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THERMAL MICROHABITAT PREFERENCE OF THE COMMON SIDE-BLOTCHED LIZARD, *UTA STANSBURIANA*

by

Maria Goller

**Thesis submitted in partial fulfillment
of the requirements for the degree**

of

DEPARTMENTAL HONORS

in

**Biology
in the Department of Biology**

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ABSTRACT

Ectotherms are especially susceptible to changing temperature conditions within their environment. To limit temperature fluctuations they must behaviorally regulate body temperature by moving between microhabitats of different ambient temperatures. By actively selecting specific substrate temperatures within a heterogeneous thermal environment, an individual could attain preferred body temperature and approach internal thermal homeostasis for periods of time. Ambient temperature dependence should thus force an individual to select those microhabitats that present optimal thermal conditions. Because dynamic thermal microhabitat structure is difficult to assess, the extent to which lizards employ behavioral thermoregulation is not well understood. Therefore, there is a need to better assess thermal habitat structure and how it relates to behavioral thermoregulation. In this study, thermal imaging was used to evaluate the dynamics in thermal microhabitat structure, lizard body temperature, and substrate preference during the warm season (July and August). Despite a broad range of microhabitat temperatures surrounding lizards (1-2 m² of surface showed a mean range of 11 °C), mean lizard temperature varied within a narrow range (36 to 38 °C). A variety of hypotheses exist for why *Uta* strongly prefer body temperatures of 37 °C, such as optimization of physiological processes. Lizards selected sites with temperatures that differed slightly yet significantly from the mean temperature around them, indicating that individuals do exhibit behavioral thermoregulation. Furthermore, lizards make use of radiative heat gain to regulate their body temperature significantly above that of their perch (mean difference of 2.6 °C). Regulation differed throughout the day. Lizard body temperature differences from before and after short- and long-distance switches in position accounted for only 15% of the variation in body temperature. These findings show that lizards are able to maintain fairly constant body temperatures for extended periods of time, during the warm season, by combining selection of a thermally favorable microhabitat with radiative regulation. Habitat structural complexity differs across the geographical range of *Uta stansburiana*, and therefore provides variable opportunity for thermoregulation. Impacts of change in temperature due to climate change may therefore vary based upon population. Our results indicate that, although *Uta* may go locally extinct due to the effects of climate change, the study population, living as it does in an area of extraordinary thermal heterogeneity, may actually benefit.

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TABLE OF CONTENTS

LIST OF FIGURES	4
INTRODUCTION	5
MATERIALS AND METHODS.....	7
Study organism and sampling.....	7
Field sampling.....	8
Analyses.....	10
Subset of measurements.....	10
Comparison to traditional thermocouple cloacal sampling.....	11
Statistical analyses	11
RESULTS	11
Thermal microhabitat structural complexity.....	11
Lizard thermoregulation	12
Seasonal variation.....	14
Daily variation.....	15
Perch temperature	15
Positional switches.....	17
Temporal temperature dynamics	19
Comparison with traditional temperature measurement	27
DISCUSSION	28
Thermoregulation in a heterogeneous environment	28
Thermoregulation and perch selection.....	29
Temporal dynamics of temperature	30
Why does Uta prefer 37 °C?.....	30
Geographic distribution of Uta and thermoregulation	31
Thermoregulatory trends.....	32
Activity and temperature	33
Behavior, territoriality, and temperature	34
.....	34
Comparison of temperature measurement methods	35
Implications for climate change.....	35
REFERENCES	37
AUTHOR'S BIOGRAPHY	41

FIGURES

Figure 1. Thermograms of temperature microhabitats.....	9
Figure 2. Thermal diversity of microhabitats and rock temperature histograms	13
Figure 3. Minimum versus maximum environmental temperature.....	14
Figure 4. Minimum and maximum temperatures versus range of environmental temperature	16
Figure 5. Thermograms of individual body temperature variability and substrate temperature.....	18
Figure 6. Distribution of environmental and mean lizard body temperatures	19
Figure 7. A) Perch temperature against difference between lizard and perch temperature; B) Mean environmental temperature against same difference.....	20
Figure 8. Seasonal change in environmental and lizard temperatures	21
Figure 9. Temperature dynamics of time of day	22
Figure 10. Daily trends of A) difference between environmental maximum and lizard body temperature and B) between lizard and perch temperature.....	23
Figure 11. A) Mean environmental against perch temperature; B) Z-scores of difference between perch and mean environmental temperature	24
Figure 12. A) Lizard body temperature before switch versus change in temperature; B) Cumulative distribution of perch and lizard body temperatures.....	25
Figure 13. Before and after body and perch temperatures for A) moves and B) shifts	26
Figure 14. Temporal dynamics of mean lizard and environmental temperatures.....	27

INTRODUCTION

Temperature affects physiological processes (Waldschmidt et al. 1986), and thus performance (e.g., Huey and Bennett 1987) and the life history of a species (Adolph and Porter 1993). Striking effects of temperature on growth and development have been well documented in different taxa (e.g., Adolph and Porter 1993; Huey 1991). Because of its universal effect on physiological and biochemical processes, temperature influences the fitness of organisms in complex ways.

Particularly in ectotherms, behavioral (active) thermoregulation is a mechanism allowing optimization of physiological processes that are directly impacted by temperature (Huey and Stevenson 1979). Thermoregulation becomes an important behavior in lizards because it directly impacts survivorship and development (Adolph and Porter 1993). Furthermore, high temperatures rapidly become detrimental (Huey and Stevenson 1979). Finding the optimal temperature for certain life stages may be challenging or dangerous for an individual. For example, female *Sceloporus* lizards may leave their home ranges to lay eggs if appropriate thermal microhabitats are absent from the area (Angilletta et al. 2009). This movement is energetically costly and potentially exposes the females to predation.

The degree of thermoregulatory capability and thermal tolerance varies largely between species. Some species will only thermoregulate behaviorally when optimal body temperature is achievable, such as *Zootoca vivipara* (Herczeg et al. 2006), while others remain passive through a wide temperature range, only regulating under extreme temperature conditions, like within the *Anolis* genus (Huey and Webster 1975, Hertz et al. 1993). However, different species of the same genus often vary in regulatory flexibility (Sinervo and Adolph 1989). Regulation may not always be possible. For example, habitat factors impact the thermoregulatory ability of geckos, such that individuals may be forced to tolerate suboptimal temperatures (Vance 1973). Therefore, an individual lizard may be unable to achieve preferred body temperature, depending on environmental conditions (Peterson 1987) and competition (Tinkle 1967). Two competing species may, however, prefer overlapping ranges in preferred microhabitats to avoidance of competition (Adolph 1990).

Thermoregulation is a highly complex optimization process, because different physiological processes and behaviors achieve performance optima at different temperatures (Huey and Stevenson 1979). Lizard activity level is highest when individuals are at optimal body temperature (Huey and Slatkin 1976), but behaviorally selecting a specific body temperature may be maladaptive in an ecological sense (Huey and Slatkin 1976). It may therefore be most beneficial for an individual to

select for intermediate body temperatures to optimize as many physiological processes as possible (Huey and Stevenson 1979).

Behavioral thermoregulation depends strongly on the presence of habitat heterogeneity (Blouin-Demers and Nadeau 2005). Availability of a range of environmental temperatures facilitates thermal choice in the context of many other competing needs in regard to microstructure of the habitat. Differences in habitat cause differences in activity level by providing varying thermal gradients to utilize (Alexander and Whitford 1968). An individual's shifts among available microhabitats may be an important way of thermoregulating (Adolph 1990), so the greater the variability in habitat, the greater the potential for precision in regulating for a preferred temperature.

The common side-blotched lizard, *Uta stansburiana*, is a small, diurnal iguanid lizard found in desert regions across western North America (e.g., Evans 1967, Parker and Pianka 1975, Irwin 1965). This species is very common and inhabits a wide range of habitats (Tinkle 1967). *Uta* are sit-and-wait predators (e.g., Parker and Pianka 1975, Waldschmidt and Tracy 1983), and therefore have ample opportunity to regulate precisely for preferred body temperature. Individual lizards engage in shuttling behavior between various microhabitats to presumably maintain appropriate temperatures (Waldschmidt 1980).

Based upon thermoregulatory ability, a question, therefore, is how *Uta stansburiana* as a species will react to climate change. Effects of changing temperatures and increase in temperature variation differ based upon an organism's physiology (Adolph and Porter 1993). Furthermore, high mortality of *Uta* has been linked to thermoregulatory ability, with survivors being more selective in activity time and habitat choice (Fox 1978), although temperature stress did not appear to heighten mortality (Wilson 1991). Ability to thermoregulate could especially impact survivorship in northern populations, where variation in climate was the most important limiting factor (Parker and Pianka 1975). Davis and Verbeek (1972) hypothesized that short-lived *Uta stansburiana* is more vulnerable to climate change than are *Sceloporus* lizards, due to potential decrease in reproductive opportunity with climate instability. As a reproducing individual accrues the highest energy demands, and foraging time decreases with rise in temperature, springtime temperature increases could be highly detrimental (Huey et al. 2010, Sinervo et al. 2010). Various Mexican lizard species, including *Sceloporus*, have recently gone extinct with similar shuttling behavior to avoid overheating (Sinervo et al 2010).

On a more local scale, winter mortality was not associated with temperature extremes, but with extended periods of snow cover (Tinkle 1967) or extended mild (warm) conditions in captive *Uta* (Zani 2008). Individual *Uta* will facultatively feed throughout the winter if temperatures are high enough (Tinkle 1967). In southern populations, thermal stress did not influence mortality, and drought conditions may actually increase survivorship by limiting predator activity (Wilson 1991). However, increase in midday temperature may force longer periods of inactivity (Zani 2008). Certain elements of lizard reproduction, such as clutch size, were not dependent on temperature, while increase in nighttime temperature accelerated development (Clarke and Zani 2011). Temperate species have greater flexibility of choice than do tropical species, which are exposed to relatively constant temperatures near their optimum in a comparatively stable environment. Thermoregulatory ability may not play a major role for these organisms (Deutsch et al. 2008). As *Uta* are flexible in timing of activity, both seasonally and across a day, it may be better able to adapt to fluctuating temperatures (Kearney et al. 2009). *Uta* populations seem adapted to local thermal microhabitats, as wood frogs appear to be (Freidenburg and Skelly 2004). The response to climate change, therefore, will undoubtedly be a complex and dynamic one, with a suite of impacting factors.

To gain an understanding of potential responses of an organism to climate changes, it is necessary to first understand its thermal environment and thermal behavior. Comprehensive studies examining these relationships are missing. The current study sought to describe the thermal complexity of microhabitats and the thermoregulatory ability of *Uta* during the hottest part of the year. A detailed map of temperatures was acquired with thermography and various temperatures were extracted from these images, including those of the environment, substrate (perch), and of the lizard. The breadth of these data allowed us to consider to what extent *Uta stansburiana* could thermoregulate and, then, to determine thermal preferences in context of the entire environmental range of temperatures available.

MATERIALS AND METHODS

Study organism and sampling

The common side-blotched lizard, *Uta stansburiana*, is a small terrestrial ectotherm ranging across the desert regions of western North America. Found in a variety of habitats, *Uta* are often one of the most common lizard species to be observed in an area. However, populations on Utah's Antelope

Island, located in the Great Salt Lake, are small and widely dispersed. The study population was on the northwestern tip of the island, around Buffalo Point. Within that area, lizards were found only in certain sections of available habitat. It remains unclear why lizards did not inhabit adjacent habitat that appeared identical, although this patchiness is a pattern consistent across much of *Uta* range. Habitat consisted of isolated boulders of variable size, surrounded by grass, small bushes, and sunflowers (Fig. 1A, B). Boulders were at varying distances apart, ranging from ten cm from the adjacent rock to isolation of several meters. Individual lizards were fairly isolated from one another because each inhabited a separate “island” of rock.

Lizards ($n = 23$) were filmed on 19 days over a two-month period from July 9th through August 22nd, 2011. Throughout the study period, individuals were filmed at various times of day, ranging from 7:30 to 19:30. This time frame covered the full period of lizard activity.

Field sampling

Different areas of the habitat were visited on subsequent days, and lizards were located and filmed as they were encountered. Unless an individual had been filmed earlier, the next encountered lizard was chosen as the subject. The lizard was approached (to within half a meter) and filmed with an infrared camera for different lengths of time. Two distinct approaches were used to assess thermal preference. Individuals were either filmed for ten to twenty-five minute periods or a single lizard was followed for several hours. To simultaneously measure environmental and lizard temperature, lizards were filmed with an infrared camera (ThermaCAM® S65HS, FLIR Systems, Wilsonville, OR, USA) at either 10 fps or 0.1 fps. Care was taken to include the environment around the lizard in each frame, such that all available thermal niches around a lizard could be assessed.

Infrared camera thermal measurements allowed noninvasive observations on thermal behavior. Although lizards were not captured and marked, the selection of locations for recording ensured that multiple sampling of the same individual was avoided. There did not appear to be significant overlap of territories since home ranges were small and individuals moved only short distances.

