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*Sceloporus Merriami***

Bruce W. Grant, Arthur E. Dunham

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## THERMALLY IMPOSED TIME CONSTRAINTS ON THE ACTIVITY OF THE DESERT LIZARD *SCELOPORUS MERRIAMI*<sup>1</sup>

BRUCE W. GRANT AND ARTHUR E. DUNHAM

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA

**Abstract.** We investigated the thermal biology of the lizard *Sceloporus merriami* in a hot, arid locality in west Texas. The effects of the thermal environment on lizard activity were hypothesized to be extensive because *S. merriami* body temperatures average lower than the body temperatures of any other North American desert iguanid (32.2°C). To test this hypothesis, we compared lizard thermal microclimate use and rates of lizard movements, feeding, and social displays with estimates of the relative availability of thermal microclimates near 32.2°. These comparisons were made throughout the lizards' morning activity period.

The thermal environment had a major impact on *S. merriami* and restricted individual activities (movement rates, feeding strikes, and social displays) to a 2-h period beginning around local sunrise (1000) and to a brief period in late afternoon. In the morning, rates of activities were maximal within 1 h after local sunrise. This activity maximum coincided with the time that the average available environmental temperature approximated the mean body temperature for *S. merriami*. Also at this time, lizards occupied thermal microclimates randomly with respect to microclimate availability on their home ranges, whereas when activity rates were lower, lizard microclimate use was nonrandom.

Thus, when thermally favorable microclimates were most available, lizard activity was least constrained. *S. merriami* timed the initiation, peak, and cessation of overall and microclimate-specific activity to coincide with the overall and microclimate-specific availability of favorable operative temperatures.

**Key words:** activity; biophysical ecology; *Sceloporus merriami*; thermal biology; thermal constraint; thermoregulation.

### INTRODUCTION

Thermal constraints on the time and energy budgets of ectothermic animals have been investigated for almost two decades (Bartlett and Gates 1967, Porter and Gates 1969, Porter and Tracy 1983). These constraints arise because the body temperature ( $T_b$ ) of an ectotherm is a complex function of its biophysical environment (Gates 1980). Thus, thermoregulating lizards are constrained to occupy specific thermal microclimates within their home ranges when they are active (to feed, defend territories, acquire mates, and avoid predators). These constraints are especially important for small lizards, with low thermal inertia, for which a failure to select an appropriate thermal microclimate for even a few minutes can result in temperature impairment or death.

Thermal constraints may be measured by comparing the pattern of thermal microclimate availability with that of use by lizards (Christian et al. 1983). For a diurnal desert lizard, thermal constraints vary in time because the physical environment is temporally and spatially variable in the intensity of solar radiation, air temperature, wind speed, etc. These climatic factors

interact with the surface heat transfer properties of a lizard (which are a function of its body size, shape, and color) to produce a distribution of available temperatures in time and space within which a lizard behaviorally discriminates. These available temperatures are "operative environmental temperatures" ( $T_e$ ) (Bakken and Gates 1975, Bakken 1980). The body temperatures a lizard will accept while it engages in activities such as foraging and social interactions, relative to the distribution of available operative temperatures, will dictate when, where, and for how long the lizard may be active (Porter and James 1979, Christian et al. 1983, Waldschmidt and Tracy 1983; see also Kingsolver 1983, Bennett et al. 1984). The constraint imposed by the thermal environment upon lizard activity and home range use at a given time may be quantified by measuring the relative spatial availability of acceptable thermal microclimates to a lizard within its home range.

We measured thermal constraints on activity and home range use during the breeding season (May–August) for a population of an iguanid lizard (*Sceloporus merriami*). We asked (1) to what extent are the observed patterns of lizard activity and home range use explained by the thermal constraints described above? and (2) how might these constraints vary for different body temperature "preferences?" To answer these

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questions, we gathered data on lizard body temperatures, rates of individual activities (movements, feeding, and social displays) and microclimate use, and thermal microclimate and operative environmental temperature availability.

## MATERIALS AND METHODS

### *Study species and locality*

*Sceloporus merriami* (Iguanidae) are small ( $\approx 5$  cm snout-vent length) saxicolous lizards that are locally common on rocky slopes among small outcrops below  $\approx 1800$  m elevation in the Big Bend region of west Texas and in Coahuila, Mexico. During the summer, males are very aggressive and are frequently observed in social interactions such as courtships and agonistic encounters with other males (Ruby and Dunham 1987). The study locality was on a west-facing slope of a wide canyon in the Grapevine Hills (29°25' N, 103°12' E, altitude 1036 m) in Big Bend National Park, Texas. The study site was 1.4 ha and had grid stakes at 10-m intervals. The population had been censused each summer since 1974 as part of an ongoing investigation of long-term variation in demography and life history (Dunham 1978, 1980, 1981, 1982, 1983). All lizards were permanently marked with unique toe-clips and were given unique paint marks (Dunham, 1981).

