JOURNAL OF THERMAL BIOLOGY
Comparative and Medical Aspects

Habitat use and activity influence thermoregulation in a tropical lizard, *Ameiva exsul*

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A B S T R A C T

We examined the contributions of alterations in daily activity and behavioral selection of microhabitat to thermoregulation in a population of the lizard, *Ameiva exsul* (Teiidae), by combining data on lizard activity with data on the availability of sun-shade patches and operative temperatures (T_e). By comparing T_e distributions predicted by "no thermoregulation" and "only thermoregulation" hypotheses to those predicted by random use of thermal habitat, we assessed the relative contributions of microhabitat selection and daily activity to regulation of body temperature (T_b). Over the course of a day lizards maintained T_b very close to optimal temperature (T_{sel}) despite T_es that deviated substantially from T_{sel}. Data demonstrating a unimodal daily activity pattern reject the hypothesis of uniform activity throughout the day. Also, lizard activity was not positively correlated with the proportion of T_es within T_{sel} nor negatively correlated with the absolute deviation of available T_e from T_{sel} (d_e) ("only thermoregulation"). Microsite use by *A. exsul* deviated significantly from predictions of the "no thermoregulation" hypothesis, but our data could not reject predictions of the "only thermoregulation" hypothesis that lizards would use sun-shade patches relative to the proportion of microsites where T_e is within T_{sel}. Also, lizards appeared to actively select sunlit and partially shaded microsites at different times of day. Thus, despite thermal constraints imposed by the habitat, *A. exsul* maintained high and relatively constant T_bs throughout its daily activity period and thermoregulated effectively. This appears to be generally representative of West Indian species of *Ameiva*.

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1. Introduction

Temperature varies both spatially and temporally. Consequently, essentially all terrestrial organisms must deal with thermal heterogeneity. Organisms cope by means of changes in the thermal sensitivity of physiological performance and/or through thermoregulation (Angilletta, 2009). Thermoregulation is critically important because it allows organisms to maintain a relatively high and constant body temperature, T_b, which favors optimal cellular and enzymatic function and whole-animal performance under natural conditions (Angilletta, 2009; Huey and Stevenson, 1979). Lizards often use behavioral adjustments (changes in activity period, shuttling between patches of sun and shade, and postural changes) to rapidly alter the exchange of energy between the animal and the environment and to allow precise regulation of T_b (Stevenson, 1985). Studies of the thermal biology of individual species provide critical baseline information

that can be used to assess potential impacts of climate change (Huey et al., 2009). This information is critical for those ectotherms inhabiting tropical regions where predicted impacts of climate change are particularly dire (Deutsch et al., 2008; Sinervo et al., 2010).

Demonstrating the extent to which animals thermoregulate is not a trivial task. Historically, correlations between air temperature and T_b have been used such that a slope less than one was indicative of thermoregulation. Although intuitive, this approach can be misleading, as inanimate objects might appear to thermoregulate under natural conditions (Heath, 1964). Researchers have developed a solution to this problem by quantifying appropriate null hypotheses for non-thermoregulating animals (e.g., Hertz, 1992). Furthermore, this latter approach not only permits a demonstration of thermoregulation, but also the behavioral mechanisms contributing to it (Bauwens et al., 1996; Díaz, 1994; Gvozdik, 2002; Hertz, 1992).

Examining the extent of thermoregulation and its contributing behaviors requires measurement of several metrics (Hertz et al., 1993): (1) an estimate of the target body temperature an animal seeks to achieve in the absence of other constraints (this metric is

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generally quantified using the selected temperature range [T_{sel}] in a laboratory thermal gradient), (2) a distribution of available temperatures a non-thermoregulating animal would achieve in the habitat (the operative temperature, T_e), (3) estimates of behaviors that might cause observed T_bs to differ from T_e, and (4) actual T_bs from animals active in nature. These metrics are then combined to assess the effectiveness of thermoregulation and can also be used to quantify the contributions of behavioral mechanisms that produce T_b (Bauwens et al., 1996; Blouin-Demers and Nadeau, 2005; Blouin-Demers and Weatherhead, 2001; Hertz et al., 1993).