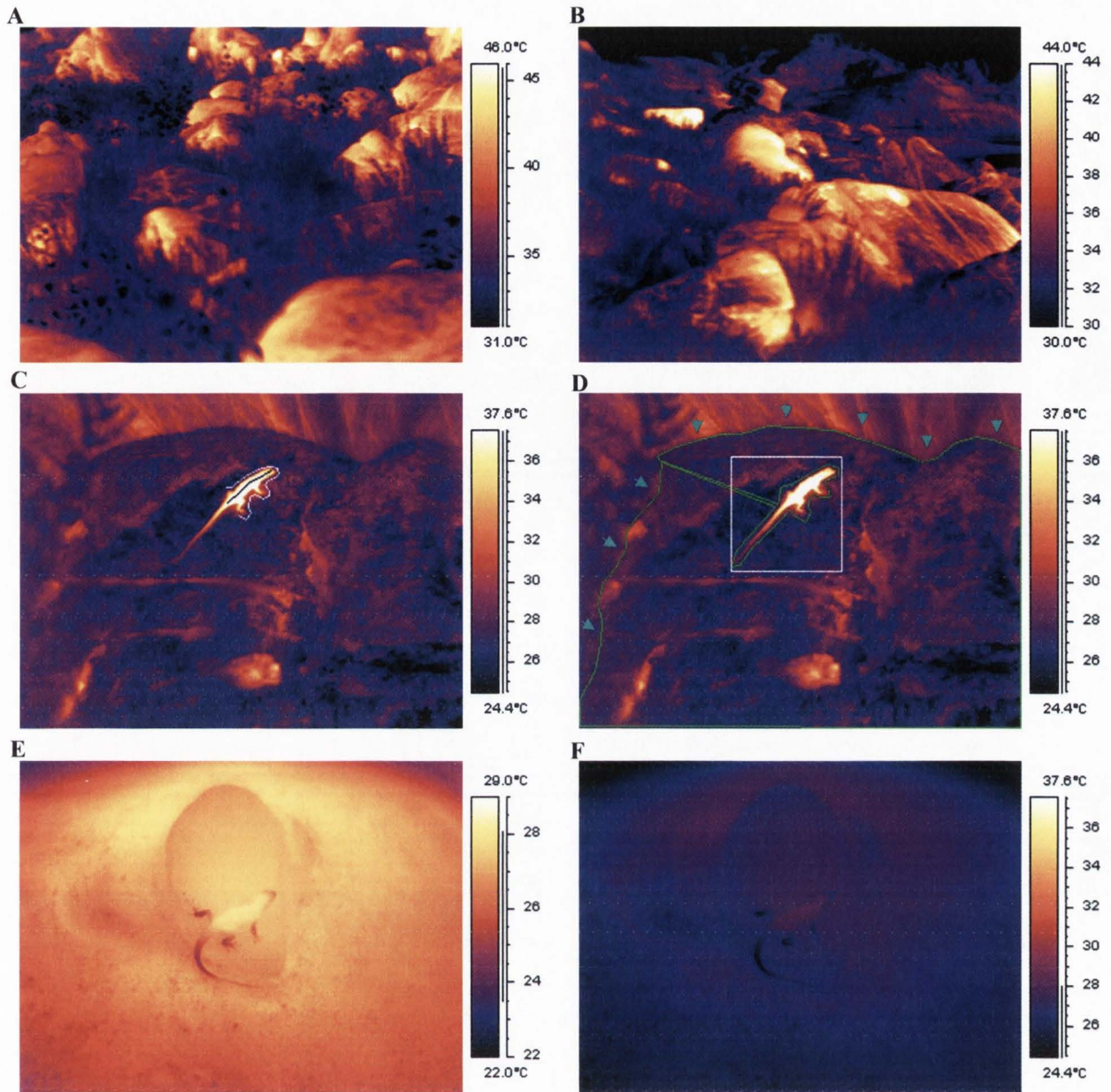


Figure 1. Thermograms of temperature microhabitats in the landscape (A-B), natural substrate including a lizard (C-D), and thermally more uniform laboratory setting (E-F). Both A and B show the overall habitat conditions (i.e., large scale) in the study area. ThermoCAM analysis is shown in C and D, as well as field microhabitat diversity. Measurement of lizard average temperature (line) and perch temperature (outline) is seen in C. Image D shows determination of maximum lizard temperature (box) and environmental maximum and minimum from the entire visible substrate available to the lizard. The rock surface comprises only part of the image (outline of the rock is indicated with arrows), and the distant background was excluded from the analysis. The homogeneous laboratory environment is shown on two temperature scales for comparison (E, F). In E, higher thermal resolution shows the range of temperatures across the body of the lizard. F is on the same temperature scale as C and D to demonstrate the lack of thermal diversity in the laboratory setting.

Analyses

Images were analyzed manually with ThermaCAM Researcher Professional 2.8 SR-1 (software accompanying the IR video camera, FLIR Systems) and various temperature measurements were taken in each frame: (1) environmental (substrate) maximum and minimum temperatures, (2) lizard mean and maximum temperatures, (3) range of lizard temperature, and (4) temperature of the section of rock upon which the lizard was sitting (perch temperature). Each frame consists of 32,000 individual temperature readings (each pixel), giving a high-resolution image of all microhabitat temperatures. Measurements from a total of 7,390 images were used in analysis. Environmental temperatures were measured by using the “draw” tool in ThermaCAM to enclose the entire visible substrate, excluding the lizard and additions (vegetation, sky; Fig. 1D). Thermal images quantified complexity of an individual’s territory by indicating all existing temperatures within microhabitats. The size of the focal area within an image varied following size differences in rock surface area. The area of the recorded substrate ranged from 100 cm² to 5,200 cm², based on estimates assuming an average snout-vent length of the depicted lizard of 50 mm.

Mean lizard temperatures were determined with the use of a line drawn down the center of the lizard, from snout to vent (Fig. 1C). Lizard maximum temperature was found by creating a box incorporating the entire lizard (if lizard temp was greater than that of perch; Fig. 1D). If the lizard was cooler than the substrate, the lizard mean line was reused for determining lizard maximum temperature. Perch temperatures were found by drawing a line around the lizard’s torso and head (Fig. 1C). The substrate beneath the tail was excluded from measurements.

Subset of measurements

A subset of 140 frames (several from each sequence, across all individuals) was used to determine mean environmental temperature and the standard deviation to assess environmental variability in more detail. These measurements - in addition to minimum and maximum temperature - were used to test whether lizards “select” perch temperature or whether the perch is selected indirectly based upon other criteria. In the latter case, perch temperature should reflect mean environmental temperature. To account for different variability in different recordings, we calculated z-scores using the standard deviation in pixel temperature for each frame. The difference between perch temperature and mean environmental temperature was then expressed relative to the standard

deviation, where a score of 1 was a difference of one standard deviation and a score of 0 was no difference between perch temperature and mean environmental temperature.

Comparison to traditional thermocouple cloacal sampling

To compare the non-contact body temperature measurements with thermocouple measurements of cloacal temperature in hand-held lizards, we performed laboratory measurements on fourteen captive male *Uta*. They were filmed in a controlled, laboratory setting with the thermal imaging camera on the afternoon of June 1, 2011. Each lizard was placed individually into an arena with a basking rock, sandy substrate, and a heat lamp (Fig. 1E, F). A representative example of the same image is shown twice to allow comparison with the image from the natural habitat. The laboratory setup produced highly uniform temperatures (as illustrated in Fig. 1F, at the same temperature scale as Fig. 1D). More detailed thermal variation is depicted in Fig. 1E, in which the laboratory setup is shown with a narrow temperature scale. Laboratory thermal conditions displayed much greater homogeneity than field habitats. After allowing for temperature equilibration in the arena (2 minutes), lizards were imaged for several seconds to allow determination of body temperature. The lizard was then removed from the arena by hand, and a thermocouple was inserted into the cloaca to determine body temperature. Cloacal temperature readings were obtained within two minutes after the lizard was caught in the arena. During this handling time the lizard was not exposed to the heat lamp, and this allowed us to assess how temperature may change in the time period required for a measurement of cloacal temperature.

Statistical analyses

Statistical analyses were performed using linear regression statistics in Sigma Plot (v. 8.2) and Kolmogorov Smirnov analyses were performed in SPSS.

RESULTS

1) Thermal microhabitat structural complexity

Lizards were found in environments characterized by high thermal heterogeneity. The landscape was a conglomeration of isolated rock “heat islands” separated by cooler vegetation (Fig. 1A, B). Larger areas therefore presented habitats with a broad temperature range, but even single rocks

typically also encompassed many different thermal microhabitats (Fig. 2). Rocks were large enough to provide many microhabitats on a single face. Most rocks were uneven, with fissures and protrusions, and vegetation growing near them creating additional thermal heterogeneity. Each rock therefore presented a different thermal microhabitat structure, which could dynamically change. Variability depended strongly on the presence or absence of direct solar radiation. Differing degrees of heterogeneity are illustrated by examples (Fig. 2) and by the overall statistics. The range of microhabitat temperatures surrounding a lizard varied from 1.3 to 37.7 °C, and the mean range (\pm 1 s.d.) was 10.93 ± 4.29 °C (Fig. 3). This range is positively related to maximal environmental temperature ($R^2 = 0.32$) and negatively with minimum environmental temperature ($R^2 = 0.073$) (Fig. 4), but these relationships leave a large portion of variation in temperature range unexplained, indicating that variation in the three-dimensional structure of the habitat and varying direct solar radiation must play important roles in generating thermal diversity.

2) Lizard thermoregulation

Lizard body temperature had the potential to vary widely across a large range of environmental temperatures at any given time (Fig. 5). Despite the broad range of environmental temperatures, overall lizard temperature was fairly constant. The mean lizard temperature across the entire data set was 37.2 ± 2.9 °C while mean maximum lizard temperature was 38.7 ± 3.1 °C. The mean range of temperature encompassed solely by the midline analysis (used for finding lizard temperature), was 2.2 °C (\pm 1.32). Maximum range in an individual's body temperature was 9 °C. Temperature of the extremities differed more clearly from that at the midline but was not measured systematically.

Mean lizard temperature varied much less than environmental temperature values (Fig. 6), indicating active or behavioral thermoregulation. Generally, lizard temperature was closer to maximum than minimum environmental temperature. The mean difference was 2.9 ± 3.8 and 8.0 ± 4.0 °C, respectively.

Lizard temperatures differed from perch temperature (mean difference of 2.6 ± 3.7 °C), indicating that individuals achieved a body temperature different from that of the chosen substrate (Fig. 7A). As average environmental temperature increased, lizard mean temperature approached perch temperature (Fig. 7B, $R^2 = 0.429$). Mean lizard average temperature also approached perch temperature as perch temperature increased (Fig. 7A, $R^2 = 0.529$). Average lizard body temperature

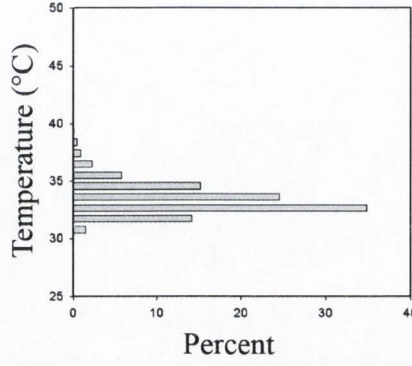
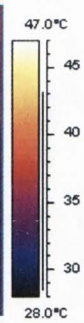
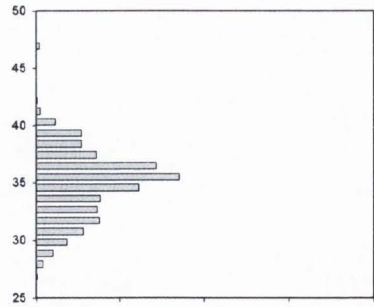
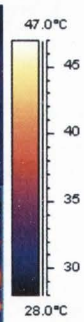
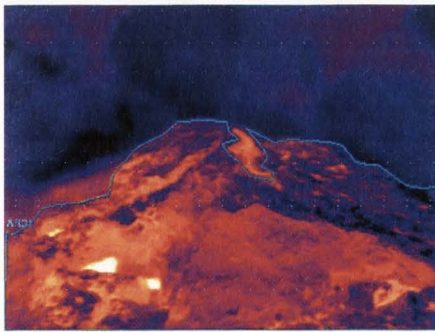
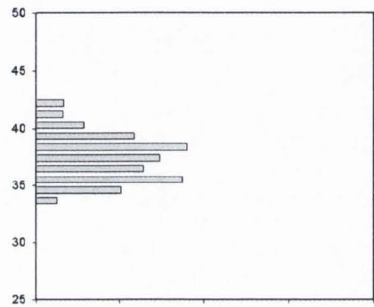
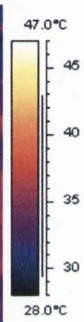
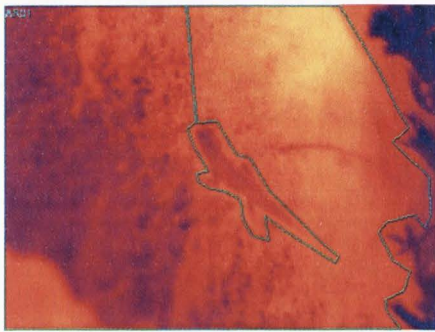
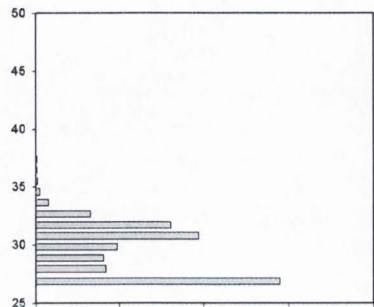
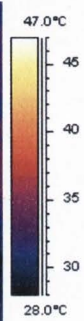
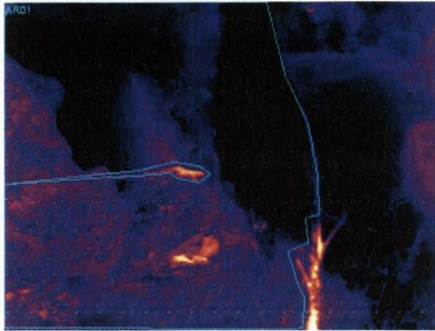
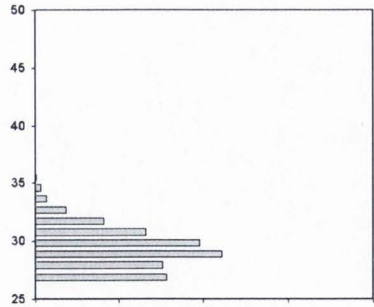
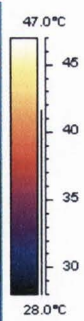
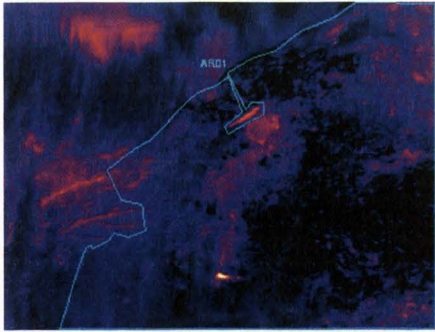


Figure 2. The thermal diversity of microhabitats and corresponding histograms of available rock temperatures within substrate surrounding different individuals. Histograms were constructed based on all pixels (measurements) within the areas drawn onto the images on the left. Temperature distributions varied within a typical range of 25 to 48 °C.