### *Temperatures exhibited by lizards*

Body temperatures (T<sub>b</sub>) were measured during the breeding seasons (May through August) of 1981–1985. Lizards were located by walking through the study site in an arbitrary direction. If a lizard was captured within the first few noosing attempts, its body temperature was measured within 20 s with a fast-reading Schulteis mercury thermometer. Time and weather conditions were also recorded. Since these captures were part of concurrent demography studies, data on sex, body size, and reproductive status (determined by palpation) were also recorded.

Operative environmental temperatures (T<sub>e</sub>) were measured at the exact location of perching lizards in 1984 with hollow-body copper models of *S. merriami*. These models were produced using techniques in Bakken and Gates (1975). We glued 0.13 mm diameter (36-gauge) thermocouples to a small plastic support in the chest area of the model, and painted each model to match the color pattern of *S. merriami*. The average spectral reflectivities of our models were within 5% of those for *S. merriami* (measured on a Beckman spectral-reflectometer). If a lizard remained stationary for 3 min, a copper model was placed in the exact same location and orientation as the lizard. The 3-min period was chosen to define lizards who were “perching.” Time and microclimate data (see below) were also recorded. After 2 min, the model temperatures had reached steady-state and were recorded using a handheld digital thermocouple reader (Omega Engineering

Model 871). Comparison of the temperatures of painted copper models with those of live lizards was performed in the field by comparing the measured body and perch temperatures for the same individual lizard.

### *Lizard time-activity patterns*

*S. merriami* activity was measured using continuous observations of individual lizards. In July 1983, five lizards (hereafter referred to as “focals”) were chosen at random for intensive observations from the pool of  $\approx 25$  socially dominant male lizards on the study site. Social status was determined by witnessing the outcomes of naturally occurring agonistic encounters. When a subordinate male encounters a dominant, only the dominant will display, and the subordinate will move away or run away if chased by the dominant (Carpenter 1961, Ruby and Dunham 1987). We chose focal lizards from the set of dominant males for two reasons. First, dominants were generally more conspicuous in their behaviors than nondominants or females, and were easier to find and monitor. Second, more information would be gained about the temporal pattern of social activity from dominant males than from nondominant males, which tend to avoid social interaction, or from females, which tend to interact much less frequently with lizards of either sex (Dunham 1981, Ruby and Dunham 1987). Undoubtedly, the absolute rates of some activities (e.g., movements and displays) differ among the dominant and nondominant males and females. Nevertheless, because their body temperatures are similar (see Results: Lizard Body Temperature), the timing of these activities should be similar among classes.

For each focal, an observer was assigned one of the five lizards to locate and watch for 30 min from a distance such that the lizard was not disturbed. During six consecutive blocks of 5 min, the observer recorded the number and distances of movements, the number of behavioral displays (push-ups or dorso-ventral flattening), and the number of feeding strikes. Observers were generally too far from the lizard to assess feeding-strike success. Normally, each of the five lizards was observed opportunistically for two nonconsecutive focal periods each morning; however, on several days we were unable to find all five lizards a second time. All focal data were recorded under cloudless and dry conditions.

Rates of movements, displays, and feeding strikes were calculated for each 5-min block of each focal. These rates were averaged at half-hourly intervals between 0900 and 1200 Central Daylight Time (CDT) by pooling blocks among all lizards and focals. During midsummer on this site *S. merriami* daily activity is bimodal with a distinct morning and evening activity period separated by several hours of midday inactivity (see Results: Lizard Time-Activity Patterns). The time period 0900–1200 was chosen to cover morning activity by *S. merriami*, and we acknowledge the possibility

of error in extrapolating interpretations of data taken in the morning to the evening.

#### *Microclimate use*

We estimated the temporal pattern of lizard microclimate use during midsummer of 1983 and 1984 using a two-dimensional matrix that describes physical aspects of the thermal environment. The first dimension had five states of perch substrate: rock faces, rock edges, gravel and stones, vegetation, and "interior" areas (caves and crevices). Rocks were distinguished from stones by a subjective estimate of size ("rocks" were > 1 m in smallest linear dimension). Rock faces were distinguished from rock edges by a subjective estimate of curvature ("faces" had less curvature than a basketball).

The second matrix dimension had seven states of incident solar radiation upon the perch substrate: full sun, oblique sun, tangent sun, sunlight filtering through vegetation, full shade of vegetation, full shade of rock and open to the sky, and full shade in an "interior" area. For "full sun," the substrate was nearly perpendicular to direct solar radiation. For "oblique sun," the angle between the normal vector to the substrate and the vector to the sun was between 20° and 70°. For "tangent sun," the substrate was nearly parallel to direct solar radiation.