In this study, we examined the contributions of alterations in daily activity and behavioral selection of microhabitat to thermoregulation in a population of the lizard, *Ameiva exsul* (Teiidae). In particular, we combined data on lizard activity with data on the availability of sun-shade patches and T_e. We followed Bauwens et al. (1996) and devised alternative hypotheses about thermoregulation. By comparing T_e distributions predicted by each hypothesis to those predicted by random use of thermal habitat, we were able to assess the relative contributions of microhabitat selection and daily activity to regulation of T_b.

2. Methods

Ameiva exsul is a relatively large (adult male snout-vent-length 70–160 mm; body mass 10–155 g) teiid lizard with a distribution comprising Greater Puerto Rico (=Puerto Rico proper, most satellite islands, and many of the U.S. and British Virgin Islands; Schwartz and Henderson, 1991). The species is a heliothermic, ground-dwelling lizard that inhabits a broad array of habitats (summarized in Henderson and Powell, 2009). We conducted our research on Guana Island, a privately owned, approximately 300-ha wildlife sanctuary in the British Virgin Islands.

Our study site included a continuous transect along established trails starting on a hillside and leading down to a beach and continuing parallel to the beach. In all, we surveyed a transect over 800 m in length and approximately 20 m in width. Habitat along the trail portion of the transect was comprised of West Indian subtropical dry forest characteristically dominated by plants in the families Rubiacaea, Euphorbiaceae, and Myrtaceae (Gentry, 1995). Habitats along the beach consisted of early successional (dominated by *Leucaena leucocephala* and *Acacia macracantha*) and mid-successional (dominated by *Coccoloba uvifera*) coastal dry forests (Rodda et al., 2001). In all, the entire transect encompassed a mosaic of sun-shade patches through which lizards willingly moved.

Data in this study were collected during one week each October 2007–2011, unless otherwise noted. We included data only for days when weather conditions were similar (low to moderate wind, nearly continuous sunshine until approximately 1400 h, some scattered cloud cover thereafter). Because we sampled only during the wet season, our inferences are necessarily limited to that time period and preclude any assessment of potentially variable seasonal patterns.

2.1. Thermal environment

We quantified operative temperatures (T_e) and the relative availability of sunlit and shaded microsites using operative temperature models (OTM) constructed from painted (gray) hollow copper tubes (7 cm long, 2 cm diameter) sealed at the ends with short lengths of silver duct tape. Each OTM contained a thermochron ibutton programmed to record temperature at one-hour intervals. Although we did not validate OTM's for *Ameiva exsul*, previous data for a closely related and similarly sized

species (*Ameiva ameiva*) indicated that equilibrium temperature attained by these OTM's closely approximates equilibrium animal temperature (mean temperature deviation ≤ 0.8 °C; Gifford and Powell, unpublished data).

In 2010, we used 52 OTM's to sample T_es available to lizards and the availability of sun-shade patches along the transect. Models were deployed at ~10 m intervals along the transect. Precise placement (right or left of transect) was determined randomly by coin flip. Due to the relative homogeneity of habitat along transects, we assumed that our model placement represented an accurate reflection of the relative availability of sun-shade microsites throughout the day. Temperatures were recorded over four consecutive days from 0700 until 1600 (10 time periods), yielding 2080 T_e measurements. This sampling regime resulted in T_e recordings prior to and after observed lizard activity at the site. During one day, we sampled OTMs hourly to record the microsite in which the model was positioned (full sun, partially shaded, fully shaded).

2.2. Lizard behavior, thermal biology, and performance

As part of a larger study of population demography, we have accumulated 102 behavioral observations and recorded body temperature (T_b) on 89 individual adult male lizards throughout the period of daily activity. The small sample size of adult females precluded their inclusion. Upon sighting, we recorded time of day and whether the lizard was resting in full sun, partial shade, or full shade, after which we attempted to capture each animal. Immediately after capture, we measured T_b to the nearest 0.1 °C with a quick-reading digital thermometer using a K-type thermocouple (Fluke 52 series; Fluke Corp., Everett, Washington). Only lizards captured within 3 min were included in the T_b data set.