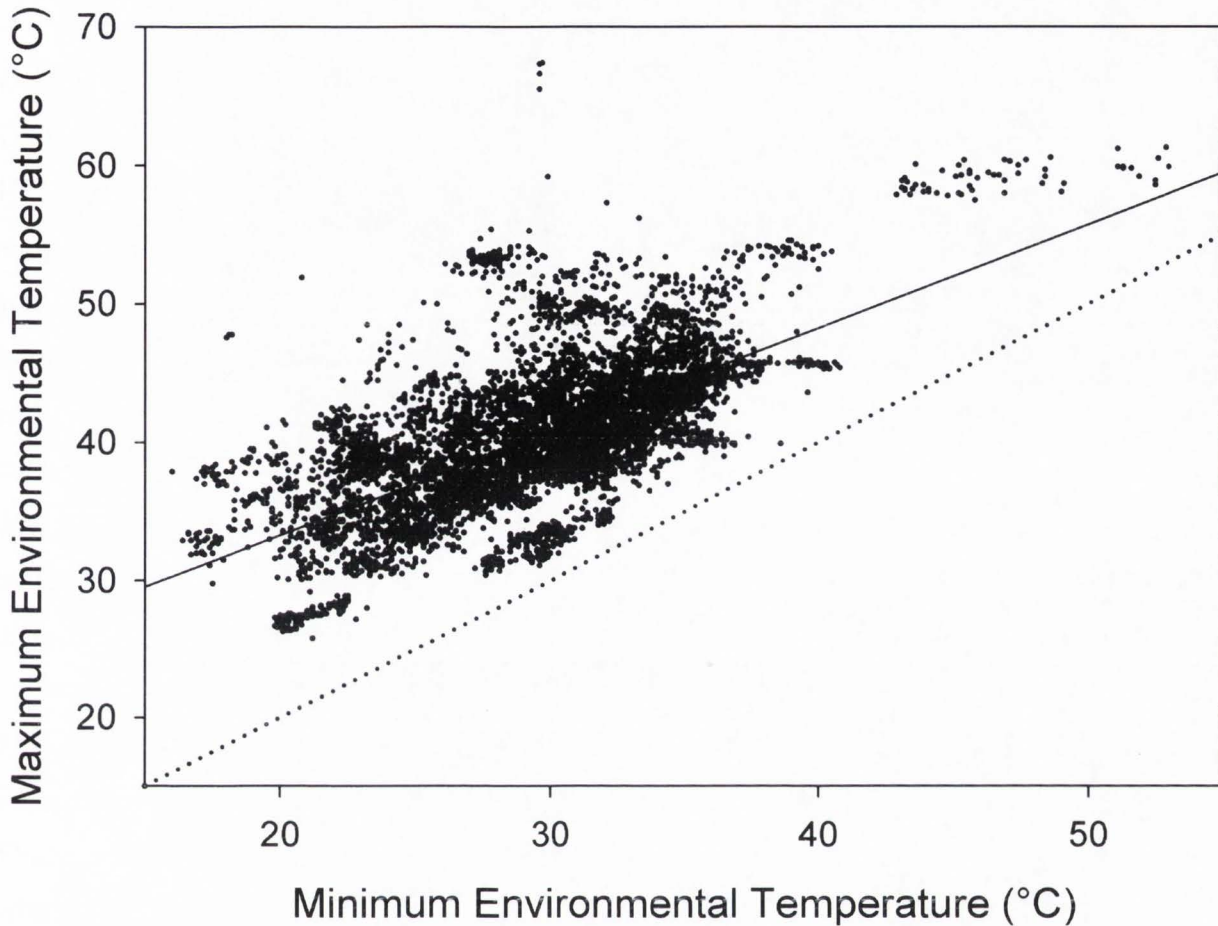


Figure 3. Scatter plot of minimum and maximum environmental temperatures with linear regression (dotted line is isothermal line for comparison). As minimum temperature increased, so did maximum temperature. Maximum temperature ranged from 25 to 60 °C and was almost 10° above minimum temperature at cooler temperatures. Minimum temperatures ranged from 15 to 55 °C. The two temperatures became more similar at high temperatures. The regression yields $\text{Max T} = 18.36 + 0.75 * \text{Min T}$; $F = 5086.2$; $P < 0.0001$; $R^2 = 0.41$.

was above perch temperature at lower substrate temperatures and below at high perch temperature (above 37 to 38 °C).

3) Seasonal variation

No clear seasonal trends were found in environmental temperature (both minimum and maximum)

between July and August (Fig. 8). Mean daytime ambient air temperatures remained fairly constant (around 31 °C), though three slightly cooler days had temperatures of approximately 27 °C. Temperature data were subsequently pooled for all days and used together for calculations and analysis.

4) *Daily variation*

Temperatures across the study period were pooled and graphed over time of day, from 07:00 to 19:30 (Fig. 9A). Environmental temperatures increased throughout most of the day, and maximum temperature peaked at 18:00, after which it decreased again. Perch temperature also increased across time, stabilizing after 16:30. Lizard average temperature increased markedly throughout the morning and then remained relatively stable for the rest of the day (Fig. 9A). This drastic change early in the morning is likely caused by the arising opportunity for direct sun exposure on the rock face. Slopes for environmental temperature variables all rise significantly over the course of the day, but that for lizard temperature remains flat (Fig. 9B), indicating substantial thermoregulation by the lizard. This thermoregulatory ability is also illustrated by the daily trend in decreasing difference between perch temperature and lizard temperature (Fig. 10).

5) *Perch temperature*

Perch temperature was close to mean environmental temperature, but different in significant ways. Three approaches were used to investigate whether perch temperature was a random selection or whether individual lizards chose specific temperatures. The mean difference between perch and environment was 0.36 °C, and, although this difference was small, was significant (paired t-test $p = 0.02$). A linear regression of perch temperature over mean environmental temperature showed a close relationship but its slope of 0.897 is significantly different from 1 (Fig. 11A, $p < 0.0001$). Furthermore, this relationship (perch temperature = $3.97 + 0.897 * \text{mean environmental temperature}$) explains 85.5% of the variation in perch temperature. For example, when mean environmental temperature = 25, perch temperature = 26.4; when mean environmental temperature = 45, perch temperature = 44.3 °C. The residual 14.5% of the variation was not significantly correlated to any other temperature variables.

In a third approach, we used the variable standard deviation of environmental temperature (calculated as the standard deviation of each pixel measurement in the environment) to standardize

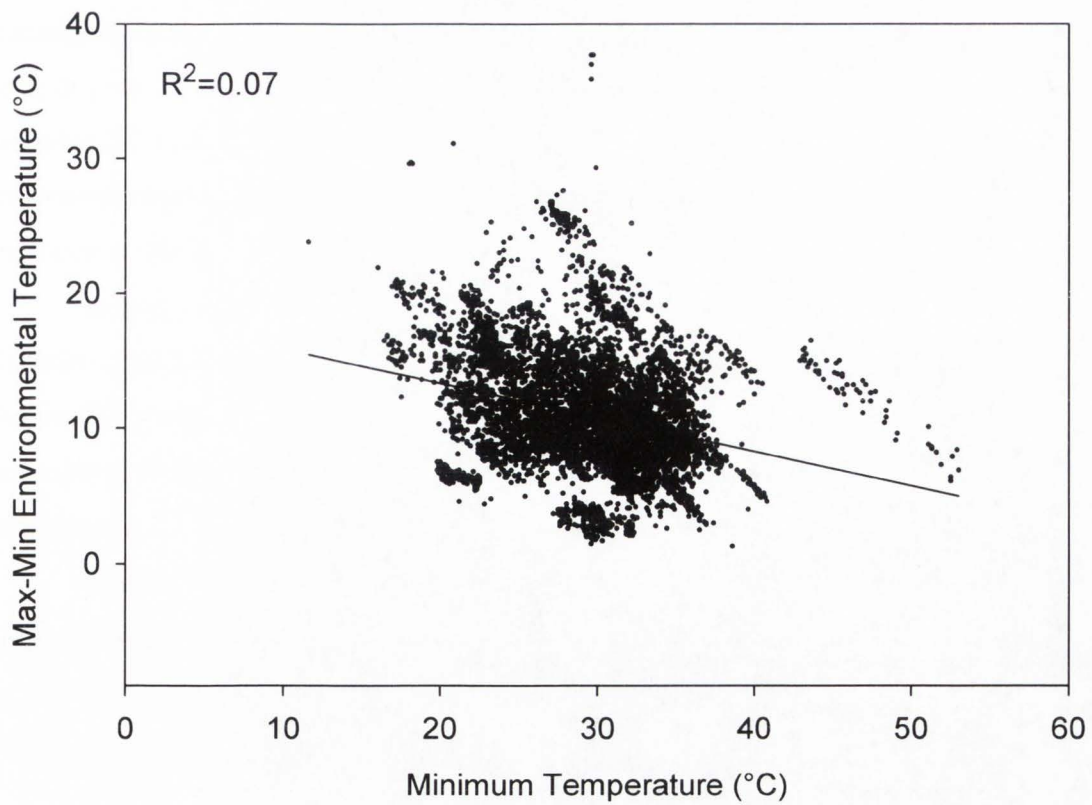
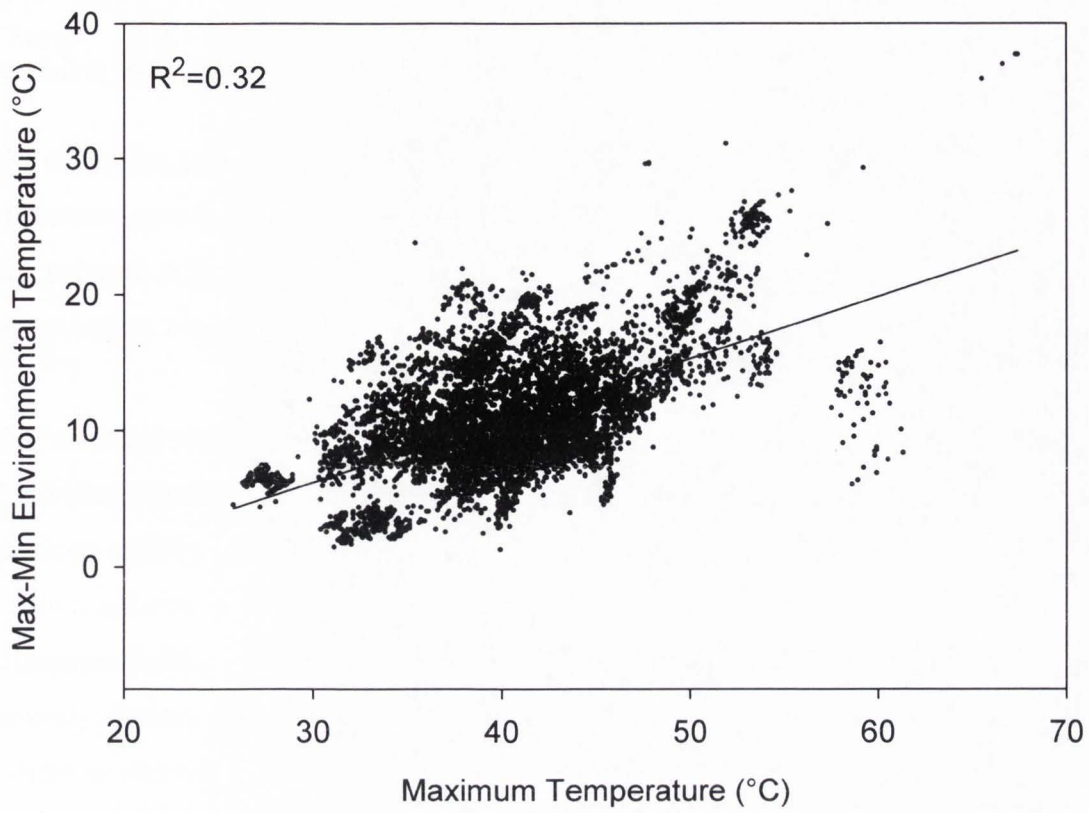


Figure 4. Maximum and minimum environmental temperatures plotted against the range of environmental (available) temperature. Range varied from 5 to 20°, increased with maximum temperature (Range = $-7.4 + 0.45 * \text{max T}$; $F = 3529$; $P < 0.0001$; $R^2 = 0.32$) and decreased with increasing minimum temperature (Range = $18.36 - 0.25 * \text{Min T}$; $F = 579.0$; $P < 0.0001$; $R^2 = 0.07$). Change in maximum temperature explained more of the observed variation in range than did change in minimum temperature.

the difference between mean environmental temperature and perch temperature (i.e., expressed the difference as x-fold of the standard deviation, i.e., a z-score). The distribution of the perch temperature differed significantly (Kolmogorov Smirnov; $p = 0.001$) from the distribution of mean environment temperatures (Fig. 11B).