Lizards were located by walking through the study site in an arbitrary direction. If a lizard was observed to be stationary for 3 min, it was assigned to one of the elements in the microclimate matrix. Time, weather conditions, and the lizard's unique paint mark were also recorded. Observations for all lizards and dates were pooled into half-hourly intervals until 1200, and into hourly intervals from 1200 to 2000. In the summer, local sunrise (LSR) on this site occurs between 0945 and 1015; consequently, observations between 0930 and 1030 were further classified as "before" or "after" LSR. Within each interval, the proportion of observations for each element in the microclimate use matrix was calculated.

#### *Microclimate availability*

The temporal pattern of microclimate availability was estimated using transect sampling. We laid out a total of 200 m of transect line segments, flush with ground and rock surfaces, in areas known to lie completely within the home ranges of three dominant male lizards in 1983. The three home ranges were selected arbitrarily from three different habitat types within the study area (a cliff area, a sloping boulder field, and near a sandy arroyo at the base of the study area). Within each home range, we laid out parallel transect segments, spaced several metres apart, where the end-points of transect segments lay on the boundary of the minimum convex polygon encompassing all ( $X$ ,  $Y$ ) observations of the resident lizard (Turner et al. 1969, Ruby and Dunham 1987). At 1-m intervals along these

transects, one sample point (small tape square) was affixed to the substrate and two more points were placed ½ m away on either side perpendicular to the transect.

All transect segments were walked at half-hourly intervals until 1300, and all 617 sample points were individually classified to one of the substrate (constant) and solar radiation (variable in time) states defined above (see Microclimate Use). Within each time interval, the proportion of observations of a given microclimate class was calculated. This technique of estimating microclimate availability samples the exposed habitat on an equal surface area basis (see Huey and Pianka 1977, for other techniques). Our methods were inadequate to sample small cracks, crevices, and other "interior" areas. No sample points were placed in any "interior" microclimate, and transect segments jumped such openings.

Comparisons of the frequencies of microclimate observations for lizards and for transect points were made using a vector space technique similar to standard overlap measures (Petraitis 1983). For each time interval ( $t$ ), we defined a  $p$  dimensional vector space for the  $p$  possible states to which a given observation may be assigned. Within the positive sector of this space there will be two vectors of unit length: one representing the frequency data on observations of lizards,  $\vec{O}(t)$ ; and one representing the observations of transect points,  $\vec{T}(t)$ . The magnitude of each vector along each axis equals the proportion of observations for that state. Thus, for a given time interval, the magnitude of the vector difference,

$$\|\vec{O}(t) - \vec{T}(t)\| = \left\{ \sum_{i=1,p} [O_i(t) - T_i(t)]^2 \right\}^{1/2},$$

may be used to measure the similarity between microclimate availability and use by lizards. Low values denote high similarity. The maximum difference is  $\sqrt{2}$ , and results if the two vectors are orthogonal.

#### *Operative temperature availability*

The temporal pattern of operative environmental temperatures available to *S. merriami* was estimated using the hollow-body copper models described above. Models were placed in locations that corresponded to four elements of the microclimate use matrix. These four were (1) rock face in full sun, (2) rock face in oblique sun, (3) rock edge in tangent sun (with the nose of the model pointed at a 45° angle from the sun), and (4) rock face in full shade and open to the sky.

Three typical (cloudless and dry) sampling dates were chosen for these measurements in the summer of 1984: 30 June and 15 and 18 July. At the beginning of each sampling date, each model to be used (between 10 and 15 models on each date) was randomly assigned to one of the four microclimate combinations. Each model temperature was taken at intervals of not less than 6 min, and no more than four times per half hour. All model temperatures were recorded using a hand-held

TABLE 1. Body temperature data under cloudless weather conditions and between local sunrise ( $\approx 1000$  Central Daylight Time) and solar noon (1353). A two-way Analysis of Covariance (with time of day as the covariate) revealed significant differences among years but not sex classes. No interactions were significant.

	1981	1982	1983	1984	1985	1981-1985
	$\bar{X} \pm 1 \text{ SD } (n)$	$\bar{X} \pm 1 \text{ SD } (n)$	$\bar{X} \pm 1 \text{ SD } (n)$	$\bar{X} \pm 1 \text{ SD } (n)$	$\bar{X} \pm 1 \text{ SD } (n)$	$\bar{X} \pm 1 \text{ SD } (n)$
Male	32.6 $\pm$ 2.6 (26)	31.5 $\pm$ 1.9 (36)	31.7 $\pm$ 2.9 (25)	32.9 $\pm$ 1.6 (30)	32.8 $\pm$ 2.2 (36)	32.3 $\pm$ 2.3 (153)
Female	32.2 $\pm$ 1.0 (8)	31.9 $\pm$ 1.6 (31)	31.7 $\pm$ 2.0 (21)	31.8 $\pm$ 1.7 (18)	32.4 $\pm$ 1.9 (31)	32.0 $\pm$ 1.7 (109)
Both sexes	32.5 $\pm$ 2.3 (34)	31.7 $\pm$ 1.7 (67)	31.7 $\pm$ 2.5 (46)	32.5 $\pm$ 1.7 (48)	32.6 $\pm$ 2.0 (67)	32.2 $\pm$ 2.1 (262)

