

Thermoregulatory accuracy, precision, and effectiveness in two sand-dwelling lizards under mild environmental conditions

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Abstract: We investigated thermoregulation and habitat use in two sympatric lizard species of the family Phrynosomatidae (side-blotched lizards, *Uta stansburiana*, and sand-dune lizards, *Sceloporus arenicolus*) in southern New Mexico to determine whether thermoregulation was necessary and detectable under mild temperature conditions, and what behavioral mechanisms the lizards used to thermoregulate throughout their daily activity. We measured lizard temperature preference (T_{sel}) in a laboratory thermal gradient as well as field body temperature (T_b) at the study site. We then calculated several indices of thermoregulation to evaluate the effectiveness of thermoregulation for both species. In addition, we recorded and compared micro- and macro-habitat use for the two species; we also compared these habitats with randomly selected microsites. *Uta stansburiana* thermoregulated less precisely in a laboratory gradient than did *S. arenicolus* and had a slightly higher preferred temperature. Environmental thermal heterogeneity occurred at both micro- and macro-habitat spatial scales, allowing lizards to thermoregulate optimally for over 10 h/day. The two species maintained mean body temperatures within their selected temperature range throughout most of the day. Two indices of thermoregulatory effectiveness revealed that both species are effective thermoregulators, and thermoregulation was easily detectable throughout the day. Lizards used the behavioral mechanisms of microhabitat choice, posture, shuttling between sun and shade, and orientation to the sun to regulate T_b .

Résumé : Nous avons étudié la thermorégulation et l'utilisation de l'habitat chez deux lézards sympatriques de la famille des Phrynosomatidae (*Uta stansburiana* et *Sceloporus arenicolus*) au Nouveau-Mexique méridional pour déterminer si la thermorégulation est nécessaire et discernable quand la température ambiante est douce et connaître les mécanismes comportementaux que les lézards utilisent pour assurer leur thermorégulation pendant leur activité quotidienne. Nous avons mesuré la température préférée des lézards (T_{sel}) dans un gradient thermique de laboratoire ainsi que les températures corporelles en nature (T_b) au site de l'étude. Ensuite, nous avons calculé plusieurs taux de thermorégulation pour évaluer l'efficacité thermorégulatrice de chacune des deux espèces. Nous avons aussi enregistré et comparé l'utilisation des microhabitats et des macrohabitats chez les deux espèces; nous avons également et comparé ces habitats à des microsites choisis aléatoirement. *Uta stansburiana* contrôle sa température avec moins de précision que *S. arenicolus* dans un gradient thermique au laboratoire et sa température préférée est légèrement plus élevée. Il y a hétérogénéité thermique environnementale aux échelles spatiales du microhabitat et du macrohabitat, permettant la thermorégulation optimale des lézards pendant plus de 10 h/jour. Les deux espèces de lézards maintiennent leur température corporelle dans l'étendue de leurs températures préférées presque toute la journée. Deux indices de l'efficacité de la thermorégulation ont révélé que les deux lézards sont des thermorégulateurs efficaces et que la thermorégulation est discernable pendant toute la journée. Les lézards utilisent les mécanismes comportementaux de choix de microhabitats, de posture, de déplacements entre les zones ensoleillées et ombragées et d'orientation vers le soleil, pour régler leur température corporelle T_b .

Introduction

Although temperature is but one of the many abiotic factors in an organism's holocoenotic environment (Allee and Park 1939), it is perhaps the most pervasive (Hutchison 1976;

Hutchison and Maness 1979). Moreover, because temperature affects all aspects of physiological performance (Hutchison and Dupré 1992), it might influence the distribution and ecology of ectotherms. During activity, certain lizard species regulate their temperatures within relatively narrow ranges

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(Bowker and Johnson 1980) and achieve control of body temperature using combinations of both behavioral and physiological means (Bowker 1984). This thermoregulation might result in potential fitness benefits. However, the benefits of thermoregulation are offset by any costs that are incurred as a result of thermoregulatory behaviors (Pianka and Parker 1975; Huey and Slatkin 1976; Huey and Webster 1976). These costs may include loss of energy due to active thermoregulation, lower food intake, lower survivorship due to predation, or a reduction in reproduction due to time spent thermoregulating (Huey 1974).

The need for and the benefits of thermoregulation are small in environments where temperatures are nearly optimal, i.e., the mean operative environmental temperature (T_e) is near or within the range of preferred body temperatures (T_{sel}). In a thought-provoking paper, Shine and Madsen (1996) suggest that for most reptiles in tropical climates (and hence most reptiles), thermoregulation is rather unimportant, owing to (i) availability of relatively high temperatures for most of the year and (ii) easy access to microhabitats with a variety of thermal opportunities. Shine and Madsen (1996) reason that in environments where thermal conditions are often close to optimal, ectothermic organisms are not likely to benefit from intensive behavioral thermoregulation.

Environmental conditions during spring and autumn in warm temperate areas of North America may be similarly benign when warm, mild temperature conditions are the norm and thermal constraints on the use of time and space are relaxed. Most studies addressing thermoregulation of lizards in North America have tended to focus on the summer season (e.g., Cowles and Bogert 1944; Pianka 1975; Schall 1977; Adolph 1990; Grant and Dunham 1990; Bashey and Dunham 1997), when temperatures are high and precise thermoregulation is required to avoid lethal temperatures. Few studies have addressed the potential importance of transitional seasons in the thermoregulatory strategies of lizards in arid habitats (but see Huey and Pianka 1977; Christian and Bedford 1995; Durtsche et al. 1997; Firth and Belan 1998). Transitional seasons may offer thermal opportunities not found during summer and winter, as well as opportunities for extended activity with relatively little need for thermoregulation, e.g., at midday, when activity is often precluded in summer (Hertz and Nevo 1981; Grant and Dunham 1988).

In addition to mean environmental temperatures, other environmental factors such as the distribution and proximity of warm and cool microsites are also important in determining the costs of thermoregulation. Environments with similar thermal opportunities but with different spatial scales of thermal heterogeneity should have differing costs of thermoregulation for diurnal reptiles because the distances that animals must move to change thermal status are different. Tropical forests and arid shrublands are examples of landscapes with different scales of thermal heterogeneity. In forested landscapes, most of the thermal variation occurs among different habitat types, with canopy disturbances, such as treefalls and riverbanks having different thermal properties than interior forest (Sartorius et al. 1999; Blouin-Demers and Weatherhead 2001). Therefore, thermoregulating reptiles in forests must live in edge habitats between canopy and open areas, or they must regularly traverse long distances to access the full range of thermal opportunities available in the landscape. However, in

arid shrublands without continuous canopies, the scale of thermal variability is much smaller. By and large, small vertebrates can experience large temperature differences by simply moving from shade under a shrub into open sunlight (Hertz 1992; Bauwens et al. 1996), and movements between macrohabitat types or use of macrohabitat edges are not necessary. It is likely that active thermoregulation carries fewer energetic costs in areas of small-scale thermal heterogeneity than in areas with large-scale heterogeneity, although this hypothesis remains to be tested explicitly. Therefore, spatial scale of thermal heterogeneity rather than absolute temperature may be a more important factor in determining whether a lizard species is a relative thermoconformer or thermoregulator. Moreover, there may be other fitness costs, such as the predation risk associated with decreased canopy coverage, associated with habitats having small scales of thermal heterogeneity.