We sampled 12 adult male lizards to quantify the selected temperature range (T_{sel}; Hertz et al., 1993). This range represents the target T_bs that lizards attempt to maintain in the field. We estimated T_{sel} as the central 80% of temperatures chosen by adult *A. exsul* in a laboratory photo-thermal gradient. We placed each animal in a gradient and recorded T_b after four hours. Thus, four animals were examined each day in two identical photo-thermal gradients. Time of day (morning vs. afternoon) did not influence estimated body temperatures (*t*-test, $P > 0.05$), so data from all individuals were pooled in analyses.

In order to explore the potential consequences of thermoregulatory behavior we assessed the thermal sensitivity of maximal sprinting speed in a sample of eight animals. Sprinting speed was measured using a 2-meter long racetrack equipped with computer-controlled photocells stationed at 25 cm intervals. Each lizard was raced three times at each of four temperatures (28, 34, 38, and 42 °C). Individual trials at a given temperature were separated by a minimum of one hour, and trials at different temperatures separated by 24 h. Prior to each trial, animals rested for 30 min inside an incubator set at the target temperature. We recorded T_b immediately prior to each trial, and returned animals to the incubator after each trial. We quantified thermal sensitivity using a thermal performance curve (TPC; Huey and Stevenson, 1979) constructed using the minimum convex polygon method of Van Berkum (1986). Based on estimates from other species of *Ameiva* (Brattstrom, 1965), we assumed a critical thermal maximum of 46.2 °C to complete the thermal performance curve.

2.3. Hypothesis testing and data analyses

We assessed the thermal suitability of microsites and the accuracy and effectiveness of thermoregulation using the methods of Hertz et al. (1993). Specifically, we examined the thermal suitability of the microsites and accuracy of thermoregulation by

calculating the proportion of T_b and T_e measurements that fell within T_{sel}. In addition we quantified the effectiveness of thermoregulation (i.e., the degree to which *A. exsul* thermoregulates) using two measures. First, we used the deviation between the thermal quality of the habitat and the accuracy of thermoregulation ($d_e - d_b$; Blouin-Demers and Nadeau, 2005; Blouin-Demers and Weatherhead, 2001). Second we calculated thermoregulatory effectiveness using E ($E = 1 - [d_b/d_e]$; *sensu* Hertz et al., 1993). In either case, d_e represents the absolute deviation of the available T_e from the selected temperature range (T_{sel}), whereas d_b represents the absolute deviation of T_b from T_{sel} (Hertz et al., 1993). Low values of $d_e - d_b$ indicate that the lizard's body temperature closely approximates the available operative environment (i.e., thermoconformer). Alternatively, high values of $d_e - d_b$ indicate that the lizard maintains a body temperature substantially different from the available operative environment (i.e., thermoregulator). Similarly, E provides an index of the relative similarity of T_bs versus T_es to T_{sel}. E-values near one indicate more effective thermoregulation.

The null hypothesis of "no thermoregulation" predicts that lizard activity time should be independent of T_e, and thus activity should be constant throughout the day. In addition, this hypothesis predicts that lizards should be distributed among microsites in proportion to their availability regardless of thermal characteristics (Bauwens et al., 1996). An alternative hypothesis ("only thermoregulation") suggests that lizard activity should be restricted to times when and locations where T_e falls within T_{sel}. Thus, this hypothesis predicts that activity should be determined by the availability of suitable thermal microsites. Statistically, this hypothesis predicts a positive relationship between lizard activity (number observed per sampling period) and the proportion of T_e values that fall within T_{sel}, and a negative relationship between lizard activity and d_e.

We tested for patterns of nonrandom microsite selection throughout the day using a selectivity index (α; Manly et al., 2003),

$$w_i = c_i / a_i$$

$$a_i = w_i / Sw_i$$

Briefly, w_i is the preference for microsite i, c_i is the proportion of lizards exploiting microsite i, and a_i is the proportion of microsite i available. Finally, selectivity of a given microsite is quantified using α_i. This index ranges from 0 to 1, with higher values indicating preference for a particular microsite. We categorized selectivity values by time (morning and afternoon) to test whether behavioral selection of each microsite type varied over the course of a day.