Omega Engineering Model 871 digital thermocouple reader. Variability in the number of models and the frequency of readings at different times and on different dates stemmed from differences in the availability of assistants. At each  $\frac{1}{2}$  h between 0900 and 1200, and at hourly intervals after 1200, each model was moved to a different location in the habitat that corresponded to its pre-assigned combination of perch substrate and incident solar radiation states. Average operative temperatures for each microclimate combination were calculated for  $\frac{1}{2}$ -h intervals until 1200, and hourly after 1200, by pooling data from different copper models and different sampling dates.

To test for differences in  $T_e$  for different substrate classes of the same solar radiation state, additional copper models were deployed on 18 July to compare rock faces with rock edges in full and tangent sun and in full shade of rock, and with gravel in full sun and full shade.

## RESULTS

### *Lizard body temperatures*

Body temperatures for adult *S. merriami* under cloudless conditions between local sunrise ( $\approx 1000$ ) and solar noon (1353) and for all years and sexes combined, averaged 32.2°C, (1 SD = 2.1°, median = 32.3°,  $n = 262$ ). Among years and sexes,  $T_b$  averages differed at most by 1.4° (Table 1). These differences were significant among years but not among sex classes (two-way ANCOVA, with time as the covariate;  $P < .02$  and  $P = .069$ , respectively; no interaction). During the morning activity period, lizards exhibited fairly consistent body and perch operative temperature averages once local sunrise had occurred (Fig. 1). The pooled within-year slope of body temperature vs. time was slightly and significantly positive (necessitating the use of the ANCOVA above), but the rate of increase was  $< 1^\circ/\text{h}$ . The average perch operative temperature between local sunrise and solar noon in 1984, the only year these data were taken, was 32.6° (1 SD = 2.2°,  $n = 113$ ), which did not differ from the average  $T_b$  for 1984 in Table 1 (ANCOVA, with time as the covariate;  $F_{1,158} = 0.196$ ,  $P > .05$ ). Further,  $T_b$  and  $T_e$  measured for the same individual lizards did not differ (two-tailed paired  $t$  test = 0.741,  $n = 27$ ,  $P > .05$ ), indicating that

lizard body temperatures reflected thermal microclimate use.

### *Lizard time-activity patterns*

Data from focal observations indicated that a broad peak in rates of lizard movements occurred between 0930 and 1130 (Fig. 2). Within this time interval, average frequencies of social displays and foraging strikes were also maximal, with the maximum for feeding slightly earlier than the maximum for displays (Fig. 3). In fact, there was a significant negative rank correlation between feeding and displays among the 179 5-min periods in which at least one of these behaviors occurred (Spearman  $R$  for large  $N$ ;  $t = 2.1237$ ,  $P < .025$ ; Siegel 1956). This pattern suggests that the focal lizards, dominant males, did not simultaneously feed and socially interact.

### *Lizard microclimate use and comparisons with availability*

*Perch substrate class.*—Although approximately half of all exposed surface area within the sampled lizard home ranges consisted of gravel and stones (307/617 transect points), all lizards were observed perching on rocks ( $n = 522$ ). Lizards will traverse gravel patches when moving between rocks within their home ranges and have been observed feeding on gravel near rocks; however they do not tarry on gravel (B. W. Grant and A. E. Dunham, *personal observation*).

The number of observations of female lizards on rock faces and edges did not differ from the expected number as determined by their occurrence in transects ( $\chi^2 = 0.111$ , for 93 females and 310 transect points on rocks,  $P > .05$ ). However, males perched on rock edges almost twice as frequently as edges occurred ( $\chi^2 = 36.58$ , for 293 males and 310 transect points,  $P < .001$ ).