In recent years, studies of ectotherm thermoregulation under field conditions have been improved by the recognition that thermoregulatory efficiency cannot be evaluated using a single measure (Hertz et al. 1993; Christian and Weavers 1996). To evaluate thermoregulation in field-active ectotherms, several indices have been developed that use three independent data types: (1) the distribution of T_e 's, (2) field body temperature (T_b) of the animal, and (3) the intrinsic temperature preference of the animal (T_{sel}). These indices have been developed to answer questions about the accuracy, precision, and effectiveness of thermoregulation in small ectotherms (Hertz et al. 1993; Blouin-Demers and Weatherhead 2001). The indices are d_e , the thermal quality of the habitat; d_b , the accuracy of thermoregulation; and E , the effectiveness of thermoregulation.

$$d_e = (T_{sel} - T_e)$$

$$d_b = (T_{sel} - T_b)$$

$$E = 1 - (d_b/d_e)$$

The index E is an estimate of the effectiveness of thermoregulation or the amount that T_b is moved in the direction of T_{sel} from the null distribution (T_e). An alternative measure of effectiveness, simply the difference between d_e and d_b (Blouin-Demers and Weatherhead 2001), may simplify interpretation of effectiveness measures, and we report both effectiveness indices throughout. Together these indices express the extent to which an organism regulates its temperature in a complex environment. However, a convincing case for thermoregulation can be made only when the indices are presented together with observations of thermoregulatory behaviors or physiological measures of thermoregulation (Heath 1964; Hertz et al. 1993).

We combined laboratory and field data to measure habitat thermal quality with indices of accuracy, precision, and effectiveness of thermoregulation for two sympatric species of lizards. We specifically addressed the following questions: (i) What is the scale of thermal heterogeneity in this habitat? (ii) Are daytime temperatures near or within the optimal ranges of these species? (iii) Are lizards distributed randomly with respect to microhabitat structural features? (iv) Is thermoregulation consistently detectable for each species at this

Table 1. Structural habitat variables used in discriminant function analyses.

Mnemonic acronym	Variable and description
SAND	Percent sand cover
ROCK	Percent rock cover
WOOD	Percent cover of woody debris (surface cover of twigs and bark over sand)
WEED	Weedy vegetation not classified in "OTHER"
OAK	Dwarf shinnery oak, <i>Quercus havardii</i>
FLOWER	White flower of dwarf shinnery oak
GRASS	Bunch grasses (family Poaceae)
ASTER	Sunflowers (family Asteraceae)
YUCCA	Soapweed yucca, <i>Yucca glauca</i>
CACTUS	Prickly pear cactus, <i>Opuntia</i> sp.
SAGE	Sand sagebrush, <i>Artemisia filifolia</i>
OTHER	Uncommon vegetation types (<i>Bahia</i> sp., <i>Arabis</i> sp., <i>Cryptantha</i> sp., and <i>Salvia</i> sp.)

time of year? (v) How effectively do these species thermoregulate throughout the day?

Because thermoregulation has a direct effect on the time of activity and the space that an organism can exploit, multi-species studies of ectotherm thermoregulation may lead to the determination of mechanisms involved in interspecific resource partitioning, which is often evaluated on the basis of time, space, and food (Pianka 1973; Vitt et al. 1998, 2000). We tested whether mild environmental temperature conditions alter a reptile's need for thermoregulation and thus reduce thermal constraints on time of activity and spatial distribution.

Materials and methods

We studied sympatric populations of *Sceloporus arenicolus* and *Uta stansburiana* in the Mescalero Sands area of Lea County, southeastern New Mexico, U.S.A. Both lizard species are phrynosomatids (Iguania), an ancient lineage retaining many features present in basal squamates, such as a sit-and-wait foraging mode, lingual prehension, and limited chemosensory abilities (Schwenk 1993; Cooper 1997; Zug et al. 2001). *Sceloporus arenicolus* inhabits a small area of semi-stabilized sand dune habitat in southeastern New Mexico and adjacent Texas (Degenhardt et al. 1996). *Uta stansburiana* is a wide-ranging generalist species of the North American desert inhabiting low- to mid-elevation sites from Idaho to central México and from coastal California to central Texas. Throughout their range, they occur in a variety of habitats from rocky hillsides and mountain slopes to sand dunes (Stebbins 1985).

The study site consisted of several square kilometres of semistabilized sand dunes. Data were collected by seven investigators on 3 and 4 October 1997. During this study, the weather was sunny, with very few clouds present, and there was no precipitation. The habitat was xeric shrubland, where most plants were separated by open sand. Vegetative cover in this area was dominated by dwarf shinnery oak (*Quercus havardii*), which formed low thickets of dense ground cover. Other common perennials included sand sage (*Artemisia filifolia*), small mesquite (*Prosopis juliflora*), soaptree yucca (*Yucca elata*), and large bunch grasses (*Aristida* spp., *Sporobolus* spp.) (Sena 1985). Overall, vegetation formed a patchy struc-

ture of low-growing cover (<1 m) separated by open sandy areas with no canopy cover.

Three investigators conducted haphazard searches for lizards throughout the active period. When a lizard was encountered, we attempted to noose it and record its T_b , using a Miller and Weber® rapid-reading cloacal thermometer, within 10 s of capture. We identified each lizard that we observed and recorded its habitat and microhabitat whether it was captured or not. We divided the study area into three macrohabitat categories based on gross topography: dune slope, dune ridge, and interdune flat. To determine the relative intensity of lizard activity patterns throughout the day, an additional investigator walked a 100 m long transect located at the center of the field site once per hour from 07:00 to 18:00, recording the total number of each species observed within 5 m of the transect line.

To better understand patterns of lizard activity and behavior, three investigators conducted focal animal studies on 40 *U. stansburiana* and 32 *S. arenicolus*. Most lizards (68) were followed for 600 s; 4 lizards were followed for periods ranging from 248 to 505 s. Each lizard was observed with binoculars from approximately 10 m, a distance at which we believed the activity of the lizards would not be disturbed. Each focal lizard was identified to species and the following behavioral data were recorded. Lizard posture was characterized using a number system based on the amount of the lizard's body in contact with the substrate: posture 1: body and tail pressed against the substrate, head on the substrate or raised; posture 2: head and chest raised, abdomen and tail pressed against the substrate; posture 3: head and body raised above the substrate with the tail raised or resting on the substrate. We predicted that posture would reflect thermoregulatory condition and that posture 1 would be used when T_e was higher than T_b and T_b was below T_{sel} or when T_e was lower than T_b and T_b was higher than T_{sel} . Posture 3 would be used when T_e was higher than T_b and T_b was higher than T_{sel} or when T_e was lower than T_b and T_b was below T_{sel} . Posture 2 is intermediate and may be used when T_e is near T_{sel} . We recorded whether each lizard was facing toward the sun, facing away from the sun, or was perpendicular to the sun when first observed. We reasoned that perpendicular orientation would increase heat gain when the lizard was basking, whereas facing toward or away from the sun would expose less body area to the sun, minimizing heat gain. We

Table 2. Summary of body temperatures (T_b), operative temperatures (T_e), habitat thermal quality (d_e), accuracy of thermoregulation (d_b), and two indices of thermoregulatory effectiveness for *Sceloporus arenicolus* and *Uta stansburiana*.