6) *Positional switches*

Individuals spent substantial periods of time sitting in one area. Other activities included shifting position slightly (while remaining in the same area and temperature) or moving larger distances (onto a different portion of the same rock or onto a new rock altogether). Occasionally a lizard disappeared into adjacent vegetation to either emerge after several minutes or remain hidden entirely. During the observation periods, individuals rarely engaged in active foraging activity, where an individual jumped into the vegetation, grabbed an arthropod, and returned to sitting. Individuals were dispersed widely across the area and home ranges did not seem to overlap. As a consequence, no intraspecific interactions were observed. Two lizards were observed on the same rock only once. Several individuals observed in July engaged in push-ups (or head-bobs) and tail-waggles (22 and 4, respectively) but no other lizards were on the rock at the time of behavior. Any movement of position associated with these territorial behaviors (17 moves and 8 shifts) was not included in the analysis of switches of perch.

A total number of 434 switches between basking spots on the rock, either over short or long distances, were documented. In total, focal lizards moved 295 times and shifted position 139 times. Perch and lizard average temperature were graphed as before/after for both categories (Fig. 12). The cumulative distribution of change in perch temperature was broader than that of lizard body temperature.

Lizards with a lower body temperature tended to grow warmer upon moving, and vice versa (Fig. 12A). The trend line illustrates a difference between before and after mean lizard temperature of 2 to -2 °C. However, there was a lot of variance in differences between the two temperatures. Furthermore, this trend in temperature change only accounted for 15% ($R^2 = 0.15$) of the variation

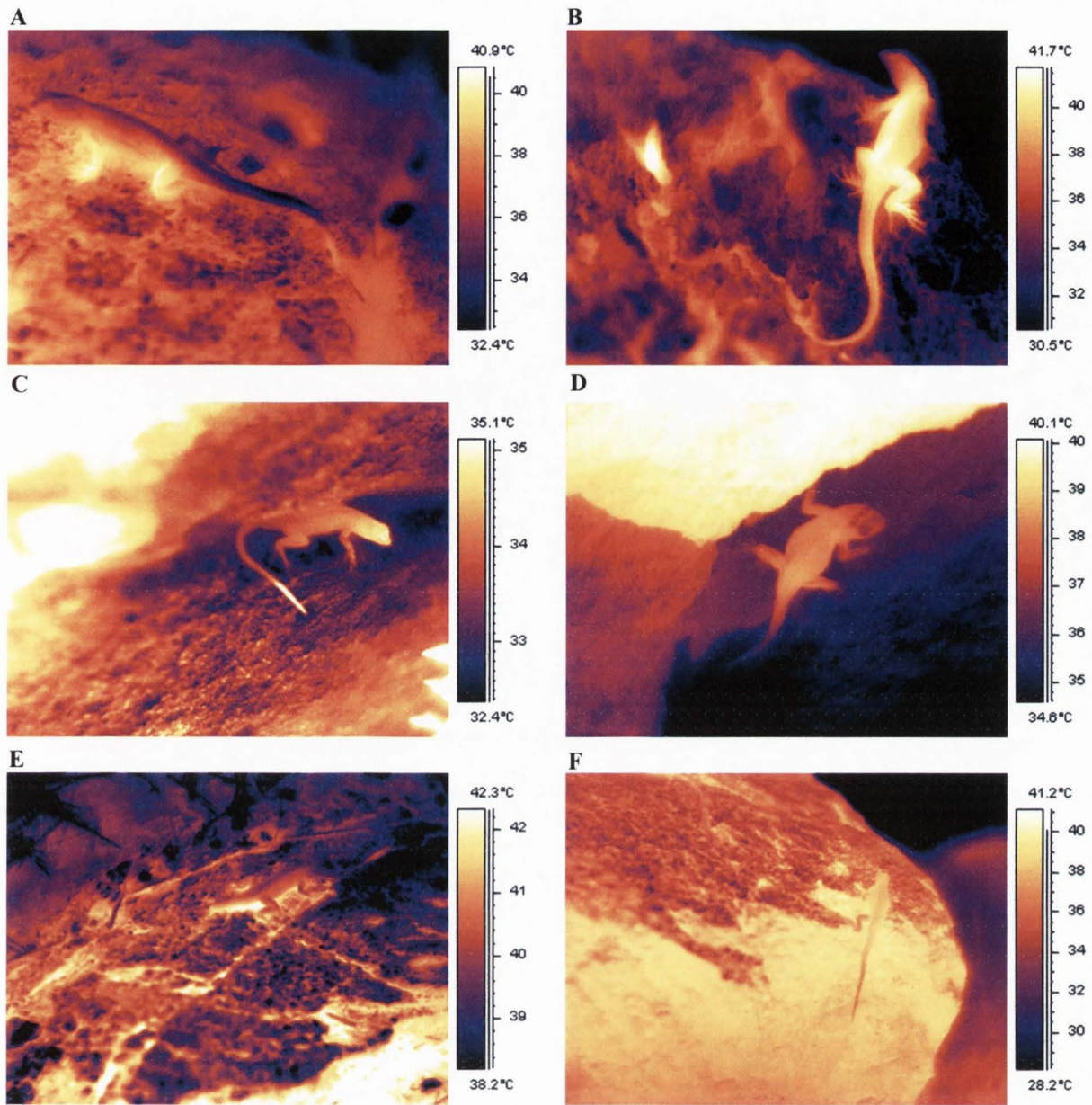


Figure 5. Thermograms of the variability in lizard body temperature and preferred substrate temperatures. Temperature across the body (length axis and extremities) of an individual could vary significantly (A, C, E) or remain largely uniform (B, F). The lizard in A had decreased contact with the substrate by pushing itself up and raising its tail, leaving its legs much warmer. In B, C, and D, temperature of the lizard's head differed from the rest of its body. The lizard in E was pressed against the substrate and the temperature of its head and tail tip approached that of the substrate.

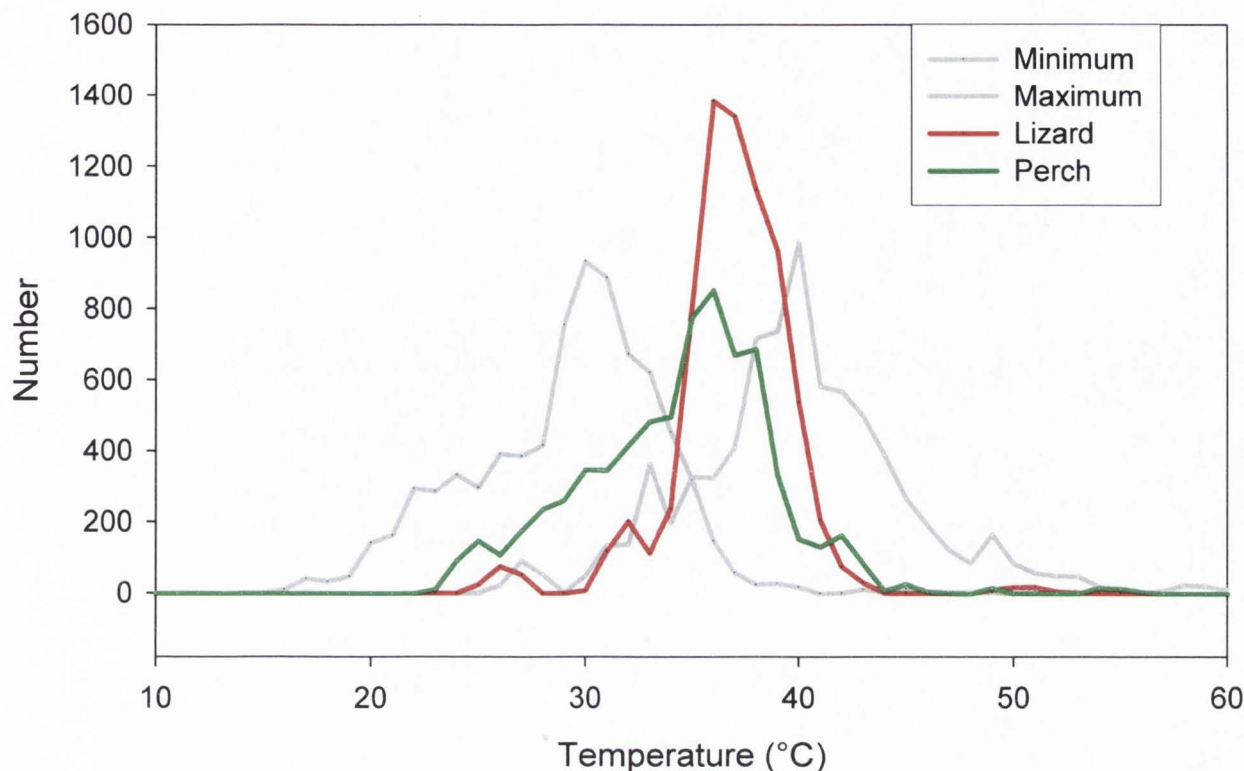


Figure 6. Histograms showing the distribution of three environmental temperatures (perch, maximum environmental, and minimum environmental) and mean lizard body temperature. Lizard body temperature had the narrowest range, with a pronounced peak at 36 to 38 °C, and was closer to maximum than to minimum temperature. The three environmental variables had similar scopes, with a minimum temperature of 30° and a maximum temperature of 40° being most common. Perch temperatures of 35 to 38 °C were most frequent, with number decreasing sharply at temperatures above and a skew toward lower temperatures.

in average lizard temperature. The variability in temperature change after a lizard moved was greater than it was after a shift in position (Fig. 13). Altering position did not play an important role in determining a lizard's temperature.

Although many switches in position were documented across the study period, there were also instances in which an individual did not move for long periods of time, ranging from 10 to 100 minutes. Lizard body temperature fluctuated even during periods of immobility.

7) Temporal temperature dynamics

Temperatures could fluctuate over the course of a minute as solar radiation changed due to cloud cover or shading (Fig. 14). Although the environment fluctuated, lizard body temperature changed much less, indicating that behavioral thermoregulation buffered the changes in environmental

temperature. A detailed analysis of the timing of temperature changes is beyond the scope of this paper.

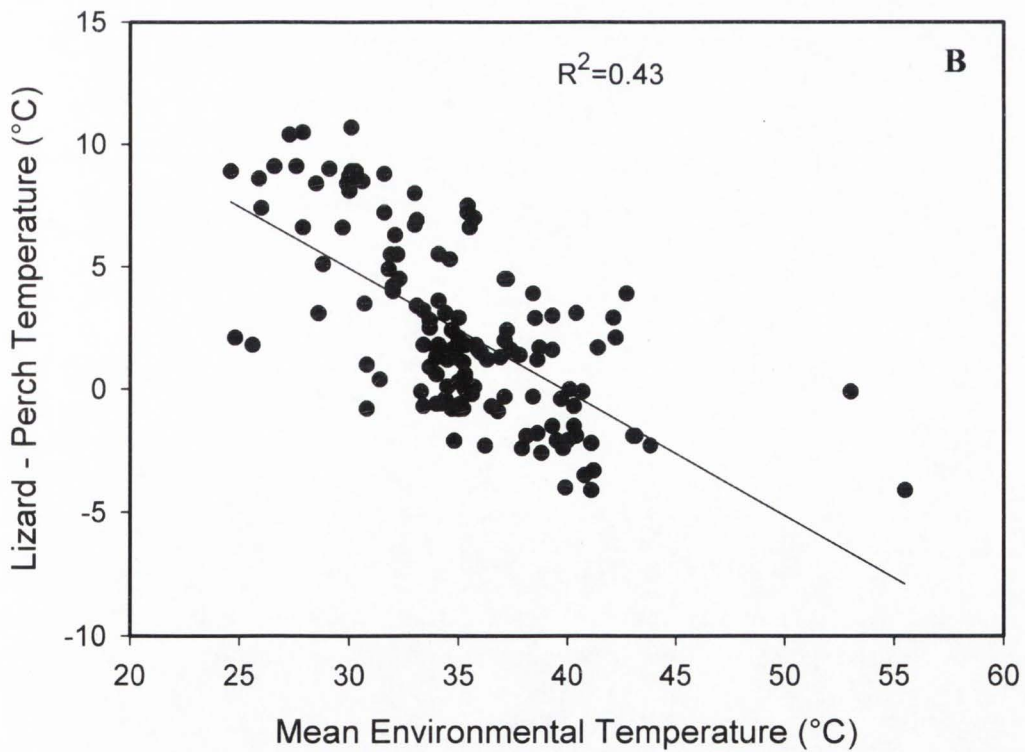
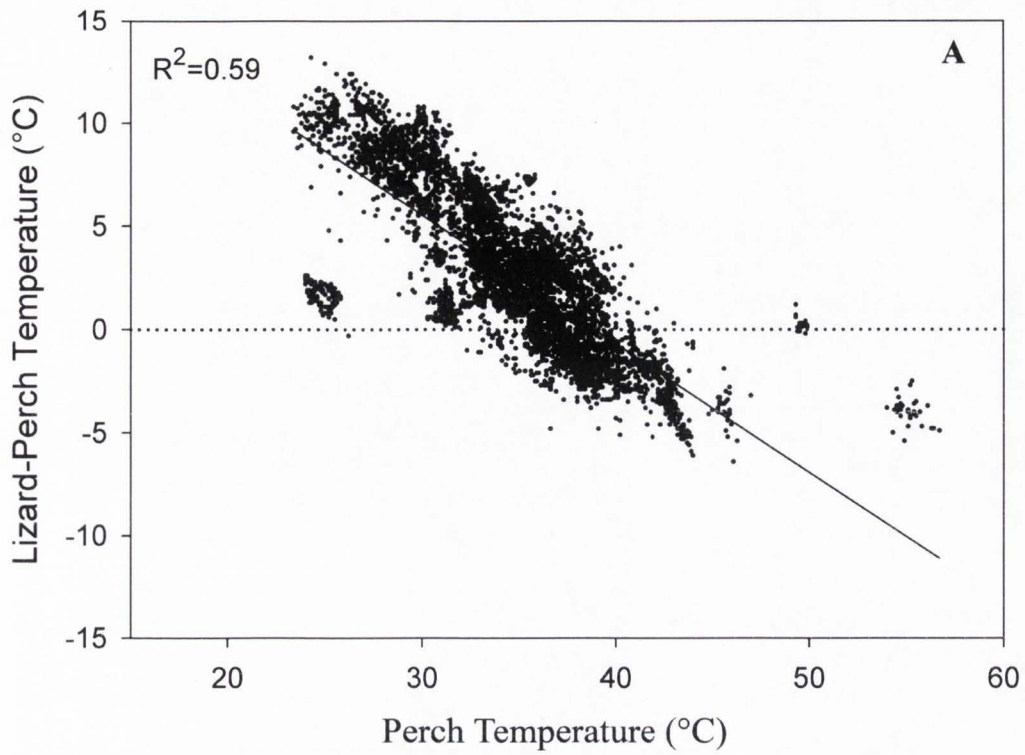