*Solar radiation to the perch substrate.*—Before local sunrise (1000), most lizards were out in open shade (Fig. 4A). Immediately following local sunrise,  $> 75\%$  of the lizards observed were perched in sun (full, oblique, or tangent) whereas only 15.5% of the exposed rock surface was in the sun at this time (Fig. 4B). For the next 90 min, lizards used the greatest diversity of microclimates, and used progressively fewer perches in the sun. At the same time the diversity of available microclimates increased, whereas the frequency of mi-

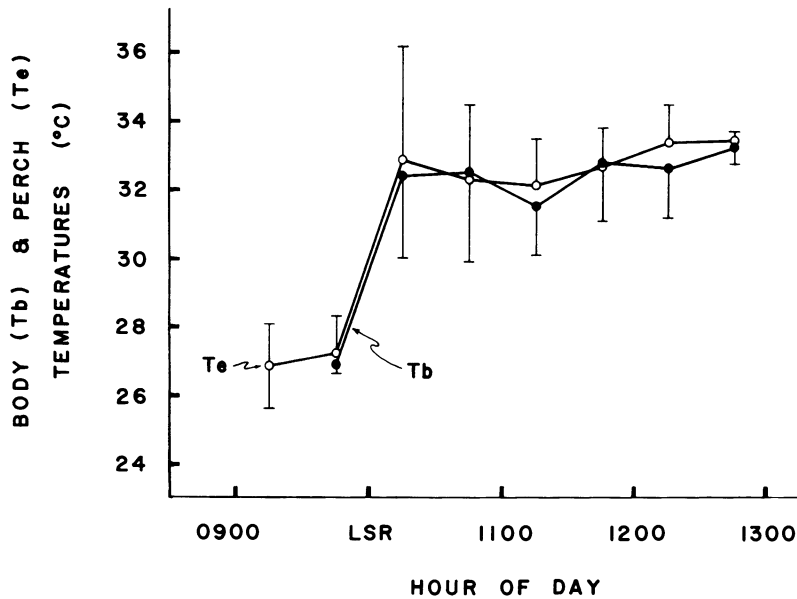


FIG. 1. Body temperature averages (●) and averages of perch operative environmental temperatures determined from painted copper model lizards (○) ( $\bar{X} + 1$  SD) between 0900 and 1300 (Central Daylight Time) for cloudless conditions in 1984. LSR refers to local sunrise.

croclimates available in the shade decreased. Between 1130 and 1300, open shade represented <30% of the habitat, while 70% or more of the lizards were perched in shade.

During midafternoon, lizards had retreated to caves and crevices. Almost all lizards observed (via our crawling) in interior areas were immobile, relatively unresponsive to approach, and many had closed their eyes. These observations suggest that lizards in interior areas were inactive. Between 1800 and sunset (2000),  $\approx 35\%$  ( $n = 42$ ) of the lizards observed emerged and occupied shaded microclimates for a brief period of activity before darkness (not shown in Fig. 4). These lizards are not abroad after darkness at  $\approx 2100$  (B. W. Grant and A. E. Dunham, *personal observation*).

It is apparent (Fig. 4) that the frequencies at which microclimates were used differed greatly from the frequencies at which microclimates were available for most of the day. To quantify this difference, we calculated the magnitude of the vector difference between the vectors of microclimate use and availability (Fig. 5A). This vector space was delineated by the six states of incident solar radiation on the substrate, with the exception of rock interiors. Immediately following LSR, the vector difference was great because the microclimate availability vector was in the region of the vector space corresponding to greater shade and the lizard microclimate utilization vector leaned more toward sun. The vectors of microclimate use and availability converged just after 1100 in 1983 and just before 1100 in 1984. After 1130, the vectors of microclimate use moved toward the region of the vector space that the availability vector occupied just after sunrise. At the

minima of the vector differences for the two sampling years and at no other times, the distributions of counts for observations of lizards vs. transect points did not differ ( $\chi^2 = 6.185$  for 29 lizards in 1983,  $P > .05$ ; and  $\chi^2 = 4.028$  for 28 lizards in 1984,  $P > .05$ ). Therefore, at the times of these minima, lizards were using microclimates at random, whereas at all other times, lizards were using them nonrandomly.

The differences between 1983 and 1984 in the timing of the minimum vector difference between microclimate use and availability may have been due to sampling error. There was no significant difference among years in average air temperature for June and July at the National Park Service Panther Junction weather station  $\approx 8$  km to the south of the study site ( $t$  test = 0.011,  $df = 120$ ,  $P > .05$ ). Further, the differences in Fig. 5A stemmed from a slightly greater usage of sunlit perches  $\approx 1100$  in 1983 than in 1984; however, body temperatures averaged slightly lower in 1983 than in 1984 (Table 1).

#### *Operative temperature availability*

The range of operative temperatures available to *S. merriami* (from microclimates in full, oblique, and tangent sun, and in full shade of rock) is presented in Fig. 6.