	<i>S. arenicolus</i>			<i>U. stansburiana</i>		
	Morning	Midday	Afternoon	Morning	Midday	Afternoon
<i>N</i>	13	16	24	28	23	30
T_b (°C)	31.9±0.91	36.1±0.52	33.9±0.83	35.4±0.52	37.8±0.25	36.4±0.47
T_e (°C)	27.5	44.9	34.8	27.5	44.9	34.8
d_b	2.55±0.730	0.537±0.190	1.788±0.580	0.461±0.201	0.270±0.094	0.467±0.200
d_e	8.70±0.16	8.95±0.24	6.23±0.13	7.80±0.16	8.06±0.23	5.38±0.12
<i>E</i>	0.71	0.94	0.71	0.94	0.97	0.91
$d_e - d_b$	6.15	8.41	4.44	7.34	7.79	4.91

Note: T_{sel} was 33.9–37.2°C for *S. arenicolus* and 32.9–38.3°C for *U. stansburiana*. Values are presented as the mean ± 1 SE. Times included in the subgroupings are as follows: morning, 08:00–11:20; midday, 11:21–14:40; afternoon, 14:41–18:00.

recorded sun exposure as in sun, in sun filtered through vegetation, or in shade. These behavioral observations served as an independent verification of thermoregulation to compare with the effectiveness indices. In addition to these data, time and distance of movements were recorded to estimate the frequency and duration of activity for each species. At the end of each 600-s observation period, an attempt was made to noose the animal and measure its T_b , but only if this could be accomplished without chasing the lizard, which potentially would alter the T_b measurement.

Structural components of each microhabitat and their percent coverage were determined by photographic analysis (see Reinert 1984) for each species as well as for randomly sampled microsites. Color photographs of microsites where lizards were first seen were made using a 35-mm single-lens camera equipped with a wide-angle lens. A metre stick placed within the center of the microsite provided a 1.0 m length scale within each photograph. Percent surface coverage by each of the 12 structural microhabitat variables (Table 1) was determined by superimposing each color slide on a 10 × 10 square grid. Randomly chosen microsites were sampled similarly for comparison with the microsites used by lizards. We selected arbitrary starting points within the study area. From these initial points, a transect was established in a random compass direction. Microsites along this transect were sampled by randomly selecting a new compass direction every 20 m and walking 5 m from the original transect in that direction. Nineteen copper lizard models equipped with temperature probes attached to data loggers were also placed randomly throughout the study site to characterize the thermal profiles of available microsites (see below). These additional microsites were also photographed and included in the microhabitat analyses.

We used discriminant-function analysis (DFA) to determine whether microsites used by *S. arenicolus* and *U. stansburiana* differed from randomly sampled microsites based on structural features. These analyses also allowed us to evaluate interspecific differences in habitat use and determine possible mechanisms for habitat and resource partitioning. Functions created by DFA of the original variables maximize separation among groups and indicate which variables contribute most to group separation where groups are preselected as microhabitat sites by lizards or randomly sampled sites. Analyses were performed using SPSS Professional Statistics 6.1 (Norusis/SPSS Inc. 1994). We used SigmaPlot 1.0 (Jandel

Scientific Software Corp. 1994) and StatView 4.5 (Abacus Concepts 1992) for graphical representations of habitat data and statistical analyses.

Concurrently with lizard observations, we recorded T_e using 19 copper lizard models painted matte gray to visually match a photo gray card (18% reflectance). Each model was connected by a thermistor probe to a miniature temperature-data logger (Onset Computer Corp.). These models were made following standard methods (Bakken and Gates 1975) and were cast using a mold cast from a preserved *Sceloporus undulatus*, a lizard similar in size and shape to the study lizards. Because this study investigated the thermoregulation of more than one species, we were unable to exactly match the reflectance, size, shape, and scale architecture of both lizards. However, the lizards in this study were very similar in respect to these characteristics, and recent studies have shown little influence of morphology and color pattern on operative temperatures of small lizards (Vitt and Sartorius 1999; Shine and Kearney 2001). Lizard models were placed in randomly selected terrestrial microsites throughout the study area. For each model we recorded substrate type and whether it was under a shrub, at the outer margin of a shrub canopy, or in an open area away from shrubs. Data loggers recorded model temperatures at 5-min intervals throughout the study period.

We determined the range of temperatures that the lizards maintain during activity (T_{sel}) by monitoring lizard T_b in a laboratory thigmothermal gradient. A sample of five *S. arenicolus* and 10 *U. stansburiana* collected at the field site at the time of the field study were acclimatized on a 12 h light : 12 h dark photoperiod for 4 days at 25°C with ad libitum water. The photoperiod during acclimatization mimicked the photoperiod of the place and time of year the lizards were captured. The lizards used in this experiment were housed and tested in accordance with the principles and guidelines of the University of Oklahoma Animal Care and Use Committee (assurance number 73-R-100) and of the Canadian Council on Animal Care. The thermal gradient was a sheet-metal disk 88 cm in diameter with a shallow (less than 0.5 cm) layer of sand covering the surface. The sand in the gradient was mixed and leveled between trials to disrupt any scent marks. An incandescent infrared bulb was placed underneath the center of the gradient and provided a concentric thermal gradient radiating from a center point of 70°C to 20°C at the periphery. Lizards were fitted with a small thermocouple probe, which was inserted into the cloaca and se-

Table 3. Summary statistics of discriminant functions and linear correlations (r) between original variables and discriminant functions.

Statistic	Discriminant function	
	1	2
Eigenvalue	0.7708	0.1569
χ^2	53.783	10.928
df	22	10
P	0.0002	0.3632
Percent variance	83.09	16.91
Linear correlation		
SAND	0.8033*	0.1966
WOOD	-0.4466*	0.0361
GRASS	-0.3738*	-0.1694
OTHER	-0.1571*	0.1084
ROCK	0.0165	0.1867*
WEED	-0.9583	0.3363*
OAK	-0.0865	-0.5019*
FLOWER	-0.1354	0.2377*
ASTER	-0.0379	0.5628*
YUCCA	-0.1406	0.1296*
CACTUS	-0.0462	-0.0499*
SAGE	0.1678	-0.2179*

*The largest absolute correlation between the variable and any discriminant function.

cured to the tail with a small (3 mm long) band of adhesive tape. Thermocouples were attached by wire to a temperature-data logger (Model 50, Electronic Controls Design Inc., Milwaukie, Oregon, U.S.A.) that recorded temperature at 5-min intervals. Lizards remained in the gradient for 3 h at times that coincided with field-measured activity (between 09:00 and 16:00). Data obtained during the first hour of the trial were not used to calculate T_{sel} . We follow Christian and Weavers (1996) in using the interquartile range of all temperatures selected in the thermal gradient to represent T_{sel} .