We examined the potential consequences of thermoregulation by weighting the T_e distribution by the proportion of lizards active during each sampling period and relative to those actually occupying each microsite. This approach produces the distribution of T_bs lizards would achieve if they did not use other behavioral or physiological adjustments to maintain their T_b (T_{ea} & T_{em}; Bauwens et al., 1996). We then compared deviations of T_{ea} and T_{em} from T_{sel} (d_{ea} and d_{em}, respectively) to d_e values assuming lizards used habitats spatially and temporally at random. We made comparisons within sampling periods and for the entire data set using appropriate mean values. Second, we assessed the proportion of maximal performance realized if lizards utilized microsites in proportion to their availability (T_e distribution), in proportion to actual microsite use (T_{em} distribution), and relative to the temperatures actually achieved by the lizards (T_b distribution). These comparisons permit us to determine the relative contribution of activity time and microsite choice, as opposed to other behavioral or physiological adjustments, to the maintenance of T_b.

We used least-squares regression, ANOVA, and chi-square to test hypotheses. In cases where assumptions of standard tests were violated (i.e., small expected sample size in chi-square tests), we used randomization tests with 9999 permutations of the data set. We computed all statistical tests in R version 2.14.1 (R Development Core Team, 2011).

3. Results

3.1. Operative and body temperatures

The mean T_b of *Ameiva exsul* in October (37.73 ± 0.23 °C, $\pm$ SE, N=89) exceeded mean T_e (32.93 ± 0.14 °C, N=2080). In addition, the distribution of T_b was substantially narrower than the distribution of available temperatures, T_e (Fig. 1). Lizards in our population exhibited a relatively narrow T_{sel} (36.30–40.13 °C). Over the course of a day lizards maintained T_b very close to T_{sel} (79% of T_b records within T_{sel}, mean $d_b = 0.83$ °C; Fig. 2), whereas T_e deviated substantially from T_{sel} (11% of T_es within T_{sel}, mean
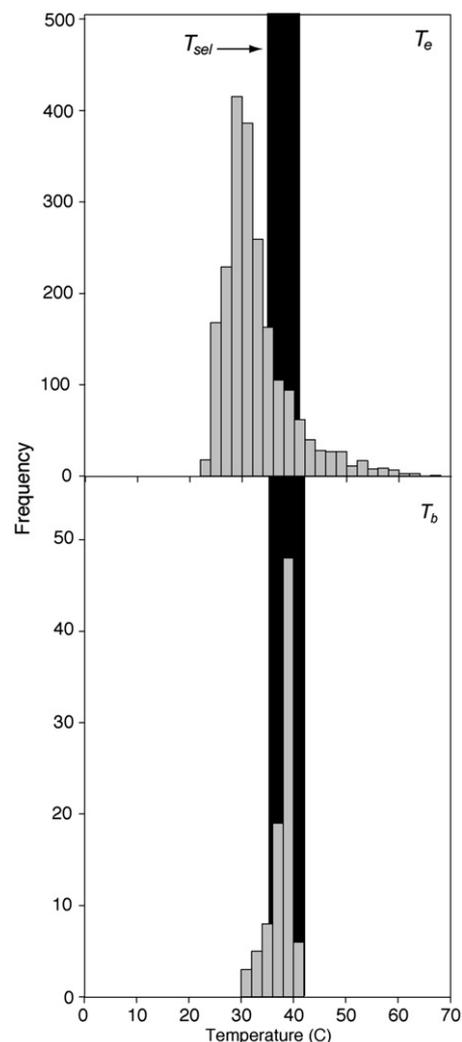

