata* at WS that ranged from 35 °C to 39 °C (no mean was published). He observed that they became inactive when soil temperatures reached 40 °C during hot summer afternoons. Hager (1998) found that WS lizards were active above the soil surface at soil temperatures ranging between 12.2 ° and 45.8 °C and documented a unimodal pattern of activity from June to August. These data demonstrate that body temperatures and some thermal relationships vary across the range of *H. maculata*.

My goal was to determine the influence of the thermal environment on *H. maculata*. I measured environmental temperatures and body temperatures, and evalutated microhabitat use of lizards in thermally divergent habitats at WS and adjacent non-gypsiferous areas in New Mexico.

METHODS

All data were collected from two sites at similar elevations (approximately 1200 m) in southern New Mexico: 1) White Sands National Monument (WS) (32°47'N; 106°11'W), and 2) Jornada Long-term Ecological Research site (JRN) (32°37'N; 106°44'W). The sites are separated by 60 km and by the San Andres mountain range. I conducted fieldwork approximately two days weekly during April-August of 1995 to 1997. Consistent afternoon and evening thunderstorms restricted work to mostly the morning and early

afternoon hours (i.e., from 0700 to 1300 h MDT). At WS, all work was conducted in the active dunes where the substratum is composed almost exclusively of white gypsum (hydrous calcium sulfate).   Plant cover in this area is sparse, although interdune depressions are dotted with various grasses (*Oryzopsis* sp., *Sporobolus* sp.), sand verbena (*Phyla incisa*), primrose (*Anogra gypsophila*), mormon tea (*Ephedra torrreyana*), yucca (*Yucca elata*), and rabbitbush (*Chrysothamnus nauseosus*). At JRN, all work was conducted in disturbed (by cattle grazing) grassland habitats composed of grasses (*Bouteloua* sp.), yucca (*Yucca elata*), mormon tea (*Ephedra torrreyana*), and various cacti (*Opuntia* spp.).

Body temperatures (T_b) were taken from active lizards that were chased less than 10 m. I assumed that all individuals were sampled once because only previously unsampled areas were visited during each survey. Lizards were noosed and T_b's taken within 10 sec from individuals handled only by the rear limbs. Measurements to the nearest 0.2°C were made using a quick reading cloacal thermometer. Air temperatures (T_a) were measured at 1 cm above the soil surface with shaded bulb. Soil temperatures (T_s) were recorded from just below the soil surface, with only approximately one layer of soil particles covering the top of the bulb. Each of these was taken at the location where a lizard was first observed.

I also recorded snout-vent length (SVL), snout-tail length (STL), and body mass (BM) for each lizard.   I calculated body condition (a representation of surface area/volume) for each population according to $BM^{1/3}/SVL$. Lengths were measured (nearest millimeter with a ruler) and body mass (BM; nearest 0.2 grams) was recorded from a 10 gram Pesola spring scale.

I used six categories to note the microhabitat where each lizard was first sighted: open (in full sun), open-hummock (in full sun on a hummock topped with short forbs or perennials), edge (< 50% estimated shade), under (> 50% estimated shade), perched (on top of low-lying forb), and arboreal (within canopy of shrub).

All statistical tests were performed on JMP software for Macintosh (SAS Institute 1995) with alpha = 0.05. For each variable the Shapiro-Wilk test (Zar 1984) was used to evaluate normality.   Where the assumptions of parametric tests were violated, nonparametric tests were used. I evaluated differences in SVL and BM between populations with Kruskal-Wallis tests. Analysis of variance was used to analyze intrapopulational differences in T_a, T_s, T_b, and body condition. For each population, I used analysis of variance to test 1) the correlation between T_b and T_a; 2) the correlation of SVL and BM with T_b; 3) the correlation of month on T_b, T_a, and T_s; 4) the correlation between microhabitat and T_b; and 5) correlation between time of day, T_a and T_s and microhabitat. I employed a t-test to compare the slopes of the regression of T_b on T_a in each population.