Comparisons of rock faces and edges revealed only slight differences in operative temperature through time. In full shade during the morning, operative temperatures for rock faces did not differ from those on rock edges (ANCOVA, with time as the covariate;  $F_{1,113} = 1.556$ ,  $P > .05$ ). However, tangent sun rock faces averaged  $\approx 1^\circ$  warmer than tangent sun rock edges (AN-

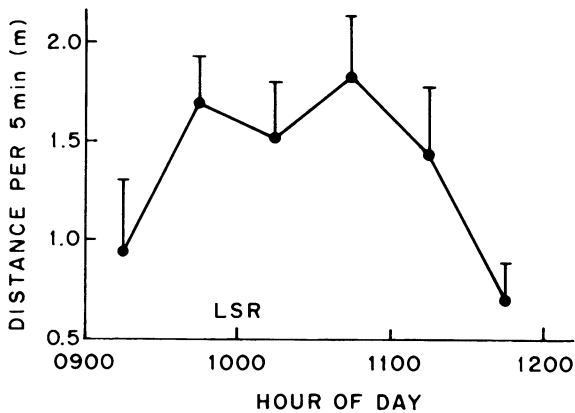


FIG. 2. Rates of lizard movement ( $\bar{X} + 1$  SD) for focal *Sceloporus merriami* between 0900 and 1200 (Central Daylight Time). LSR refers to local sunrise.

COVA, with time as the covariate;  $F_{1,113} = 12.748$ ,  $P < .01$ ). In full sun, the pattern was slightly more complex since the linear regressions of  $T_e$  vs. time for faces and edges crossed. However, immediately after LSR when lizards were seen perching in full sun microclimates, rock faces in full sun were slightly warmer than edges (by  $\approx 1^\circ$ ).

Gravel patches in full shade throughout the morning were consistently cooler by  $\approx 2^\circ$  than rock faces in full shade (ANCOVA, with time as the covariate;  $F_{1,135} = 237.5$ ,  $P < .001$ ). Gravel patches immediately after sunrise exhibited fairly cool operative temperatures (on the order of tangent sun rock edge in Fig. 6). However, gravel in the sun heated very quickly and had operative temperatures  $10^\circ$  above the highest measured on rocks by 1230 (compare with full sun in Fig. 6). The highest  $T_e$  recorded was  $66.0^\circ$  and was on gravel at 1544.

#### DISCUSSION

Many of the lizard behavior patterns described above may be explained wholly or in part by patterns of temperature availability. For example, Fig. 6 offers specific predictions about when thermoregulating lizards should be active and in what specific microclimates activity should occur in order to maintain  $T_b$  near  $32.2^\circ\text{C}$ .

1) Activity should begin at local sunrise when favorable operative temperatures are first available. Our activity data generally support this prediction (Figs. 2 and 3). There was a large increase in movements, displays, and total distance traveled for times near local sunrise. Interestingly, most lizards were on the surface and in open shade well before LSR (Fig. 4A), and many were moving about their home ranges at body temperatures of  $27^\circ$  and lower (see below).

2) Microclimates in full oblique sun should only be used immediately following LSR for basking because the operative temperatures for these microclimates greatly exceeded  $32.2^\circ$ . It is clear that the lizards used these classes most at this time (Fig. 4A). Also, note

that the high variance in average  $T_b$  and perch  $T_e$  for the time interval LSR-1030 (Fig. 1) is consistent with observations of basking (Fig. 4A). Between 1030 and 1200, some individuals were still found in full and oblique sun. Of 21 observations of lizards perched in oblique sun after 1030, 11 also included an estimate of perch  $T_e$ . The average  $T_e$  for this group was  $34.2^\circ$ , which is well below the averages for available oblique sun in Fig. 6. Thus, many of these lizards were perched in very cool locations relative to most other locations of the same microclimate type.

3) Microclimates in tangent sun should be maximally used between 1100 and 1130, when the average  $T_e$  of this microclimate type roughly equaled  $32.2^\circ$ , and tangent sun should be abandoned by  $\approx 1200$ . These predictions are generally supported in Fig. 4A. Similar to prediction (2), lizards perching in tangent sun microclimates between 1200 and 1300 tended to perch in cool locations (average perch  $T_e$  of  $34.0^\circ$ ) relative to average tangent sun operative temperatures after 1200 ( $35.8^\circ$ ; Fig. 6).