Figure 7. A. Perch temperature plotted against the difference between lizard mean body temperature and perch temperature. Individual lizard temperature differed from that of the chosen substrate (perch), with temperatures above perch at low perch temperature and temperatures below perch at high perch temperature. Average body and perch temperatures grew more similar as perch temperature increased. Regression equation: Lizard-Perch T = 24.23 - 0.62 * Perch T; F = 9628; P < 0.0001).
 B. The difference between lizard and perch temperature decreases with increasing mean environmental temperature (of the subset). Around environmental temperatures of 40 °C, lizard temperature is below that of the perch. Regression equation: Lizard-Perch T = 20.02 - 0.5 * Mean Env T; F = 102.3; P < 0.0001).

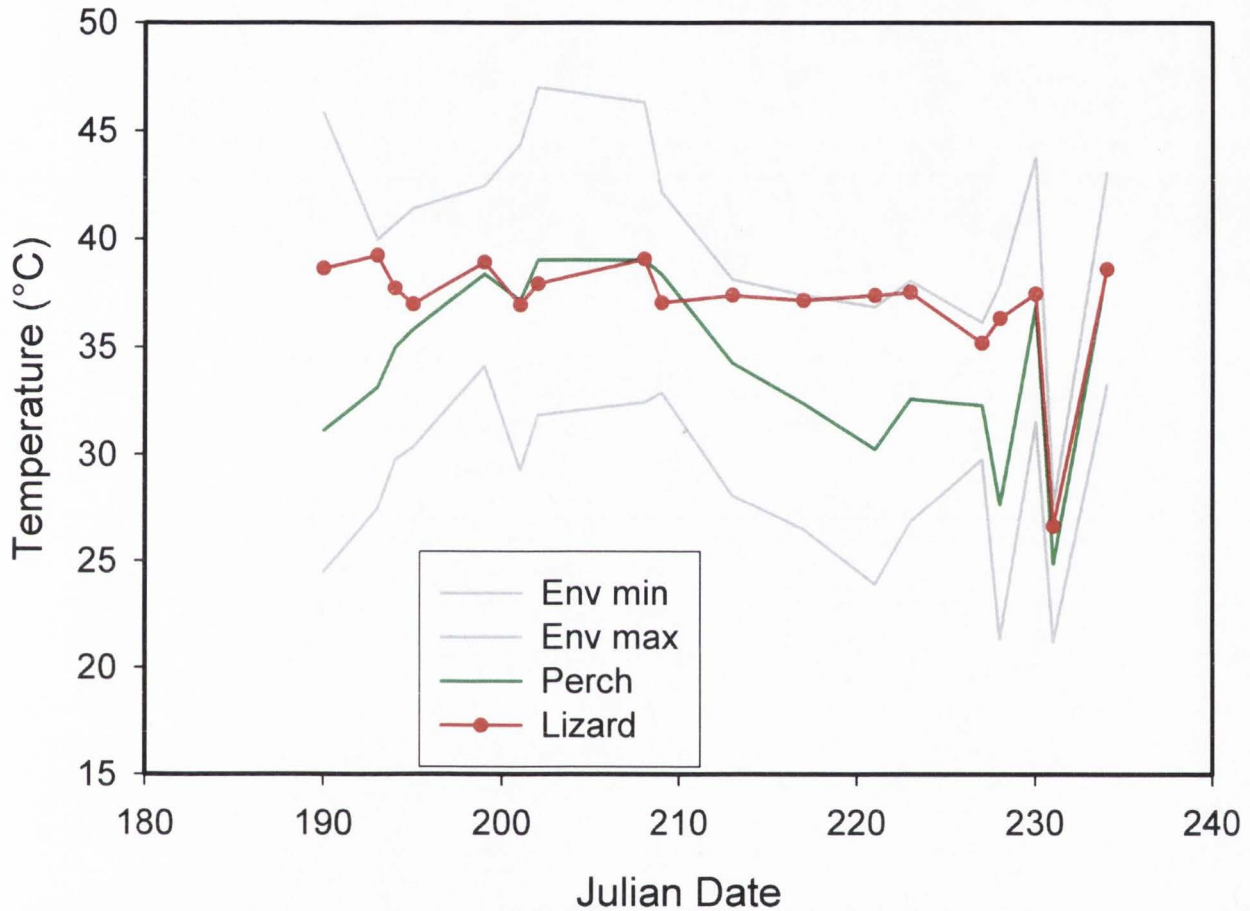


Figure 8. Changes in environmental (minimum, maximum, perch) and mean lizard body temperatures across the study period. There were no significant trends within July or August, and no clear differences between the two months. As environmental temperatures fluctuated, lizard temperature remained fairly constant (around 37°). Perch temperatures were above lizard temperature at the end of July but remained below body temperature for all other days.

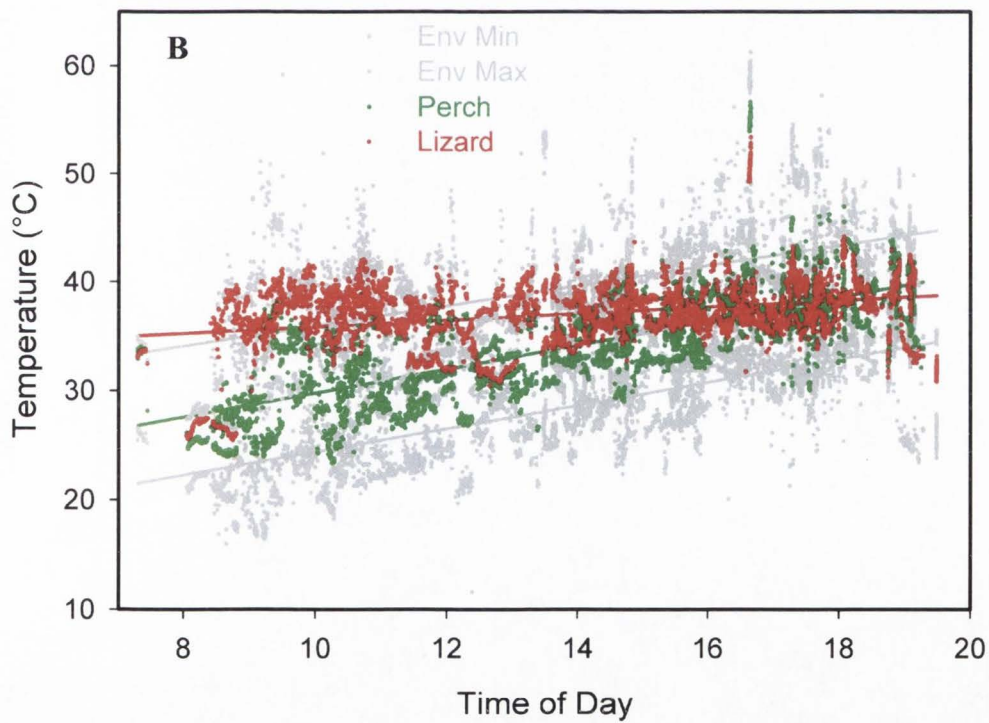
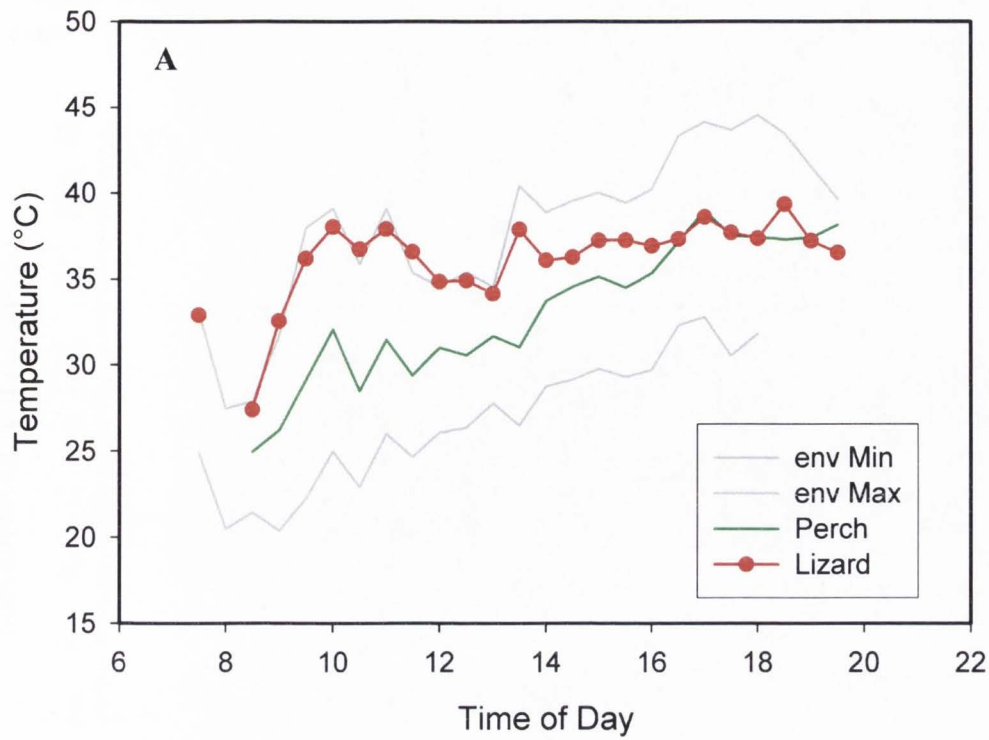


Figure 9. Temperature dynamics as a function of time of day, graphed as average temperature for every 30-minute period (A) and all data points (B). Average lizard body temperature increased early in the morning

and then quickly stabilized for the rest of the day. The slope of environmental variables (B) is much steeper than that of body temperature. Lizard T: slope = 0.3, $R^2 = 0.1$; Min Env T: slope = 1.07; $R^2 = 0.51$; Max Env T: slope = 0.93; $R^2 = 0.29$; Perch T: slope = 1.1; $R^2 = 0.54$.