RESULTS

Holbrookia maculata at WS had significantly lower T_b's than those at JRN (Table 1). Air temperatures were also significantly lower at WS than at JRN, as were T_s's (Table 1). Body temperature was positively correlated with T_a at both WS and JRN, although T_b followed T_a more closely at WS than at JRN (WS: df = 188, r^2 = 0.59, P < 0.0001; JRN: df = 68, r^2 = 0.48, P < 0.0001); the slopes of the regressions differed significantly (t = 6.36, P = 0.001) (Figure 1).

Body temperatures of lizards at WS and JRN were not related with SVL (WS: P = 0.84, JRN: P = 0.71) or BM (WS: P = 0.10, JRN; P = 0.91). At WS, T_b (P = 0.13), T_a (P = 0.45), and T_s (P = 0.98) did not vary among months. Conversely, T_b ($F_{3, 85}$ = 4.79, P = 0.004), T_a ($F_{3, 67}$ = 6.70, P = 0.0005) and T_s ($F_{3, 72}$ = 4.71, P = 0.0005) were influenced by month at JRN.

Microhabitat was correlated with T_b at WS ($F_{5, 161}$ = 6.70, P < 0.0001), but not at JRN (P > 0.33) (Figure 2). Microhabitat selection varied with time of day in both populations (WS: $F_{5, 130}$ = 42.4, P = 0.003; JRN: $F_{5, 51}$ = 37.9, P = 0.009) (Figure 3). In the early morning hours WS lizards basked in direct sunlight in the open hummock and open microhabitats (Figure 3A). In each of these, lizards were positioned with the dorsum facing the sun and the venter applied to the ground. As T_b's increased lizards were found in the open (still in direct sunlight) but with their heads facing the sun and their venters held above the ground. Above T_b's of 36.6°C, lizards shuttled between partial (edge) or full shade and the open. The highest mean T_b's were taken from perched individuals. White Sands lizards were never observed in the arboreal microhabitat, even though this microhabitat was present. *Holbrookia maculata* at JRN showed no relationship between T_b's and microhabitat (Figure 2). Generally, lizards basked in the open and perched on vegetation in the early morning (Figure 3B). The edge and arboreal microhabitats were used increasingly during late and early afternoon hours. Individuals used *Ephedra* exclusively for arboreal perches. The open/hummock microhabitat was not present at JRN. Air temperatures were related to microhabitat at both WS ($F_{4, 114}$ = 6.85, P < 0.0001) and JRN ($F_{4, 66}$ = 3.96, P = 0.007). Microhabitat also influenced T_s's at WS ($F_{4, 134}$ = 4.10, P = 0.004), but not at JRN (P = 0.10).

DISCUSSION

Variation in body temperature (T_b) and thermoregulatory behavior within species are attributable to differences in the thermal environment via changing seasons, microhabitat selection, and altitude (Adolph 1990; Grant and Dunham 1990; Smith et al. 1993; Smith and Ballinger 1994; Van Damme et al. 1989, Van Damme et al. 1990). However, no studies have shown differences in these thermal relationships across populations at similar elevations and seasons. I found that two populations of *Holbrookia maculata* inhabiting

thermally divergent environments, separated by only 60 km and at similar altitudes, showed differences in T_b's and thermoregulatory behavior.

Temperature regulation in lizards may be evaluated by examining the variance in T_b's of field-active individuals (Huey 1982). At WS, T_b's were significantly lower than the T_b's of lizards at JRN. This suggests that lizards at WS cannot regulate body temperatures as effectively as individuals at JRN. The environmental properties (biotic and abiotic) of the white gypsum dunes may hamper significant increases in T_b's. For example, T_s's at WS were lower than T_b's. Consequently, lizards at WS may be mostly restricted to direct heat uptake from solar radiation (heliothermically basking).   In contrast, T_s's at JRN were higher than T_b's, suggesting that relatively more heat energy is stored in the substrate during the day at JRN than at WS. This would allow the JRN population to exploit another heat source in addition to solar radiation. A more complete picture of thermoregulation may be obtained by examining how T_b's vary with environmental temperatures.