We used the indices developed by Hertz et al. (1993) and elaborated by others (Bauwens et al. 1996; Christian and Weavers 1996; Diaz 1997) to describe lizard thermoregulatory activities. The index d_b represents the accuracy of thermoregulation and is calculated as the average deviation of T_b from T_{sel} . A high d_b value indicates that optimal temperatures are seldom maintained. The index d_e is the average deviation of T_e from T_{sel} . This is a complementary index to d_b and is a measure of the thermal quality of the habitat. A high d_e value indicates a habitat with few optimal temperatures, whereas a d_e of 0 indicates a habitat where thermoregulation is unnecessary for the maintenance of optimal T_b . The index E is an estimate of the effectiveness of thermoregulation and generally varies from 0, indicating no thermoregulation, to 1, indicating highly effective thermoregulation. This is a measure of the degree to which the lizard takes advantage of the thermal opportunities found in the environment to move its T_b closer to T_{sel} . We also report the index proposed by Blouin-Demers and Weatherhead (2001), the deviation of d_b from d_e . This index is similar to E but is not undefined when d_e is 0 and is not sensitive to small changes in d_b or d_e . We compared T_b and d_e data using t tests. When multiple comparisons were performed on the same dataset, we employed a

sequential Bonferroni correction procedure (Rice 1989) to maintain the probability of Type II error at 0.05.

Results

In the field, both species maintained T_b within a narrow range, especially when high temperatures prevailed (Fig. 1) ($34.1 \pm 0.59^\circ\text{C}$ (mean \pm SE), $n = 43$; and $36.5 \pm 0.27^\circ\text{C}$, $n = 78$, for *S. arenicolus* and *U. stansburiana*, respectively). In t tests, T_b was significantly higher in *U. stansburiana* than in *S. arenicolus* in the morning ($t_{[38]} = 3.82$, $P < 0.0005$), at midday ($t_{[38]} = 3.42$, $P = 0.0015$), and in the afternoon ($t_{[52]} = 2.75$, $P = 0.0082$) after sequential Bonferroni correction. The d_e index varied greatly throughout the day (Table 2, Fig. 2). For both species, the d_e index showed high values (low thermal quality) early and late in the day, with a lower peak at midday. There were low index values at 10:00 and again at 17:00. Owing to the similarity in T_{sel} for these species, d_e indices were also similar. The d_b index for both species was lower than d_e throughout the day (Table 2, Fig. 3). Morning d_e indices for *U. stansburiana* were significantly lower than those for *S. arenicolus* ($t_{[38]} = 3.90$, $P = 0.0004$). These differences disappeared at midday ($t_{[38]} = 1.22$, $P = 0.228$). Afternoon differences in d_e were nearly significant after sequential Bonferroni correction ($t_{[52]} = 2.34$, $P = 0.023$). These results show that *U. stansburiana* was better able to maintain T_b near or within T_{sel} than *S. arenicolus* during times of overall low T_e . At midday, when T_e was generally high, no differences in d_b were indicated. Our transect data indicate that we observed *U. stansburiana* approximately 25 times as often as *S. arenicolus* (Fig. 4). Owing to the low number of *S. arenicolus* observed, hourly patterns of activity intensity cannot be determined from our data. *Uta stansburiana* was observed during all transect runs and appeared to maintain a stable high level of activity until 17:00, when optimal T_e 's were no longer available and lizards sought shelter in underground retreats.

Posture use varied consistently with our predictions for thermoregulation (Fig. 5), i.e., lizards used postures that placed their bodies in contact with the ground during the cooler morning and afternoon hours and used elevated postures more often at midday. Both species used posture 1 most often. The use of posture 1 declined at midday, when postures 2 and 3 became prevalent. Likewise, our orientation data show probable thermoregulatory tendencies for *U. stansburiana*; they are less convincing for *S. arenicolus*. *Uta stansburiana* used orientation category 2 (perpendicular to the sun) much more often in the morning and afternoon than at midday (Fig. 6). Our observations of lizard exposure to the sun show that both species used sunny microsites more often in the morning and afternoon than at midday (Fig. 6). The use of shade peaked at midday for *U. stansburiana* and in the last hour of the day for *S. arenicolus*, because some lizards were active after local sunset.

The DFA indicated that one of two discriminant functions was statistically significant. These results and the linear correlations (r) between the original variables and the discriminant functions are presented in Table 3. The discriminant function (function 1) accounted for 83% (Table 3) of the total variance, indicating that open sand significantly separated each of the group mean centroids (Fig. 7). The second discrimi-

Fig. 1. Hourly field body temperatures (T_b) of *Sceloporus arenicolus* (a) and *Uta stansburiana* (b) plotted with hourly mean and minimum and maximum operative environmental temperatures (T_e) measured concurrently with lizard sampling. The shaded bar indicates the preferred body temperature range (T_{sel}) in a laboratory thermal gradient.

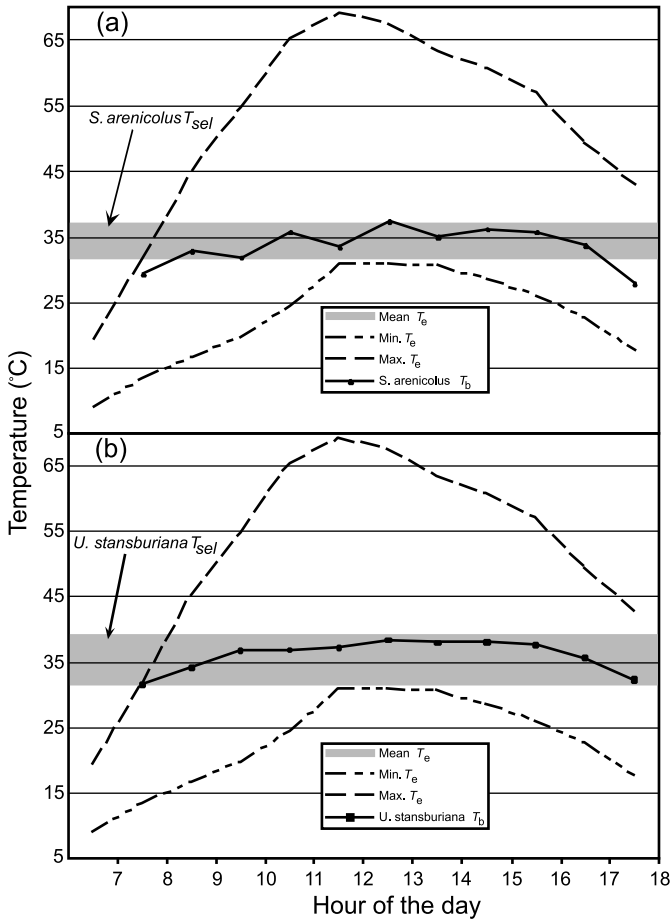


Table 4. Classification results.