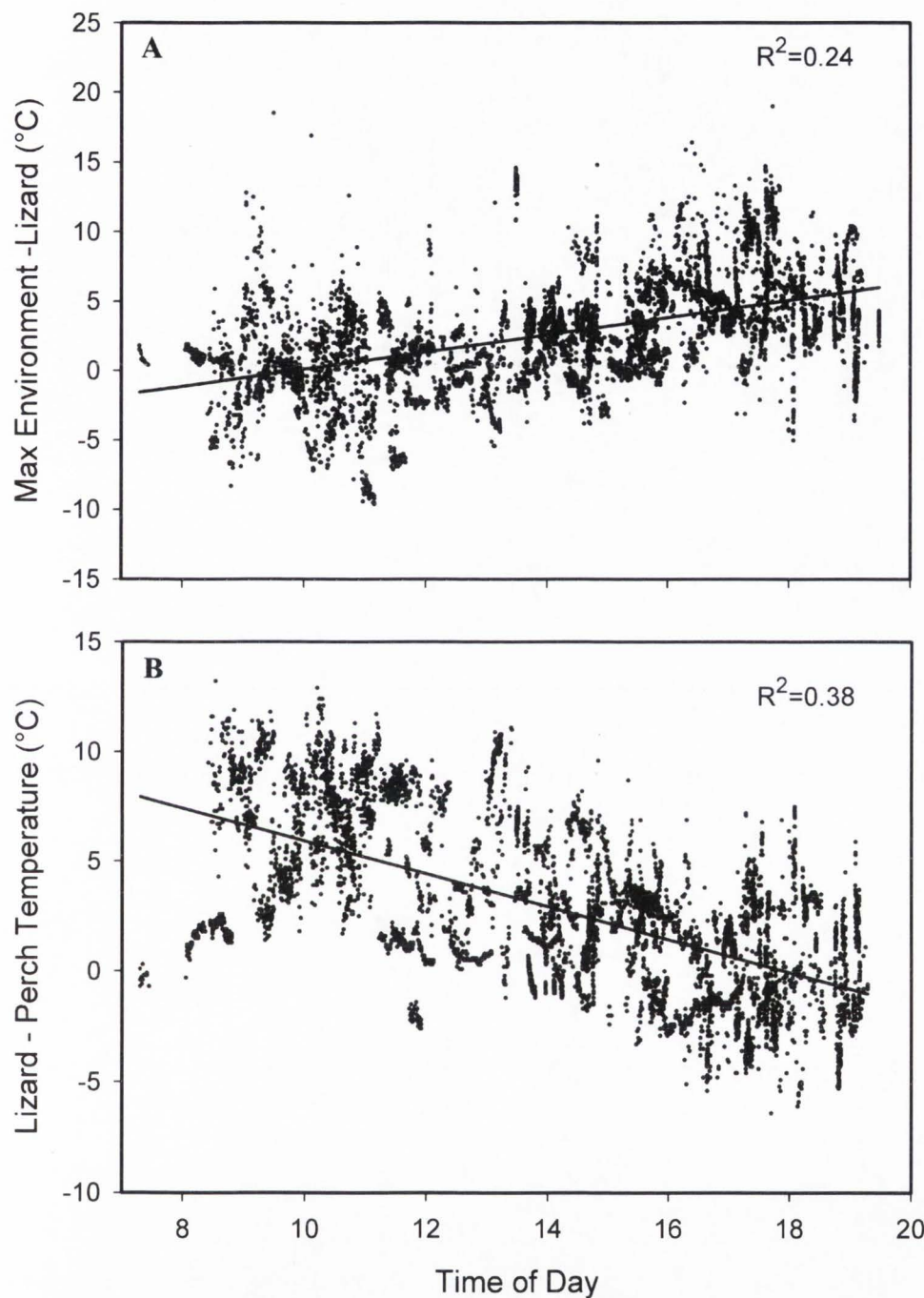


Figure 10. Daily trends of the differences between environmental maximum temperature and lizard body temperature (A), and between lizard and perch temperature (B). As time progresses, maximum temperature grows increasingly different from body temperature ($R^2 = 0.24$). Lizard body temperature was higher than perch temperature in the morning and became increasingly similar throughout the day ($R^2 = 0.38$).

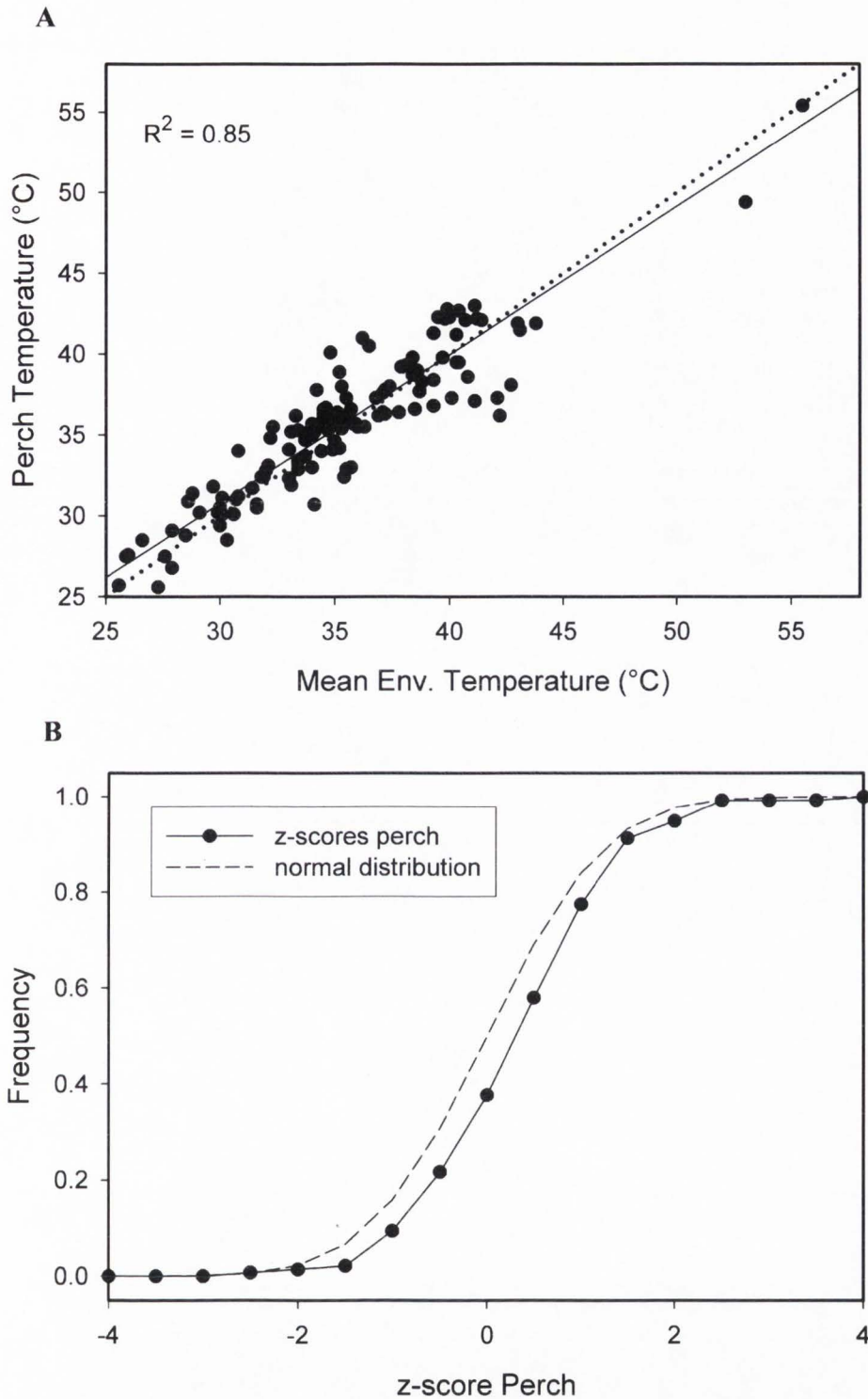


Figure 11. A. Mean environmental temperature (of the subset) plotted against perch temperature. Perch temperature had a strong positive correlation with mean environmental temperature (equation: Perch T = $3.97 + 0.897 * \text{Env T}$; $F = 803.0$; $p < 0.0001$; slope is significant at $p < 0.0001$; intercept at $p < 0.006$; $R^2 = 0.85$). B. Distribution of the differences between perch and mean environmental temperature expressed as z-scores (x-fold standard deviation of environmental temperatures of each frame of the subset) compared to a

normal distribution. The distribution of z-scores differed significantly from that of a normal distribution (Kolmogorov Smirnov, $D = 0.174$, $p = 0.001$), indicating selection of perch temperature.

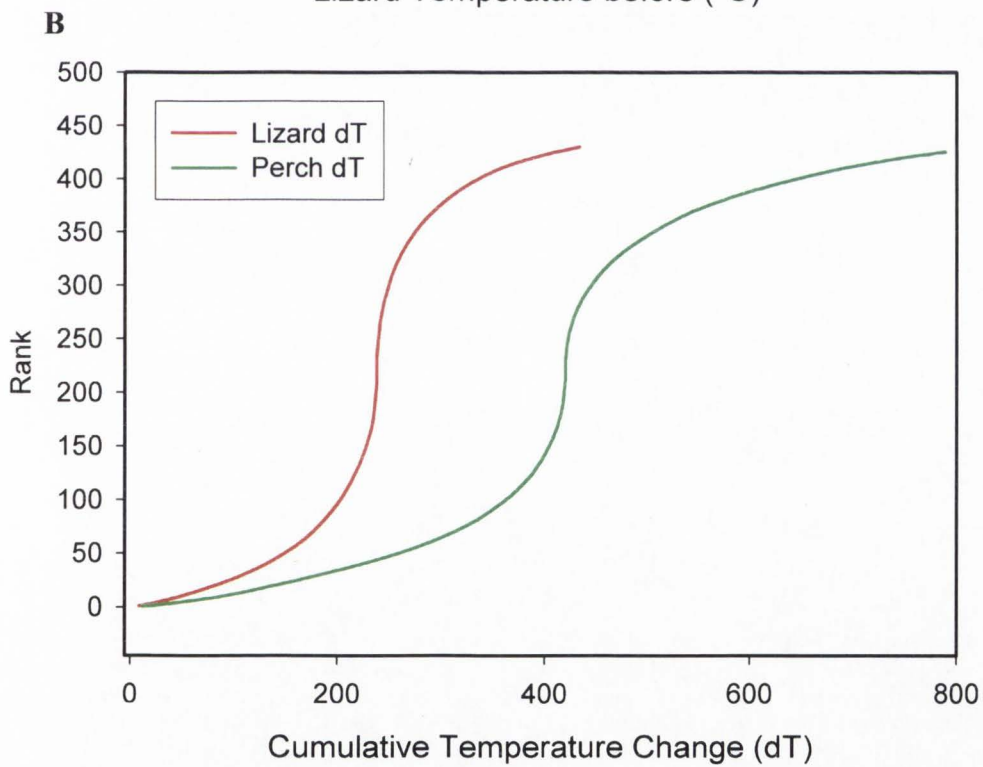
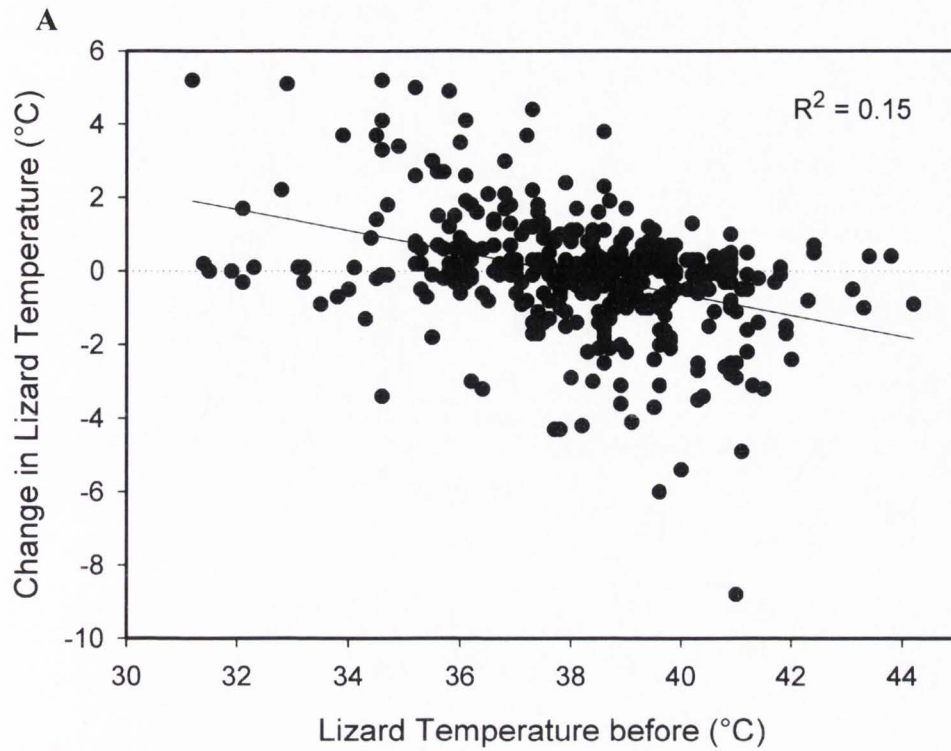


Figure 12. A. Lizard mean body temperature before the switch in position plotted against the change in body temperature (body temperature after – body temperature before). Lizards with high body temperature before moving tended to have a slight decrease in temperature after moving, and vice versa. Lizards with a body temperature of 38 °C did not have a change in temperature upon moving. B. Cumulative distributions of perch and lizard body temperatures illustrate the broader distribution of perch temperature change.