Fig. 1. The distributions of available operative temperatures (T_e) and body temperatures (T_b) for a population of *Ameiva exsul* on Guana Island (British Virgin Islands) during October. The vertical black bar indicates the selected temperature range for this population (T_{sel}).
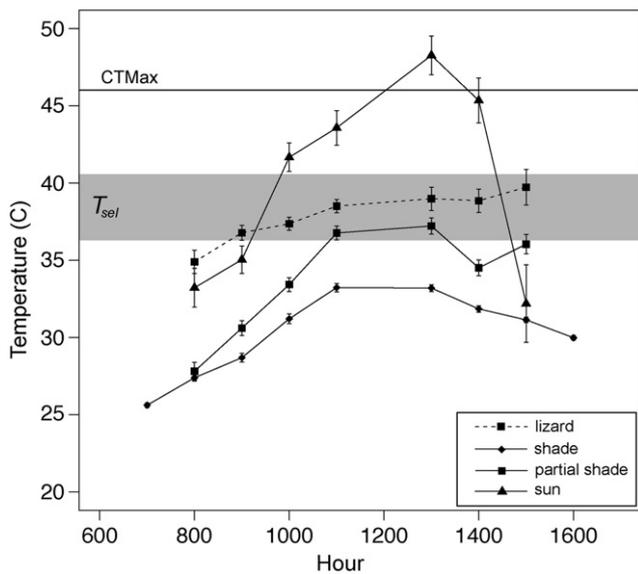
Fig. 2. Hourly variation in body temperature of *Ameiva exsul* and habitat temperature for each available microsite. Data are represented as the mean ± 1 SE.

Fig. 3. The number of lizards observed along the sampled transect during each hour of the day. The 1200 h is left blank because of unequal sampling intensity over the course of this study.

$d_e = 5.96 \, ^\circ C$). Therefore, during October, *A. exsul* thermoregulates very effectively ($d_e - d_b = 5.13 \, ^\circ C$; $E = 0.87$).

During most hours of the day (0800–1500 h), some T_es were within T_{sel}; therefore, lizards had the potential to attain T_b within T_{sel}. However, a very small proportion of microsites had T_es within T_{sel} during any one time-period (range=4–23%). Regardless, a large proportion of T_bs fell within T_{sel} during each hour of activity (range=23–100%). Thus, despite thermal constraints imposed by the habitat, *A. exsul* maintained high and relatively constant T_bs throughout its daily activity period and thermoregulated very effectively ($d_e - d_b$ range=4.5–5.6 $^\circ C$; E range=0.67–0.98).

3.2. Lizard activity

The "no thermoregulation" hypothesis predicted a uniform level of lizard activity throughout the day independent of thermal constraints. Our observations indicated that *A. exsul* exhibits a unimodal period of activity with a peak in the late morning (1000–1100 h; Fig. 3). Because we did not sample during the 1200-hour, we cannot determine if activity is maintained at a high level during that time. However, previous data on activity for this population (Nicholson et al., 2005) are consistent with ours, although their peak in activity is extended to 1300 h. We note also that their data included observations on adults and juveniles, whereas ours are restricted to adult males. Activity patterns of different age classes might vary incongruously because large size and lower surface-area:volume ratios might impair heating/cooling rates. Regardless, our data reject the hypothesis of uniform activity throughout the day ($X^2 = 30.34$, $P < 0.001$).

The "only thermoregulation" hypothesis predicted that lizard activity should be positively correlated with the proportion of T_es within T_{sel} and negatively correlated with d_e per sampling period. Our data do not confirm these predictions. Although lizard activity trends in the predicted directions relative to T_e and d_e, these relationships are not statistically significant ($r = 0.52$, $df = 7$, $P = 0.15$; and $r = -0.55$, $df = 7$, $P = 0.12$).