4) All activity should cease between 1300 and 1400, and lizards should retreat from open shade into caves and crevices. Sunlit areas were totally abandoned by 1300, and most of the lizards were perched in rock "interior" areas (Fig. 4A). Although we do not have quantitative activity data past 1200, it is apparent that activity had rapidly declined by this time (Figs. 2 and 3). In fact, it appears as if animals abandoned activity and sought interiors earlier than would be predicted by temperature constraints alone. Since our activity indices were based on lizard movements and behaviors rather than lizard conspicuousness, it may be that individuals did not move very much for times approaching 1200 because thermally favorable microclimates became rare. Open shade represented  $<20\%$  of the habitat (Fig. 4B), and the average distance per move

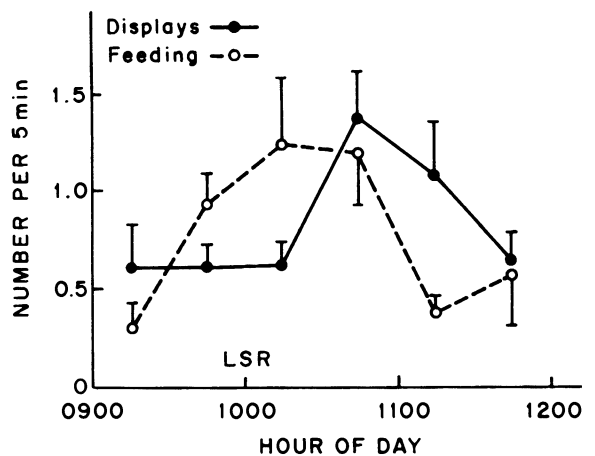


FIG. 3. Frequencies of behavioral displays and feeding strikes ( $\bar{X} + 1$  SD) for focal *Sceloporus merriami* between 0900 and 1200 (Central Daylight Time). LSR refers to local sunrise.

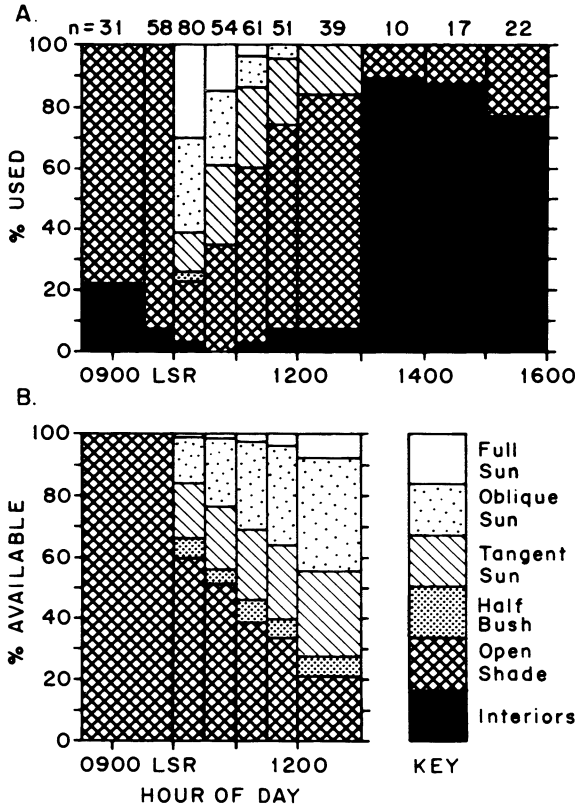


FIG. 4. (A) The temporal pattern of microclimates used by perching lizards under cloudless conditions. All observations of perching lizards were from rock microclimates. For this figure, data for 1983 and 1984, and for males and females, were pooled. Also, rock faces and rock edges were pooled for each solar radiation state, and full shade of vegetation was pooled with open shade of rock. Sample sizes (*n*) of observations of perching lizards per time interval are indicated across the top. (B) The temporal pattern of microhabitats available to lizards on rocks. Data were pooled as in (A). All proportions are based on the same set of 310 transect points on rocks. LSR refers to local sunrise.

was maximum at this time. Toward noon, thermally favorable microclimates tended to be surrounded by thermally stressful ones. Thus lizard movements and home range use appear to be constrained by the overall distribution of available operative temperatures rather than the range per se, even though individuals occupy only one microclimate at a time.

To quantify this suggestion, we combined data from Figs. 4B and 6 to estimate the average available operative temperature per time by summing the product of the microclimate temperatures times their relative abundance. Because we did not estimate operative temperatures for all microclimates, we lumped all rock faces and edges for each state of incident solar radiation, and lumped all open shade classes. Our estimate of the average available operative temperature appears in Fig. 5B.

Note that when the average available operative tem-

perature approximately equaled 32.2° at ≈1100, the vectors of microclimate use and availability did not differ (Fig. 5A). Also at this time, lizard movements, displays, and feeding were near maximal rates (Figs. 2 and 3). Thus when the average available operative temperature is most similar to the average lizard activity temperature, home range use by *S. merriami* is least constrained, lizards use microclimates randomly, and activity is at its peak. In summary, the observed patterns of overall activity and microclimate use with respect to substrate solar radiation are generally consistent with predictions based on patterns of temperature availability.