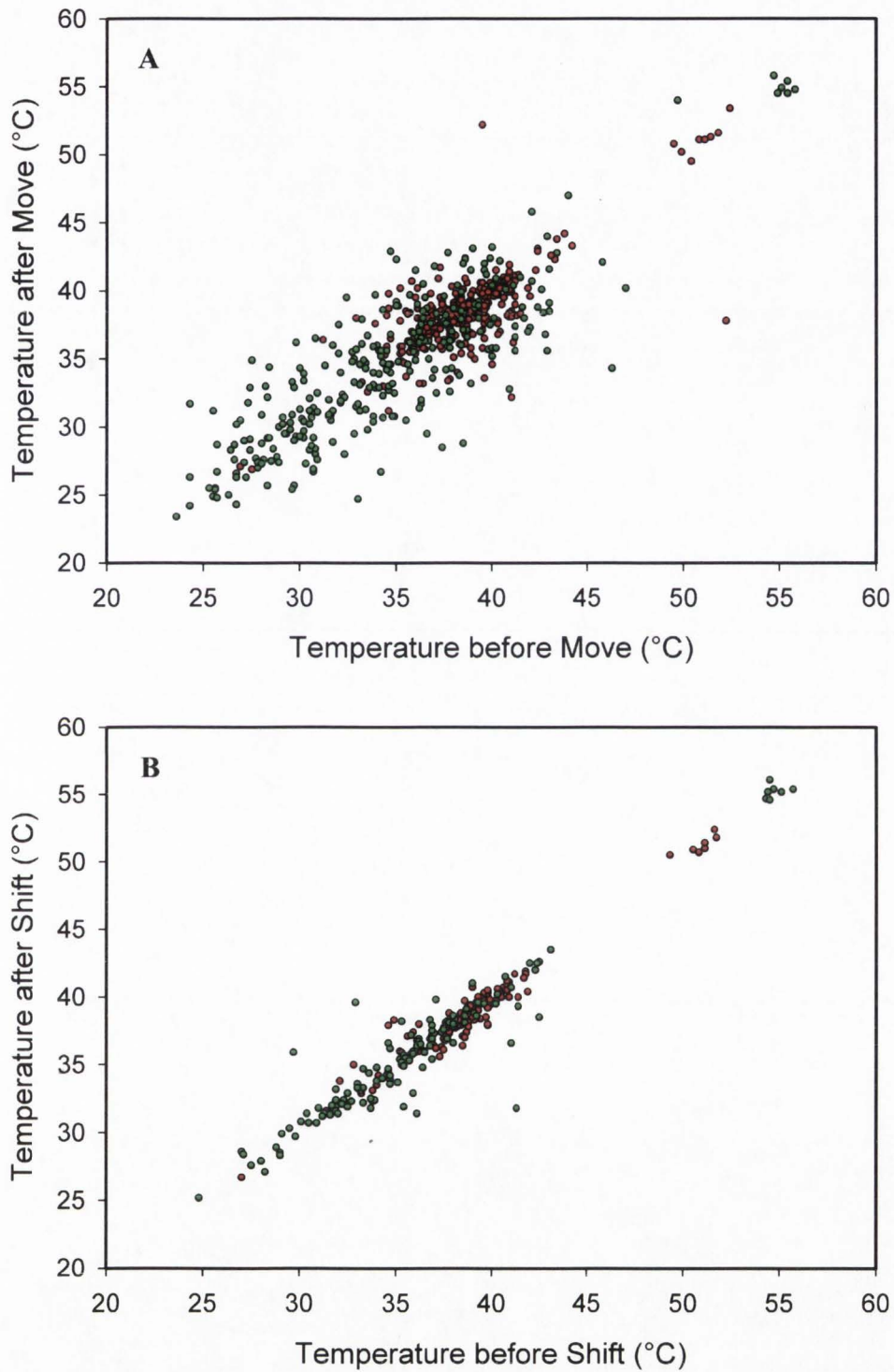


Figure 13. Relationship between before switch and after switch body temperature (red) and perch temperature (green) of selected switches. Moving to a new location (A) resulted in greater variation in body and perch temperatures than when individuals only shifted position slightly (B). Both datasets demonstrate that lizard body temperatures tended to be higher than perch temperature.

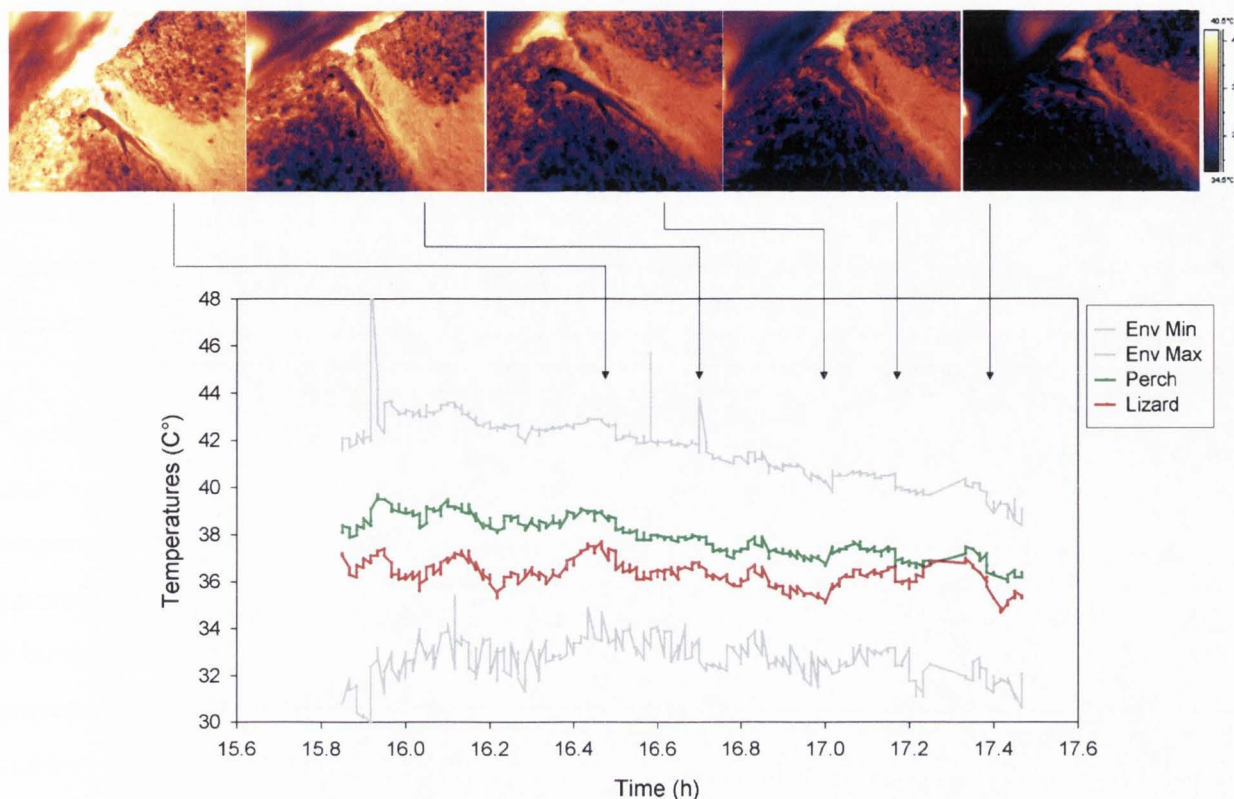


Figure 14. Temporal dynamics of mean lizard body temperature, of an individual, and environmental temperature. Changes in the four variables are graphed as a function of time. The sequence of thermograms documents change in microhabitat temperature over a period of inactivity (in which no switches occurred).

8) Comparison with traditional temperature measurement

Body temperatures measured in the lab with a cloacal thermometer differed significantly from those measured by ThermaCAM software (paired Student's t-test; $p < 0.0001$). Differences between infrared and thermocouple temperature readings ranged from 0.5 to 5.3 °C. Cloacal temperature was always lower than lizard exterior temperature. When taking cloacal readings, lizards were removed from the heat lamp and held in the hand. Readings took a variable amount of time (up to several minutes), during which body temperature would have been decreasing. Furthermore, the difference between the two readings varied largely even when repeatedly measuring the same individual's temperature. ThermaCAM measurements appear to be more precise than traditional cloacal

measurements. However, there may be real biologically important differences between core versus surface measurements due to radiative heat gain.

DISCUSSION

The goal of this study was to relate body temperature of *Uta* to the thermal mosaic of its habitat. The results show remarkable variation in environmental temperature within the habitat both in a space and over time. Despite this variation, *Uta* effectively regulated body temperature through behavioral thermoregulation. In the following, the nature of this behavioral thermoregulation will be discussed in relation to its physiological and ecological importance.

Thermoregulation in a heterogeneous environment

Little variation in mean body temperature in the face of broad shifts in available microhabitat temperatures is seen as evidence of behavioral thermoregulation (Adolph 1990, Huey 1982). *Uta* maintained an average body temperature of 37 °C in environments that varied broadly with a mean difference between minimum and maximum temperatures of at least 10 °C and mean environmental temperatures spanning a range of 20 °C. The maximum temperature within the environment accounted for more of the variation in the environmental range than the minimum, which suggests that patterns of solar radiation on the structured microhabitat are largely responsible for determining the range. This heterogeneity produced by solar radiation and the microstructure of the habitat creates the basis for effective behavioral thermoregulation.

Uta, like other lizards (e.g., *Sceloporus* species; Adolph and Porter 1993), makes use of the heterogeneous thermal environment and solar radiation to regulate body temperature, whereas other species do not seem to regulate as closely (Huey 1982). Although typically *Uta* body temperature was somewhat below the maximum environmental temperature in its close vicinity, occasionally a lizard could achieve body temperatures that exceeded that of the environment. Lizard body temperature was routinely significantly above or below the perch temperature. The most likely explanation for these differential temperatures is that lizards, by being elevated above the substrate, could either gain more heat through solar radiation than the underlying substrate or lose heat to a cooler air.

Uta demonstrated a clear preference for a narrow range of body temperature (from 36 to 38 °C). This range is slightly higher than that of 34 to 36 °C favored by the larger *Sceloporus* species (Adolph 1990). Thermal selectivity in some species is less precise, as demonstrated by the lack of a strong preference in geckos within the range 26 to 33 °C (Vance 1973), whereas other tropical species show more specific preference (e.g., iguanas, *Conolophus pallidus*, Wilhoft 1958) as do many other species (e.g., common lizard, *Zootoca vivipara*, Herczeg et al. 2006; garter snakes, *Thamnophis elegans*, Huey 1991, Peterson 1987).

The microstructure in the habitat also results in diverging temperatures of different body parts of the lizards. The difference between maximum and minimum temperatures across the body of a lizard was up to 9 °C with a mean of 2.2 °C. This variation probably results from the fact that the surface area of the lizard or extremities could be exposed to differing surface temperatures and to differential solar radiation.

Thermoregulation and perch selection

Within this range of available environmental temperatures, lizards selected a perch temperature that differed from the preferred body temperature (37 °C) by only a few degrees. Perch temperature was also close to the mean temperature of the thermography image of the habitat. It is therefore of interest to evaluate whether or not the temperature or the perch plays a role in where the lizard chooses to sit.

Perch temperature was similar to, yet significantly different from, mean environmental temperature. Active selection of perch temperature is suggested by several findings. First, temperature varied widely even within very small areas of substrate. Although mean environmental temperature may be close to perch temperature, patches of mean temperature may be small and randomly distributed across the monitored surface. Without understanding the complex nature of the substrate, the close relationship between mean environmental and perch temperatures could be misconstrued as an indication of thermo-conformity. Furthermore, perch temperature may deviate as much as ± 6 °C from mean environmental temperature.

Second, though the linear relationship with environmental temperatures explains 85.5% of the variation in perch temperature (Fig. 11A), 15% are unexplained. The fact that these residuals were found not to correlate with other variables, such as time of day, lizard body temperature, and

so on, is indicative of further thermoregulation through an unknown mechanism. Further research is necessary to understand this aspect of thermoregulation.

Third, the distribution of z-scores confirms that perch temperature significantly deviates from the expected normal distribution, supporting the interpretation that the temperature plays a role in why a particular perch is chosen. Of course, choice of perch also must accommodate other important needs such as protection from predation, opportunity to observe, etc...

Further evidence that temperature plays a role in perch selection can be derived from the lizards' movements between perches. The difference in perch temperature before and after a move was substantially greater than the change in lizard body temperature. The ability to maintain body temperature after the change of perch suggests strongly that thermoregulation played a role in the selection of the new perch.

Temporal dynamics of temperature

During the two-month observation period, overall environmental temperature conditions did not show a seasonal trend. However, weather conditions did result in large fluctuations from day to day or hour to hour. Lizards were able to maintain a fairly stable body temperature throughout these conditions.

Similarly, *Uta* showed remarkably stable body temperatures, with the exception of the early morning hour, despite a diurnal trend toward warmer environmental temperatures. The fact that lizard temperature was lower in the morning is most likely caused by less availability of direct solar radiation to elevate temperature above that of the environment.

On a shorter time scale, the time series data reveal that environmental temperature profiles on rock substrate can change rapidly. As expected, cloud cover and resulting changes in solar radiation as well as orientation of crevices with respect to the sun can cause fairly rapid and substantial temperature changes. Lizard temperature, however, remained more stable relative to environmental temperature fluctuations. Dynamic changes in an individual lizard's body temperature over time and the corresponding changes in environmental variables will appear elsewhere.

Why does Uta stansburiana prefer 37 °C?

For many species, optimization of physiological processes occurs within a narrow temperature

range that corresponds to preferred body temperature (Blouin-Demers and Nadeau 2005, Huey 1982, Angilletta et al. 2002). Mean body temperature of active *Uta* is constant across its entire geographic range (Parker and Pianka 1975) and this constancy in preferred temperature may confer a number of advantages. Waldschmidt and Tracy (1983) found that *Uta* have the highest sprint speeds at body temperatures between 35 and 38 °C. Peak in activity occurred at body temperatures between 36 and 38 °C (Tinkle 1967), and may allow individuals to be more active while limiting danger of predation. This coincidence between locomotor performance and chosen temperature is, however, not ubiquitous. Some species of Australian skink prefer temperatures that are not associated with optimum sprint speed (Huey and Bennett 1987). Maintaining a relatively high body temperature may allow maximum exploitation of available food sources (Waldschmidt et al. 1986). Consumption rate, which is directly linked to locomotor performance, was highest when body temperature was between 32 and 36 °C, close to 37°, though individuals foraged at temperatures above 28 °C (Waldschmidt et al. 1986). It is likely that digestion processes are also optimized at a relatively high temperature (Waldschmidt et al. 1986). Because lizards in this study for the most part were not foraging or engaging in any other dynamic behavior, processes related to general physiological maintenance may be an important factor in explaining the thermal preference (Angilletta et al. 1999, Hutchinson and Maness 1979).