3.3. Microsite availability and selection

Microsites varied significantly in thermal properties ($F_{2,2073} = 575.61$, $P < 0.001$, repeated measures ANOVA). In addition, a Tukey HSD *post hoc* test indicated that all microsites differed significantly
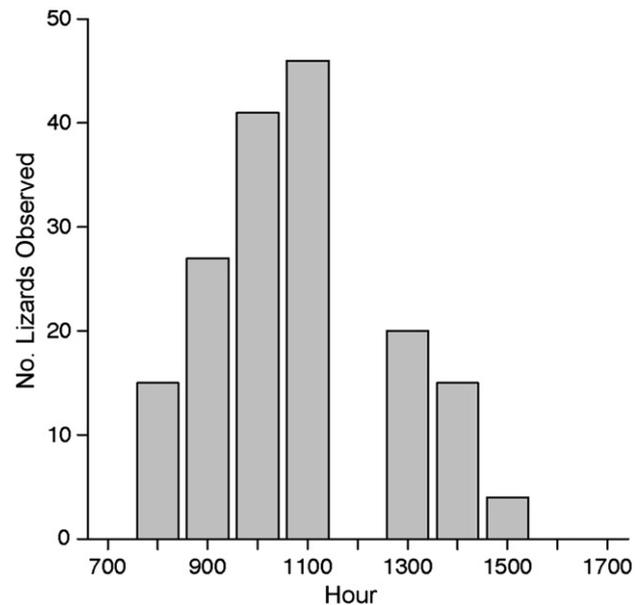
from one another ($P < 0.05$). Shaded habitats provided the coolest and least variable T_es over the course of a day (Fig. 2). The overwhelming majority of T_es in shaded microsites fell below T_{sel} (95.6%), whereas only a small fraction fell above and within T_{sel} (0.9 and 3.5%, respectively). Partially shaded microsites provided warmer and more variable T_es throughout a day (Fig. 2). The majority of T_es at these sites also fell below T_{sel} (70.5%), with a roughly equal fraction above and within T_{sel} (13.02 and 16.5%, respectively). Only a small number of partially shaded sites had T_es that exceeded CT_{max} (3.9%). Sunlit microsites provided the warmest and most variable thermal conditions throughout a day (Fig. 2). In contrast to T_es in the other two microsite categories, only 38.9% of T_es fell below T_{sel}, whereas 16.7% of T_es were contained within T_{sel}. Further, a large proportion of T_es in sunlit patches exceeded T_{sel} (48.7%) with many exceeding CT_{max} (29%). Thus, all three alternative types of available microsites provided thermally suitable habitats to varying degrees throughout a day.

The "no thermoregulation" hypothesis predicted that lizards should use microsites (sun-shade patches) in proportion to their availability irrespective of thermal conditions. Microsite use by *A. exsul* deviated significantly from predictions of this hypothesis ($X^2 = 143.67$, $P = 0.003$; based on 9999 permutations of the data set). Alternatively, the "only thermoregulation" hypothesis predicted that lizards would use sun-shade patches relative to the proportion of microsites where T_e is within T_{sel}. Our data cannot reject this alternative ($X^2 = 64.90$, $P = 0.41$; based on 9999 permutations of the data set).

We further explored microsite selection to assess the contribution of behavioral factors to thermoregulation by this population. We used Manly's α to quantify selectivity of each microsite type during each hour of activity. Selectivity of shaded microsites was consistently low throughout a day and did not differ significantly between morning and afternoon time periods ($t = 1.54$, $df = 5$, two-tailed $P = 0.384$). In contrast, lizards appeared to actively select sunlit and partially shaded microsites at different times of day (sunlit: $t = 3.33$, $df = 5$, two-tailed $P = 0.02$; partial shade: $t = 6.04$, $df = 5$, two-tailed $P = 0.002$). During morning hours, lizards actively selected sunlit patches more frequently than their availability, whereas in the afternoon, lizards actively sought partial shade (Fig. 4).
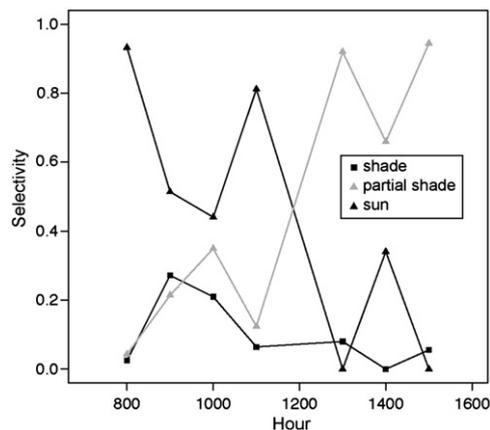
Fig. 4. Microsite selection by _Ameiva exsul_ estimated using Manly's α (Manly et al., 2003). Selectivity was calculated for each microsite type for each sampling period.

