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*<sub>e</sub>). By comparing *T*<sub>e</sub> 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*<sub>b</sub>). Over the course of a day lizards maintained *T*<sub>b</sub> very close to optimal temperature (*T*<sub>opt</sub>) despite *T*<sub>e</sub>s that deviated substantially from *T*<sub>opt</sub>. 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*<sub>e</sub>s within *T*<sub>opt</sub> nor negatively correlated with the absolute deviation of available *T*<sub>e</sub> from *T*<sub>opt</sub> ("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*<sub>e</sub> is within *T*<sub>opt</sub>. 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*<sub>b</sub>s 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*<sub>b</sub>, 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*<sub>b</sub> (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*<sub>b</sub> 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...
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 \(T_e\) (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 along the transect. 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 \(T_p\).

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 composed of West Indian subtropical dry forest characterized 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 mearnsii) 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 \(\leq 0.8^\circ C\); Gifford and Powell, unpublished data).

In 2010, we used 52 OTM’s to sample \(T_{bs}\) available to lizards and the availability of sun-shade patches along the transect. Models were deployed at \(\sim 10\) 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 OTM’s 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 \(^\circ C\) 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 \(^\circ C\)). 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* (Bratststrom, 1965), we assumed a critical thermal maximum of 46.2 \(^\circ C\) 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 $T_{set}$. 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 ($T_{set}$), whereas $d_b$ represents the absolute deviation of $T_b$ from $T_{set}$ (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 $T_S$ versus $T_{set}$. $E$-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 $T_{set}$. 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 $T_{set}$ 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 ($z$; 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 $z$. 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 $T_S$ lizards would achieve if they did not use other behavioral or physiological adjustments to maintain their $T_S$ ($T_{eo}$ & $T_{em}$; Bauwens et al., 1996). We then compared deviations of $T_{eo}$ and $T_{em}$ from $T_{set}$ ($d_{eo}$ 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 ($T_{eo}$ 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 $T_e$.

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 $T_e$ of Ameiva exsul in October ($37.73 \pm 0.23 ^\circ C$, N=89) exceeded mean $T_b$ ($32.93 \pm 0.14 ^\circ C$, 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 $T_{set}$ (36.30–40.13 ^\circ C). Over the course of a day lizards maintained $T_b$ very close to $T_{set}$ (79% of $T_b$ records within $T_{set}$, mean $d_b=0.83 ^\circ C$; Fig. 2), whereas $T_e$ deviated substantially from $T_{set}$ (11% of $T_S$ within $T_{set}$ mean

![Fig. 1](image-url). 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 ($T_{set}$).
from one another ($P < 0.05$). Shaded habitats provided the coolest and least variable $T_{\text{S}}$ over the course of a day (Fig. 2). The overwhelming majority of $T_{\text{S}}$ in shaded microsites fell below $T_{\text{sel}}$ (95.6%), whereas only a small fraction fell above and within $T_{\text{sel}}$ (0.9 and 3.5%, respectively). Partially shaded microsites provided warmer and more variable $T_{\text{S}}$ throughout a day (Fig. 2). The majority of $T_{\text{S}}$ at these sites also fell below $T_{\text{sel}}$ (70.5%), with a roughly equal fraction above and within $T_{\text{sel}}$ (13.02 and 16.5%, respectively). Only a small number of partially shaded sites had $T_{\text{S}}$ that exceeded $CT_{\text{max}}$ (3.9%). Sunlit microsites provided the warmest and most variable thermal conditions throughout a day (Fig. 2). In contrast to $T_{\text{S}}$ in the other two microsite categories, only 38.9% of $T_{\text{S}}$ fell below $T_{\text{sel}}$, whereas 16.7% of $T_{\text{S}}$ were contained within $T_{\text{sel}}$. Further, a large proportion of $T_{\text{S}}$ in sunlit patches exceeded $T_{\text{sel}}$ (48.7%) with many exceeding $CT_{\text{max}}$ (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 $A. \text{exsul}$ 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 $T_{\text{sel}}$. 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 $\chi$ 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 ($t = 1.54, df = 5, P = 0.384$). 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).

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
3.4. Consequences of thermoregulation

We explored the thermal consequences of nonrandom microsite selection by weighing T σ measurements by the observed lizard activity pattern and by lizard habitat use. This approach yielded two new operative distributions, Tσm and Tσn, which described the temperatures lizards would experience based on their activity pattern 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 Tσm and Tσn from Tσ (δσm and δσn, respectively) to those of random Tσ records (δσ). The mean δσ was 2.34 °C lower than the mean δσ, whereas the mean δσn was 2.64 °C lower than mean δσ. 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 Tσ than were Tσs 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; Tσs), in proportion to availability of microsites with temperatures within Tσ (only thermoregulation, Tσm), and relative to body temperatures achieved by lizards (observed Tσ). The “no thermoregulation” hypothesis suggests that lizards would suffer a 6% reduction in performance relative to the “only thermoregulation” hypothesis (81% versus 75%, respectively, t = 2.1, P < 0.05). However, based on observed Tσ 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 Tσ.

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 Tσs that differed substantially from the Tσs 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., Tσ within Tσm). However, lizards at our site had very few opportunities to exploit this strategy as very few sites had thermal conditions that resided within Tσm. 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 Tσ.

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; Govdzik (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 Tσ 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 Tσs that are 2.34 °C closer to Tσm than are randomly available Tσs. 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 Tσ.

We detected a similar positive effect on thermoregulation for microsite use. Non-random microsite use resulted in predicted Tσs that were 2.64 °C closer to Tσm than randomly distributed Tσs. 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 Tσ in shaded microsites never reached Tσm; 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 Tσs near Tσm (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, Tσs in these sites averaged well below Tσm (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. chrysoleuca_ 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 Tσs 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 support rejection of the “no thermoregulation” hypothesis. So, despite the possibility that species 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 $T_b$ 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 $T_b$ 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 thermocoforming counterparts.

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