This choice may of course reflect optimization of multiple factors or trade-offs in thermal optima of different factors. For example, *Uta* tend to maintain a 5-degree buffer between body temperature and their critical temperature maximum (lethality around 42 °C) (Tinkle 1967). Furthermore, the preferred temperature range does not necessarily lead to optimization of all physiological processes (Huey 1982), thus requiring performance trade-offs. More work on the physiological and fitness consequences of body temperature fluctuations in *Uta* is required to fully address this question.

Geographic distribution of Uta and thermoregulation

Uta is a species found throughout western North America across latitudes and altitudes, in a large variety of habitats (Tinkle 1967, Nussbaum and Diller 1967). It is ecologically flexible (Tinkle 1967) and therefore can adapt to a variety of structural microhabitats. The population studied here was found in an area of boulder "islands" with a large range in available thermal microhabitats. Each rock had multiple facets of different temperature. Substrate temperatures fluctuated over time,

largely due to change in the level of solar radiation and the three-dimensional habitat composition of each home range. Colorado and Oregon habitats were similarly fragmented and dimensionally complex while Texas habitats tended to be more homogenous and two-dimensional (Nussbaum and Diller 1967), consisting mostly of sand and isolated vegetation (Irwin 1965). Although habitat similar to that preferred by *Uta* in Texas is found on Antelope Island, lizards were not observed there. If given a choice, could this species prefer habitats with more complex temporal structure, which allows them to thermoregulate more consistently? Similarly, other widely distributed species, such as the European common lizard (*Zootoca vivipara*), may exhibit greater habitat selectivity to avoid thermal challenges (Herczeg et al. 2006).

Habitat structural complexity not only impacted ability to thermoregulate, but also seemed to impact survivorship of *Uta* (Fox 1978). Survivors tended to occur in territories with greater diversity of microhabitat and open areas allowing those body temperatures at which sprint speed was maximized (Fox 1978). Escape and foraging behaviors also varied depending on habitat availability (Smith and Ballinger 2001). Furthermore, habitat was related to physiological and ecological fitness of an organism (Huey 1991). The study population, therefore, appears to exist in the ideal habitat for *Uta*, with the potential to maximize a variety of behaviors. As extent of possible behavioral thermoregulation is reliant upon available habitat thermal quality (Blouin-Demers and Nadeau 2005), our heterogeneous environment provided ample opportunity for individuals to regulate.

Thermoregulatory trends

Uta did not show differing patterns of thermoregulation between the months of July and August, the hottest part of the summer. Other seasons have greater fluctuation in temperature and regulation may change as a necessary response. For example, proportion of individuals in the shade has been observed to vary depending on monthly air temperature (Waldschmidt 1980). In the current study, however, air temperature remained fairly constant. This population may have varying temperature preferences across the seasons, as do some *Sceloporus* species (Adolph 1990). Spring and fall temperature changes might cause *Uta* to abandon thermal homogeneity in favor of acclimation. This study illustrates that air temperature is not necessarily a good indicator of experienced temperature, and it is therefore not surprising that no correlation was found between air temperature and body temperature in *Uta* (Soulé 1963), as it was in *Anolis* species (Huey and Webster 1975).

Activity and temperature

The reported activity period of *Uta stansburiana* is from shortly before sunrise (Evans 1967) through sunset (Tinkle 1967). This range was supported by our observations, though lizards were seen sitting exposed on rocks as late as 19:30. In various populations, *Uta* activity followed a bimodal distribution, with activity peaking mid-morning and mid-afternoon (Waldschmidt and Tracy 1983; Wilson 1991). However, time of highest activity level varies between populations. Our population did not appear to have significant differences in activity across a day. Southern populations have shorter periods of daily activity, remain active longer seasonally, and tend to be most active in the late afternoon (Tinkle 1967), while other northern *Uta* have a longer period of daily activity (Parker and Pianka 1975, Wilson 1991) and highest activity mid-morning (Nussbaum and Diller 1967). Morning activity in some Texas populations was always less than in the afternoon, even if air temperature was the same, and this difference was attributed to variation in solar radiation (Irwin 1965).

Activity increased if the hottest parts of the day were overcast (Irwin 1965) or on days after rainstorms (Tinkle 1967). Populations in Texas and Colorado moved into the shade to escape the highest intensity of solar radiation (Irwin 1965, Waldschmidt 1980). *Uta* on Antelope Island did not often retreat into shade. Only several individuals retreated to a shaded area, most likely in response to increase in temperature of their selected microhabitat. In areas of extreme summer temperatures, lizards relied upon shade provided by cover to extend activity into the hottest parts of the day (Alexander and Whitford 1968, Davis and Verbeek 1972). In Texas, lizards were active at temperatures ranging from 25 to 42 °C (Irwin 1965). *Uta* are very vulnerable both to lengthy cold exposure and to overheating (Huey 1982), which can cause death in under a minute (Tinkle 1967). "Shuttling" behavior between shade and sun (Waldschmidt 1980, Fox 1978) is therefore a key component of *Uta* behavioral thermoregulation.

Our study population differed in that individuals were active (sitting visibly on rocks) throughout the day. There was no midday retreat into shelter, as observed in other regions of the species' range (e.g., Texas, Irwin 1965, and Colorado, Waldschmidt and Tracy 1983), which has been taken as a sign of behavioral thermoregulation (Waldschmidt 1980). This was most likely due to the fact that the thermal heterogeneity of the environment consistently provided suitable thermal conditions that were not as extreme as in more homogeneous habitats farther south. Furthermore, larger *Sceloporus* species have been found to spend more time in the shade than the smaller *Uta*

(Waldschmidt 1980), suggesting either that *Uta* may have a higher tolerance for warmer conditions, or that *Sceloporus*, being larger, may not be able to utilize microhabitat heterogeneity as effectively.

Activity has been shown to vary based upon what microhabitats are available (Alexander and Whitford 1968). Since the habitat was highly heterogeneous, individuals in the study population might not have needed to be more active, as locating preferred substrate temperature was easier.

Behavior, territoriality, and temperature

Lizard thermoregulation is generally through two mechanisms: choosing when to be active throughout the day and season (Stevenson 1985, Adolph and Porter 1993), and shuttling between microhabitats of differing temperatures (Stevenson 1985), though other factors also play a role (Huey and Slatkin 1976, Huey and Stevenson 1979). Many ectotherms follow a daily cycle of thermal microhabitat preference (Hutchinson and Maness 1979, Stevenson 1985). Microhabitat complexity serves as a limiting factor of potential body temperatures (Huey and Slatkin 1976, Soulé 1963) and therefore of thermoregulatory ability (Stevenson 1985, Adolph 1990, Smith and Ballinger 2001). Precision of regulation varies with thermal habitat quality, generally decreasing in high quality environments (Blouin-Demers and Nadeau 2005). *Uta* are late spring to early summer breeders (Davis and Verbeek 1972), and this may be reflected in the observed inactivity of individuals in July and August in some populations.

In the current study, individuals sat motionless for long periods of time and were rarely active, suggesting that favorable microhabitats were readily available. *Uta stansburiana* has been characterized as sedentary, with individuals preferring specific parts of their home range (Tinkle 1967, Irwin 1965). Switches in position were either slight shifts (in which a lizard generally remained in the same microhabitat) or moves to a new thermal microhabitat, as seen by the broader variation in differences between before and after temperatures. However, a surprisingly small amount of the variation in lizard average temperature (15%) was accounted for by these differences. Clearly, factors other than thermoregulation play a role in an individual's decision to move location. This is surprising because earlier findings suggest that lizards thermoregulate mainly through changing habitat (Adolph 1990).

Uta have various territorial behaviors, including push-ups, head-bobs, tail-waggles, and charges (e.g., Tinkle 1967, Tinkle et al. 1962, personal observation). Only one instance of intraspecific interaction was witnessed, as well as several displays when no other lizards were

present as in Tinkle (1967), but territoriality and aggressiveness vary among populations, especially based upon population density (Parker and Pianka 1975, Nussbaum and Diller 1967).

Comparison of temperature measurement methods

This study is unique in the use of a thermal imaging camera to collect precise spatial and temporal information on thermal profiles of the environment and the lizards. Past studies have relied upon thermometers or implanted thermocouples for measurements of ambient air and body temperature (Tinkle 1967, Angilletta et al. 1999). Other authors used biophysical models to determine possible body temperatures at a given time (Huey 1991, Hertz 1992). Data sets often included three measurements: cloacal temperature, temperature of air above substrate, and the substrate temperature where the animal was sitting (Tinkle 1967) or a subset of these three (Soulé 1963). To survey available environmental temperatures, hollow lizard models were used and placed throughout a lizard's home range (Blouin-Demers and Nadeau 2005, Hertz 1992, Hertz et al. 1993, Angilletta et al. 1999, Huey 1991).

The thermal imaging camera not only allowed detailed mapping of the temperatures of all available microhabitats but also allowed simultaneous recording of variation in surface body temperature across a lizard. Though surface body temperatures may deviate slightly from that of the core, ThermaCAM imaging allowed measurement of lizard temperature while an individual was in its environment. This was an integral part of the study.

The cloacal measurement technique is not necessarily a precise indicator of the body temperature of an individual in its environment. An individual's body temperature may change between capture and time of measurement, and readings may therefore vary based upon handling time. Temperature readings differed significantly from ThermaCAM measurements, which indicate surface temperature. Thermal data for cloacal measurements were more variable even for repeated measurements on the same individuals, suggesting a lower precision than when using a thermal camera. Further discrimination requires the simultaneous investigation of an individual's surface and core body temperatures.

Implications for climate change

Climate change is expected to cause greater variability and fluctuation in temperatures across North America. A direct result of these changes will be greater variation in temperature across the range of

Uta. Based upon this study, some populations of *Uta* already preferentially select areas of exceptional breadth in thermal complexity. More thermally uniform habitats similar to those inhabited by *Uta* in other areas of their range are also found on Antelope Island, however, no *Uta* were observed in them. Many factors may affect *Uta* distribution, such as variable predation pressure and availability of suitable lookout points, however, a habitat consisting of sand dunes and isolated vegetation may not provide sufficient thermal diversity for the species. Ability to thermoregulate by moving into shaded microhabitats can serve as an important buffer of climate change (Kearney et al. 2009), and complex habitats will be more likely to retain some level of shade with large-scale increases in environmental temperature. If more diverse habitat is available these less favorable habitats may be avoided. Thermal microhabitat diversity is important because complexity may allow populations to adapt to varying temperature conditions. Habitats of lesser thermal heterogeneity, such as southern *Uta* home ranges, could provide unsuitable microhabitats with rising temperatures due to climate change, and therefore lead to local extinctions of *Uta stansburiana*. Critical thermal maximum was proposed as a barrier to adaptation, because an increase in preferred body temperature, with its necessary increase in basking, would cause overheating (Sinervo et al. 2010).

Our measurements predict that changes in temperature may prove not detrimental, and even beneficial, to the study population of *Uta* in northern Utah. During July and August, individuals preferred substrate temperatures close to the maximum environmental temperature. Cooler substrate was available at all times but was largely avoided. These areas could serve as retreats against overheating if average temperatures rise. However, several caveats should be kept in mind. First, in this study we only looked at temperature preferences of a particular age group over the hottest months of one season. As maximum summer temperatures are expected to remain similar with climate change (Zani 2008), these data may not be as applicable. Temperature increases during the reproductive season may have the greatest negative impact by decreasing effective foraging time and therefore limiting energy gain (Huey et al. 2010, Sinervo et al. 2010). Furthermore, reproductive individuals often demonstrate different thermal preferences than do non-reproductive individuals. For example, air temperature and the rate of maximum temperature change were correlated with extinction in Mexican lizards during the breeding season (Sinervo et al. 2010). However, our results indicate that substrate temperature is more critical than air temperature as a determinant of lizard body temperature. Second, specific physiological and ecological needs may

vary between populations, and thermal thresholds may exist for critical life stages (i.e., reproduction) that were not observed. The potential benefits and costs of climate change vary between seasons and years (Zani 2008). Sinervo et al. (2010) proposed that thermoregulatory responses evolved by lizard species also might not be sufficient when faced with rising temperatures. Nevertheless, the present results on behavioral thermoregulation suggest that climate change may cause local extinctions of populations found in more homogeneous environments, while other populations, such as the one on Antelope Island, found in an area of extraordinary thermal complexity, may remain unaffected or even benefit.

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AUTHOR'S BIOGRAPHY

Maria Goller was born during a thunderstorm in South Bend, Indiana, on the evening of April 23rd, 1991, to Austrian parents. At the age of three months she helped drive the moving truck with her family's possessions to just outside of Bloomington. For the next six years of her life, Maria lived in an old, dilapidated farmhouse in the country, where she discovered her love of nature and animals (of frogs, homeless dogs, fishing bats, birds, grasshoppers, and, above all, of crayfish). Sadly, this peaceful, pastoral lifestyle was not to continue. The Goller family packed up pets and belongings in 1998 and headed west, arriving in Salt Lake City, Utah. Although none of the six were thrilled enough to exclaim that "this was the place", they quickly settled into their new home. All four children attended and graduated from West High School, Maria in the spring of 2009. From there she attended Utah State University as a Research Fellow for four years, traveling to Thailand and studying abroad in Salzburg, Austria, for a semester. Maria will be graduating in Spring 2013 and is thrilled to be leaving Logan.

With endless amounts of energy and boundless curiosity about the natural world, Maria spends long periods of time outdoors hiking and observing wildlife. To put these interests to good use, she will be pursuing a PhD in animal behavior in a natural setting. As a compassionate and conscientious animal lover and environmentalist, she refuses to participate in experimentation on laboratory animals. Maria will, however, be taking a year off from school to travel and work as a field assistant in the Sierra Nevadas, before subjecting herself to four (or more) years of school.