A regression of T_b on T_a is another method of evaluating temperature regulation in lizards (Huey 1982). The slope from this linear relationship can indirectly identify the extent of thermoregulation. A slope near 0 suggests more precise regulation, whereas a slope near 1 suggests that body temperature depends upon ambient temperature. The slope calculated for *H. maculata* at WS is high (0.63) compared to the slope calculated for *H. maculata* at JRN (0.36), as well as compared to the slopes for other lizard species of the desert southwest. For example, reported slopes for *Sceloporus jarrovi* were 0.40 (Middendorf and Simon 1988) and 0.37 (Smith and Ballinger 1994). Smith et al. (1993) calculated a slope of 0.23 for *Sceloporus scalaris* and the slope for *Urosaurus ornatus* was 0.30 (Smith and Ballinger 1995). Sena (1978) reported a slope of 0.645 for *H. maculata* from eastern New Mexico. Interestingly, the slopes are similar for lizards at WS and at the quartz dunes of eastern New Mexico. Of those lizards studied, it appears that most species are relatively precise thermoregulators, whereas *H. maculata* shows interpopulational differences in control over thermoregulation.

Body temperature regulation via behavioral adjustments allows lizards to maintain fairly constant T_b's in an environment. Lizards of thermally heterogeneous environments have the potential to increase and maintain optimal T_b's that maximize performance, such as locomotion (Bennett 1980). However, when the thermal conditions are relatively homogeneous lizards could experience less that adequate thermal conditions (Huey and Bennett 1987) or remain inactive for extended periods of time (Grant and Dunham 1988, 1990). I found that microhabitat use, an index of behavioral thermoregulation, was different between lizards at WS and JRN, and that microhabitat influenced T_b's at WS, but not the T_b's at JRN. This suggests that the WS habitat is more thermally homogeneous than the environment at JRN. Moreover, the lizards at WS appear to thermoregulate in a limited sense by increasing T_b's throughout the morning and remaining active into the afternoon. In contrast, lizards at JRN appear to thermoregulate more carefully by obtaining activity T_b's at a relatively faster rate in the

morning, then behaviorally regulate T_b's throughout the rest of the afternoon by shuttling between thermally appropriate microhabitats.

The morphology of *H. maculata* at WS may preclude significant increases in T_b's. First, lizards at WS are significantly lighter in dorsal coloration relative to those dorsal hues recorded from lizards at JRN (Hager 1998). Heat gain by a "white" lizard occurs at slower rates than the rate for darker individuals (Norris 1967; Porter et al. 1973). I observed lizards at WS to darken dorsally for only a short period of time in the early morning, but in a relative sense they do not darken to levels of lizards from areas outside WS (Hager 1998). Furthermore, heat gain and loss is influenced by the surface area to volume ratio of an animal (Porter et al. 1973; Stevenson 1985). Differences in body condition between each population suggest that lizards at WS have a lower surface area to volume ratio than lizards at JRN. Coloration and body size may reduce rates of heat gain in lizards at WS.

The data presented in this paper are preliminary, but they suggest that T_b's and thermoregulation vary between populations of *H. maculata* found in diverse thermal environments. At WS, it appears that relatively low air and soil temperatures, white body coloration, and a low estimate of body condition (a representation of the ratio between surface area and volume) may further influence T_b's. The precision, accuracy, and effectiveness of thermoregulation in *H. maculata* can be addressed by examining the relative distributions of lizard T_b's and operative temperatures of behaviorally-inert model lizards (Bakken 1992; Hertz et al. 1993). Furthermore, identifying the observed distributions of lizards into habitat categories relative to the actual distribution of the available habitat area into habitat categories is needed to more rigorously assess habitat selection (Grant and Dunham 1988).

ACKNOWLEDGMENTS

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