Group	n	Predicted group membership		
		1	2	3
Random	42	29 (69.0)	6 (14.3)	7 (16.7)
<i>S. arenicolus</i>	19	1 (5.3)	4 (21.1)	14 (73.7)
<i>U. stansburiana</i>	22	1 (4.5)	17 (77.3)	4 (18.2)

Note: The numbers in parentheses are percentages of cases that were grouped correctly. The percentage of grouped cases correctly classified was 72.3%.

minant function (function 2) was correlated with percent coverage of sunflower (Asteraceae) and oak (Fagaceae) within microhabitats but was found to be not significant in separating group means. Based on discriminant functions 1 and 2, *U. stansburiana* used more open sand habitats than *S. arenicolus*, while *S. arenicolus* was associated more with shinny oak cover (Fig. 7). Table 4 indicates that the three groups (i.e., random, *S. arenicolus*, and *U. stansburiana* habitats) were each correctly classified with 72.3% accuracy. This shows that our analysis was able to identify interspecific differences in microsites based on structural elements.

Fig. 2. Hourly means for the d_e index, a measure of the thermal quality of the habitat, for *S. arenicolus* (a) and *U. stansburiana* (b) in each habitat type. Error bars represent ± 1 SE.

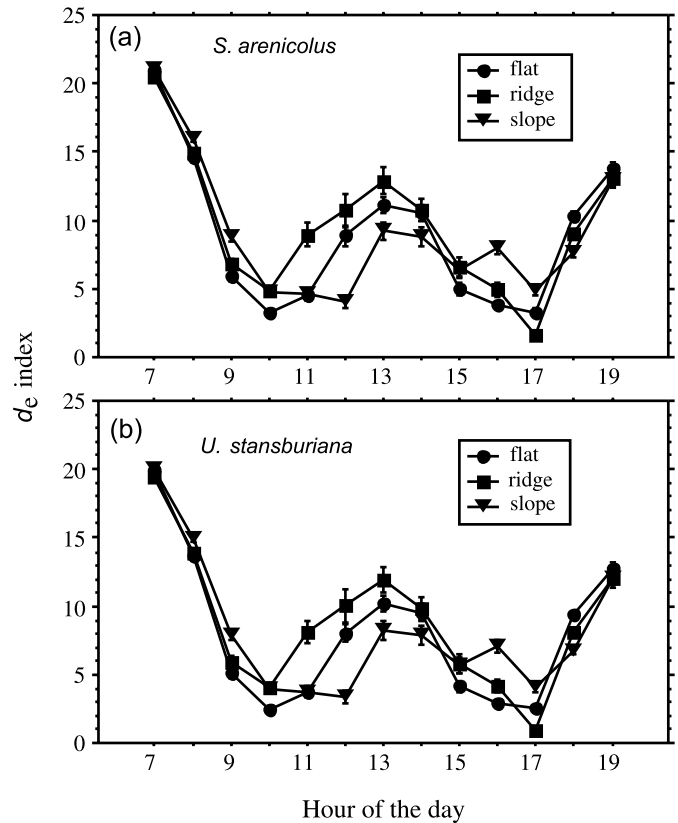
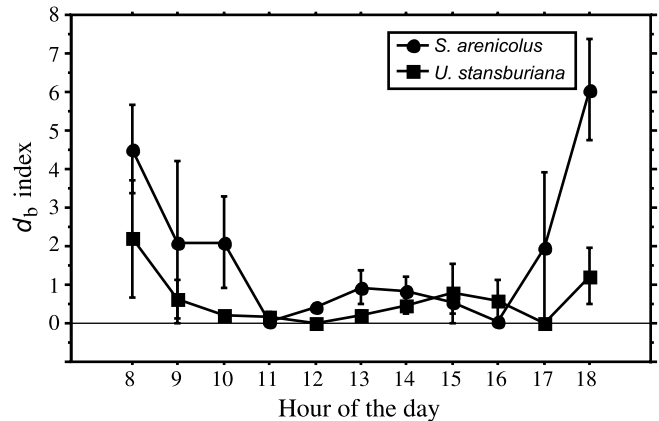
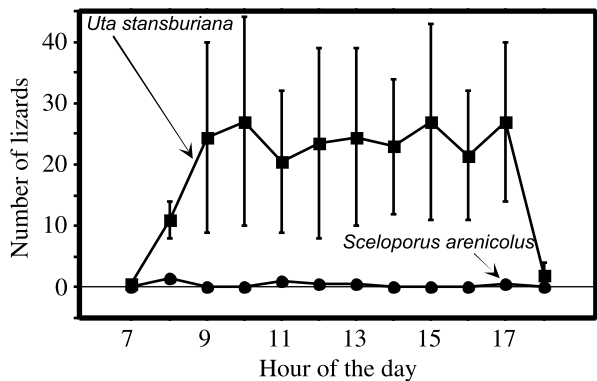


Fig. 3. Hourly means for the d_b index, a measure of the accuracy of thermoregulation, for *S. arenicolus* and *U. stansburiana* over all habitat types. Error bars represent ± 1 SE.



T_e 's ranged from 8.9°C at 07:00 to 69.1°C at 12:20 ($33.1 \pm 0.180^\circ\text{C}$ for 07:00–18:00, Table 2). Of the three habitat types, ridge had the highest maximum, mean, and minimum temperatures, followed by slope and then by flat habitats (Fig. 8). Differences between macrohabitat types were small relative to the overall variation within each of the habitat types (Fig. 8), thus thermal heterogeneity occurred at two spatial scales relevant to lizard thermoregulation: microhabitat and macrohabitat. All habitats offered temperatures above, below, and within the selected range for both species at all times after 09:00;

Fig. 4. Hourly variation in lizard activity determined from data collected while walking a 100 m long transect once per hour over 2 days. Each point indicates the mean number of lizards counted; error bars represent ± 1 SE.



hence, the spatial scale of thermal heterogeneity was small enough that all lizards had access to microsites with T_e both above and below T_{sel} at all times between 09:00 and 17:00. Temperatures varied with sun exposure throughout the day. Early and late in the day, T_e 's were equal among microsites or slightly higher in microsites under shrubs (Fig. 9). Mid-day T_e 's were higher in microsites exposed to the sun and lower in shaded sites (Fig. 9).