3.4. Consequences of thermoregulation

We explored the thermal consequences of nonrandom microsite selection by weighting T_e measurements by the observed lizard activity pattern and by lizard habitat use. This approach yielded two new operative distributions, T_{ea} and T_{em}, which described the temperatures lizards would experience based on their activity patterns and observed microsite use. The contribution of activity time and microsite selection to thermoregulation by these lizards was then examined by comparing the absolute deviations of T_{ea} and T_{em} from T_{sel} (d_{ea} and d_{em}, respectively) to those of random T_e records (d_e). The mean d_{ea} was 2.34 °C lower than the mean d_e, whereas the mean d_{em} was 2.64 °C lower than mean d_e. Therefore, restriction of activity and microsite selection would result in operative temperatures during times of day and at sites chosen by lizards that were 2.34 and 2.64 °C closer to T_{sel} than were T_es randomly available at random in the habitat. These patterns were consistent throughout a day.

We also tested the consequences of microsite use for thermoregulation by examining the proportion of maximal performance lizards would attain by using microsites in proportion to their availability (no thermoregulation; T_e), in proportion to availability of microsites with temperatures within T_{sel} (only thermoregulation, T_{em}), and relative to body temperatures achieved by lizards (observed T_b). The "no thermoregulation" hypothesis suggests that lizards would suffer a 6% reduction in performance relative to the "only thermoregulation" hypothesis (81% versus 87%, respectively, $t=2.1$, $P < 0.05$). However, based on observed T_b values, lizards in this population enjoyed a performance advantage of 14% over that predicted by the "no thermoregulation" hypothesis and an 8% advantage over predictions of the "only thermoregulation" hypothesis (all $P < 0.05$). Consequently, although microsite selection influenced thermoregulation by these lizards, other behavioral and/or physiological mechanisms also appear to be important for regulating T_b.

4. Discussion

Ameiva exsul on Guana Island is an effective thermoregulator during the month of October. Our estimated metrics of thermoregulatory effectiveness were high and indicated that, during most parts of a day, lizards maintained T_bs that differed substantially from the T_es available to them. One strategy of thermoregulation would be to restrict activity to times and places where the thermal conditions are most favorable (i.e., T_e within T_{sel}). However, lizards at our site had very few opportunities to exploit this strategy as very few sites had thermal conditions that resided within T_{sel}. In fact, at a maximum, only 17% of the habitat had thermal conditions that met

this criterion during any part of a day. Regardless, lizard activity exhibited a distinct peak in the late morning (Fig. 3), possibly extending into early afternoon. Therefore, available temperatures were neither too hot nor too cool to preclude activity. Thus, lizards most likely used alternative behaviors to regulate T_b.

Three (non-exclusive) mechanisms have been identified as modes of behavioral thermoregulation (Stevenson, 1985; Bauwens et al., 1996). These include: (1) alteration of activity times (e.g., Grant, 1990; Grant and Dunham, 1988; Hertz, 1981; Hertz and Huey, 1981), (2) habitat selection (both microhabitats and sun-shade patches; e.g., Adolph, 1990; Christian et al., 1983; Grant and Dunham, 1988; Gvozdík (2002); Dias and Rocha, 2004; Harvey and Weatherhead, 2010; Hertz, 1992; Huey et al., 1977), and (3) physical adjustments, such as shifts in posture or orientation, that alter the rates of energy exchange with the environment (e.g.,Van Damme et al., 1986). Previous data for a population of _A. exsul_ on Puerto Rico indicated that this species typically alternates between sun and shade patches for T_b regulation (Rivera-Vélez and Lewis, 1994).

The daily activity pattern exhibited by lizards in this population differed significantly from the "no thermoregulation" hypothesis. Therefore, non-random activity suggested thermoregulatory behaviors. However, this observation alone cannot demonstrate a contribution to temperature regulation, as other factors potentially influencing lizard behavior might also vary non-randomly in time (e.g., resources, predators, competitors). The observed activity time yields predicted T_bs that are 2.34 °C closer to T_{sel} than are randomly available T_es. Therefore, activity adjustments had a measurable impact on temperature regulation in this population. This observation agrees with Stevenson's (1985) proposal that alterations in activity can play an important role in regulating T_b.

We detected a similar positive effect on thermoregulation for microsite use. Non-random microsite use resulted in predicted T_bs that were 2.64 °C closer to T_{sel} than randomly distributed T_es. Most habitats offered lizards a mosaic of sun-shade patches that were clearly exploited throughout a day. However, lizards showed a distinct preference for alternative microsites during different parts of a day (Fig. 4). Lizards appeared to avoid fully shaded microsites at all times of day, likely as a consequence of unsuitable thermal conditions (mean T_e in shaded microsites never reached T_{sel}; minimum deviation=3.08 °C; Fig. 2). In contrast, lizards actively sought sunlit microsites during morning hours and avoided these in the afternoon. During the morning, these microsites had T_es near T_{sel} (mean absolute deviation=2.34 °C), whereas in the afternoon, sunlit sites approached the critical thermal limit (mean absolute deviation=5.83 °C). The opposite pattern was evident for lizard use of partially shaded microsites. Partially shaded sites were avoided in the morning, but lizards selected these sites in the afternoon. In the morning, T_es in these sites averaged well below T_{sel} (mean absolute deviation=4.06 °C), whereas in the afternoon, partially shaded sites provided thermally suitable conditions (mean absolute deviation=0.51 °C). Therefore, non-random microsite selection played a role in temperature regulation in this population.

Activity patterns of West Indian species of _Ameiva_ include both unimodal and bimodal patterns (summarized in Henderson and Powell, 2009), but peak activity is almost always during late morning regardless of season and age of individuals. In species with bimodal activity patterns (e.g., _A. chrysolaema_ on Hispaniola; Schell et al., 1993), the lesser second period of activity is during late afternoon (after the hottest time of day). Consequently, restricted activity periods to some extent allow lizards to avoid times of day when T_es are most unsuitable and thermoregulation presumably would be most difficult or energetically expensive (the "activity times strategy"; e.g., Hertz, 1981; Hertz and Huey, 1981).

Similarly, although detailed data are lacking for West Indian congeners, observations of shuttling between sun and shade abound, as do records of lizards spending more time in sunny

patches during morning hours and individuals exploiting often tiny sunny patches in otherwise shaded habitats (summarized in Henderson and Powell, 2009). So, effective use of thermally variable microsites (the "habitat selection strategy"; e.g., Hertz, 1992) appears to be common in species of *Ameiva*, although evidence is largely in the form of anecdotal observations. Nevertheless, like our data, these indications of non-random microsite selection playing an apparently substantive role in temperature regulation supports rejection of the "no thermoregulation" hypothesis. So, despite the possibility that specifics might vary by season or that individuals of different ages or sizes might exploit habitats a bit differently than large adults, we suggest that our findings for *A. exsul* on Guana Island in October are generally representative for West Indian species of *Ameiva*.

Studies such as this are useful because they demonstrate the degree to which ectotherms thermoregulate and the contributions of different behaviors to maintenance of T_b. Ongoing global climate change is predicted to have detrimental effects on ectotherms on a world-wide scale, particularly for those inhabiting tropical regions (Deutsch et al., 2008; Huey et al., 2009; Sinervo et al., 2010). Environmental warming could cause even partially shaded microsites to reach the upper limits of T_{sel} during some afternoon hours for *A. exsul*. This could cause a behavioral shift to an occupation of more shaded habitats or to alterations of activity times. Because *A. exsul* is a very effective thermoregulator, and because thermal refugia might remain available as climate changes, perhaps this species can escape the fate predicted for their thermoconforming counterparts.

Acknowledgments

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