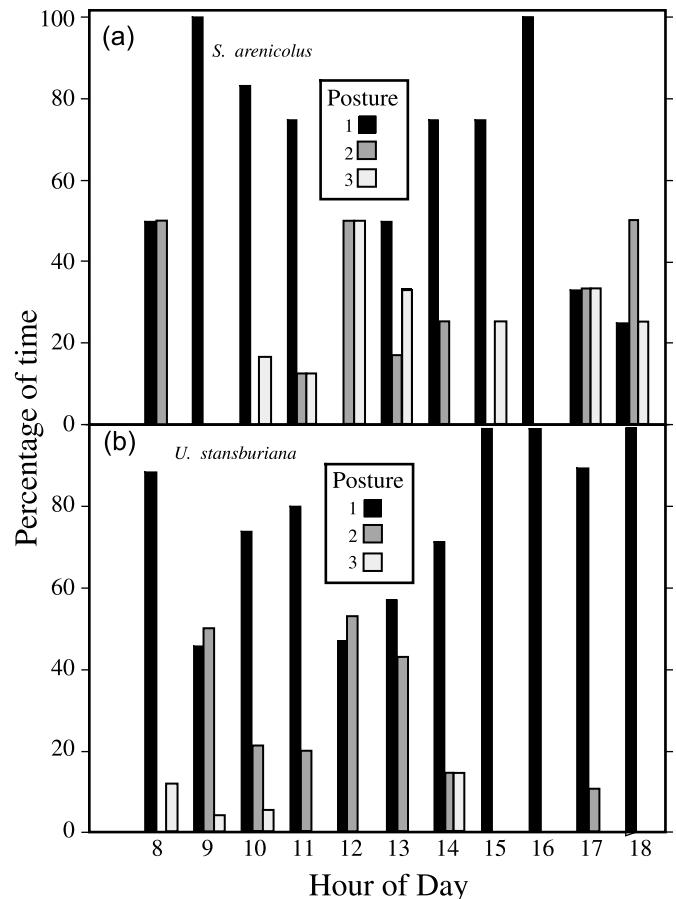
Both species selected narrow temperature ranges relative to the total variation available in the laboratory gradient. T_{sel} 's for eight *S. arenicolus* ranged from 33.9 to 37.2°C (mean = 35.8°C; median = 35.9°C); T_{sel} 's for 10 *U. stansburiana* ranged from 32.9 to 38.3°C (mean = 35.5°C; median = 36.2°C). The temperature range for *U. stansburiana* corresponds well to the ranges that are optimal for sprint speed in this species (35–38°C; Waldschmidt and Tracy 1983), evidence that lizards in the gradient were thermoregulating optimally. Variance was higher for all individual *U. stansburiana*, resulting in a broader T_{sel} .

Overall, E was high, with means of 0.95 and 0.82 for *U. stansburiana* and *S. arenicolus*, respectively, indicating that despite the highly variable environment, the two species were able to maintain a temperature much closer to their respective T_{sel} than was T_e (Table 2, Fig. 10). When the day's samples were split into morning, midday, and afternoon, *U. stansburiana* was found to have maintained a higher E in all three periods, with the greatest difference between the species occurring in the morning and afternoon, when E decreased to 0.71 for *S. arenicolus* and remained above 0.9 for *U. stansburiana*. The results for $d_e - d_b$ were also high, although they did not directly mirror E . For *S. arenicolus*, $d_e - d_b$ values were higher at midday and lower in the morning and afternoon, indicating that at midday, *S. arenicolus* deviated more from thermoconformity than did *U. stansburiana*. There was general agreement between the E and $d_e - d_b$ indices in that both indicated that the effectiveness of thermoregulation was relatively high at all times.

Discussion

Both *S. arenicolus* and *U. stansburiana* are primarily terrestrial and occurred on sandy substrates. These species were not distributed randomly with respect to habitat structure:

Fig. 5. Hourly summary of postures used by *S. arenicolus* (a) and *U. stansburiana* (b) throughout the day from focal-animal observations. Postures areas follows: 1, body and tail pressed against the substrate, with head raised or against the substrate; 2, head and chest raised, with abdomen and tail pressed against the substrate; 3, head and body raised above the substrate, with tail in contact with or raised above the substrate.



U. stansburiana microsites typically had more open sand and *S. arenicolus* microsites contained more vegetative cover. This spatial pattern could have significant effects on thermoregulation or alternatively may represent thermoregulatory decisions by each species. The d_b index was consistently lower than d_e throughout the day for both species, despite widely fluctuating T_e 's. This result, combined with our behavioral observations, suggests that the deviation from random microhabitat use by both species is partially the result of temperature-based microhabitat selection. The exposure data show that *U. stansburiana* was found in open sun more often than *S. arenicolus*, which may explain the low E values for *S. arenicolus* during late morning and late afternoon. If *S. arenicolus* is less willing to expose itself to predation, we would expect a reduction in thermoregulatory activities that require exposure when the benefits of thermoregulation are low.

Our data for sand-dwelling lizards in October clearly indicate that thermoregulation occurs throughout the day, even in this season of mild temperature conditions and high availability of microsites with optimal temperatures. The two species differed little in mean temperature preference, with

Fig. 6. Hourly summary of the percentages of time that lizards spent in the sun, in filtered sun, or in shade and the lizard's direction of orientation to the sun (1, facing the sun; 2, body perpendicular to the sun; 3, facing away from the sun) throughout the day, from focal-animal observations.

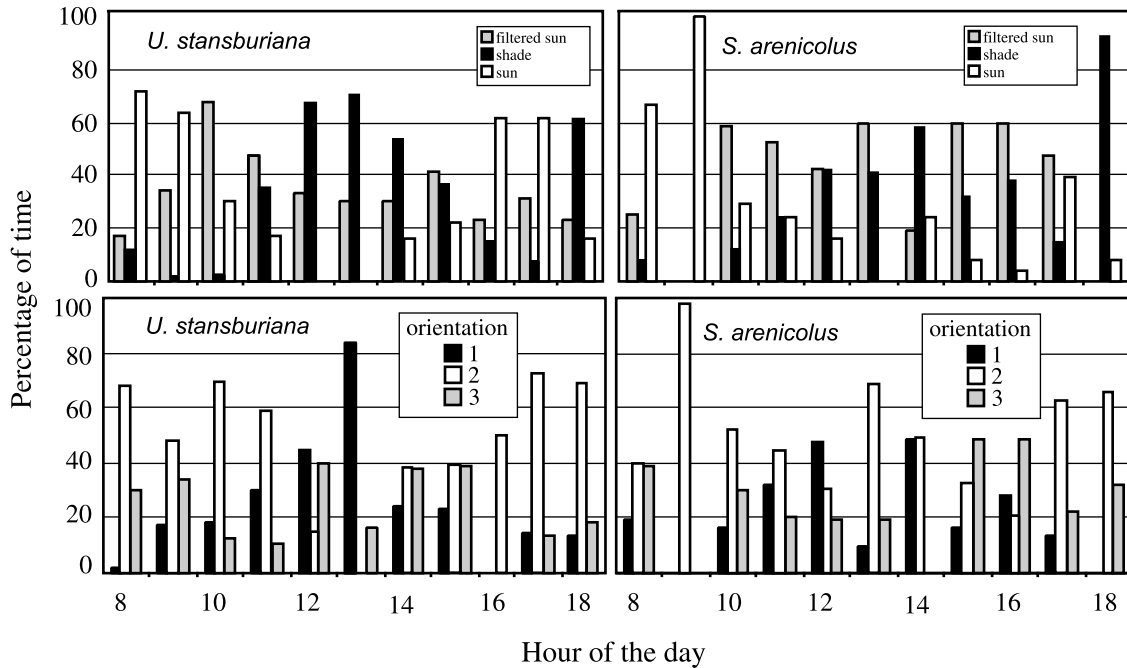
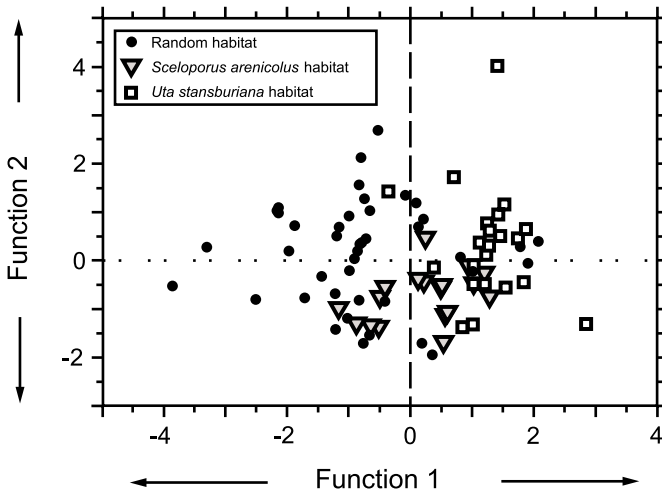


Fig. 7. Functions 1 and 2 from the discriminant functions analysis (DFA) performed on the habitat-use data for *S. arenicolus* and *U. stansburiana*, as well as on data from randomly chosen sites. Function 1 is positively loaded on the variable SAND, whereas function 2 is positively loaded on Asteraceae and negatively loaded on Fagaceae.



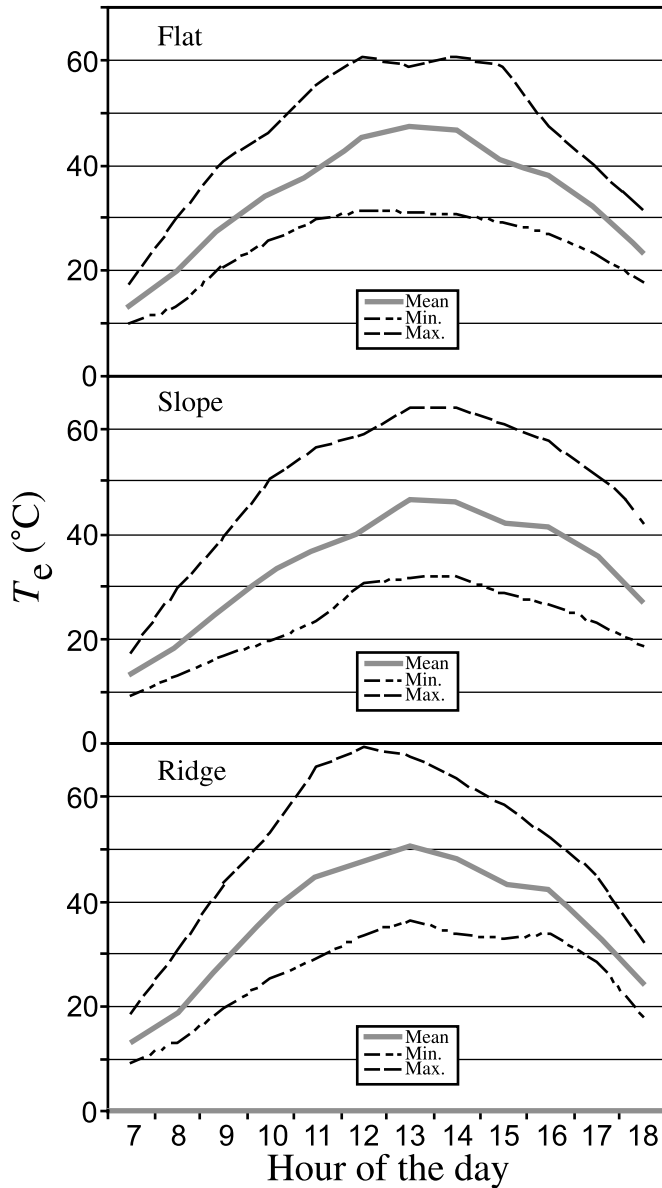
U. stansburiana having a wider T_{sel} with both lower and higher endpoints. Both species maintained T_b closer to T_{sel} than to T_e throughout the day. *Uta stansburiana* maintained a high E value (>0.9) throughout the day, whereas *S. arenicolus* maintained a high E value at midday and a lower E value in the morning and afternoon. Low E values are likely due to the high availability of optimal temperatures at this time and the consequent reduced necessity for thermoregulation. Overall, both species were able to maintain near-optimal tempera-

tures for most of the active period, and this was accomplished through preferential use of optimal microhabitats, postures, and orientations.

The spatial scale at which thermoregulatory decisions are made and the distances required for thermoregulatory movements have a direct effect on the cost-to-benefit ratio of thermoregulatory strategies that animals use. Heterogeneous environments in which the scale of thermal heterogeneity occurs within the sensory resolution ability of the animal and also within the range of its daily movements have the most utility in comparative studies of behavioral thermoregulation. Xeric shrublands are ideal for lizard thermoregulation because the spatial scale of thermal variation is often small (~1–4 m) and movements between macrohabitats are not required to change thermal status. Our data show that the bulk of the thermal variation at the site was found among microhabitats (small scale) rather than among macrohabitats. Moreover, shifting sun exposure contributes to thermal heterogeneity in xeric shrublands, producing microsites that may exhibit a wide range of temperatures throughout the day that are not closely tied to the overall macrohabitat temperature, a situation that is less likely in an environment with larger scale heterogeneity (e.g., closed canopy forest), where sun exposure is consistent over large areas (Sartorius et al. 1999; Blouin-Demers and Weatherhead 2001).

This study was conducted during October, a month in which temperatures are usually transitional between the extremes of summer and winter in southern New Mexico. Under these circumstances, it might be expected that daytime temperatures would be close to optimal for lizards and that thermoregulation would be difficult to detect. Recent investigators have questioned the importance of thermoregulation for reptiles living in habitats with generally high ambient temperatures and having accessible microhabitats with dis-

Fig. 8. Maximum, mean, and minimum operative environmental temperatures (T_e) for three macrohabitat types sampled at the Mescalero Sands area, southern New Mexico, U.S.A.



tinctive temperatures (small-scale heterogeneity) (Shine and Madsen 1996). Our study site had minimum temperatures that were lower than and maximum temperatures that were similar to those at sites reported in other studies of tropical lizards (Christian and Weavers 1996; Shine and Madsen 1996; Sartorius et al. 1999), so the thermal environment is not perfectly analogous to tropical habitats. However, mean temperatures for much of the day were within T_{sel} for both species. In addition, warm and cool microsites were in close proximity throughout the site, facilitating behavioral thermoregulation by shuttling lizards. Thermoregulation under these circumstances was easily detected.

Environmental temperature regimes have been implicated as a constraint on the activity time of desert lizards (Grant and Dunham 1988; Grant 1990; Grant and Dunham 1990).

Fig. 9. Hourly mean operative environmental temperatures (T_e) for three habitat types sampled in the open space between shrubs, at the edge of the shrub canopy, or under a shrub. Error bars represent ± 1 SE.

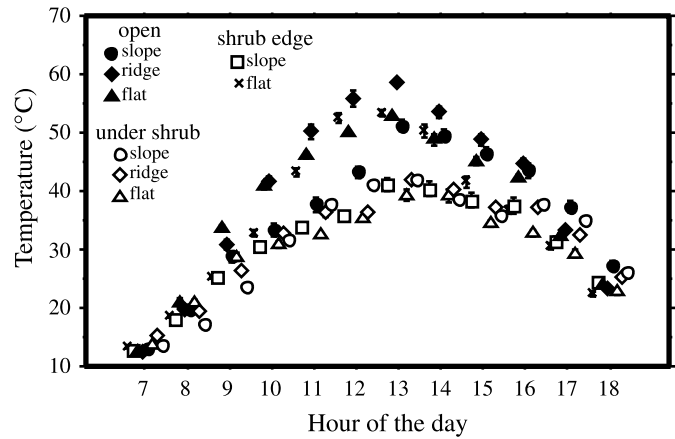
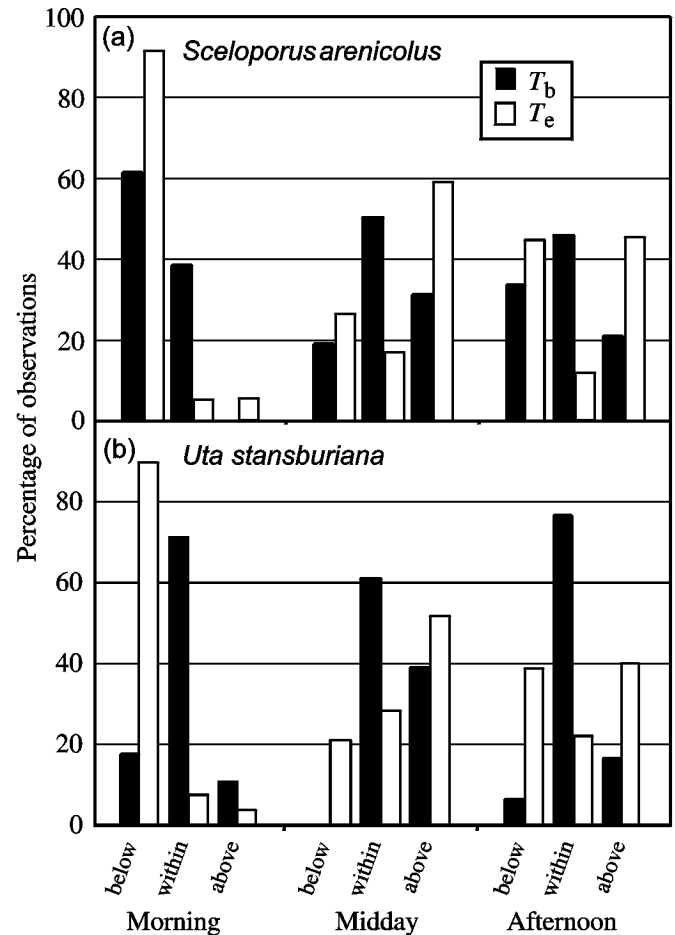


Fig. 10. Percentages of field body temperatures (T_b) or operative environmental temperatures (T_e) that were within the preferred body temperature (T_{sel}) range for *S. arenicolus* (a) and *U. stansburiana* (b) during the morning (08:00–11:20), at midday (11:21–14:40), and during the afternoon (14:41–19:00) over the entire study period.



These studies show that high midday temperatures preclude surface activity during the warm season in most or all microhabitats. Our study indicates that the period of diurnal activity is not severely restricted for these species at the time and place studied. In addition, there was no decline in activity levels at midday, when high temperatures often constrain lizard activity in deserts during summer. Indeed our data show that optimal temperatures are available for approximately 10 h during the day and are abundant for 2 h in mid-morning and another 2 h in late afternoon. Seasonal shifts in activity time are well documented in lizards (Huey and Pianka 1977). In hot environments, such as warm deserts, increased opportunities for activity in spring and fall may represent a benefit that overshadows the costs associated with the loss of midday activity in summer, especially if the loss of midday activity is accompanied by extended activity in early morning and late afternoon during the warm season (Grant and Dunham 1990). This is in contrast to higher latitudes or elevations where the highest thermal habitat quality (and the highest level of lizard activity) occurs at midday during summer (Grant and Dunham 1990; Christian and Weavers 1996; Grbac and Bauwens 2001). Conversely, in areas or times of high predation intensity, the period of activity may be minimized to avoid exposure to predators rather than exposure to adverse conditions.

The spatial distribution of reptiles is affected by many interacting factors, including interspecific interactions (Pianka 1973, 1975; Vitt et al. 2000), predator avoidance (Carrascal et al. 1992; Martin and López 1999), environmental temperature (Huey et al. 1989; Adolph 1990; Sartorius et al. 1999), reproduction (Anderson 1993), foraging (Durtsche 2000), and others. Our results suggest an interaction between different predator-avoidance strategies and differences in thermoregulatory effectiveness between species. *Sceloporus arenicolus* had a lower T_{sel} than *U. stansburiana*. In the field, *S. arenicolus* used microsites with lower T_e 's throughout the day and had a resulting low mean T_b . This microhabitat choice made *S. arenicolus* a less effective thermoregulator than *U. stansburiana* during those times of the day when T_e was low (morning, afternoon), despite its lower T_{sel} ; however, it was equally effective at thermoregulating at midday, when T_e 's were generally high, even in shaded microsites. The use of open space by *U. stansburiana* may confer a thermoregulatory advantage over *S. arenicolus* during periods of low temperature, but *S. arenicolus* may have the advantage during periods of high temperature. The ability to exploit lower temperatures is a potential fitness advantage in cool seasons or at high elevations for this widespread habitat generalist. To determine the relative influence of thermoregulation on community structure, future studies should focus on the extent to which species within an assemblage use different thermoregulatory strategies while pursuing similar resources.

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