A different conclusion results when microhabitat use with respect to substrate class is compared with temperature availability. For example, male lizards non-

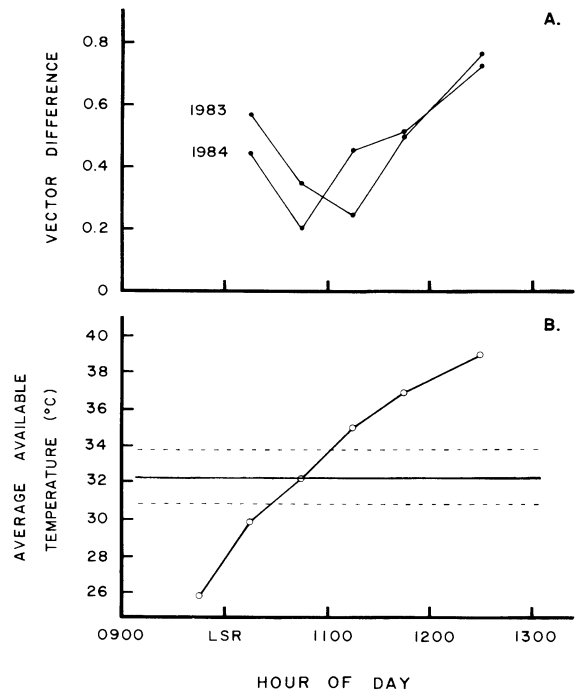


FIG. 5. (A) The magnitude of the vector difference between the vectors of microclimate use by perching *Sceloporus merriami* and rock microclimate availability. This vector difference is defined within a six-dimensional space delineated by six states of incident solar radiation on the substrate: full sun, oblique sun, tangent sun, sunlight filtered by vegetation, full shade of vegetation, and full shade of rock but open to the sky. Low values of this vector difference denote high similarity between the vectors of use and availability. (B) An estimate of the average rock surface operative temperature available to *S. merriami* through time. This estimate was made by summing the product of microclimate- and time-specific average temperatures times their relative abundance. Because we did not estimate temperatures for all microclimates, we pooled all substrate classes for each state of incident solar radiation. The solid line at 32.2°C is the average morning body temperature of *S. merriami*, and the dotted lines at 30.8° and 33.8° enclose 50% of all Tb records. LSR refers to local sunrise.



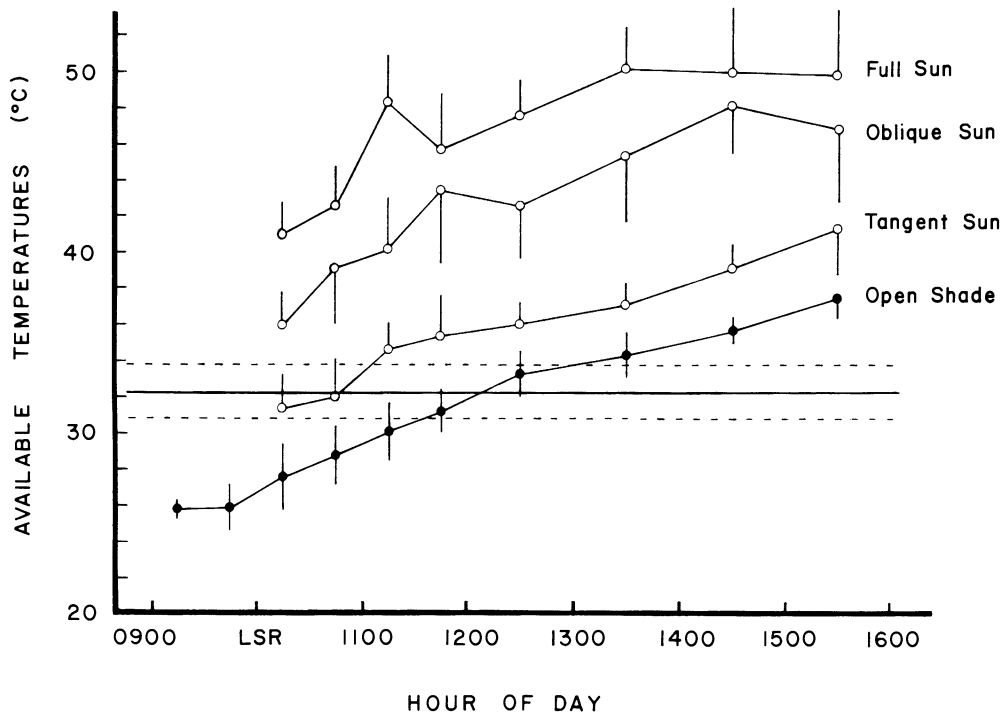


FIG. 6. Average operative environmental temperatures ( $\pm 1$  SD) available to *Sceloporus merriami* in four microclimate types. Each point represents 12 or more measurements of painted copper model lizards. The solid line at 32.2°C is the average morning body temperature of *S. merriami*, and the dotted lines at 30.8° and 33.8° enclose 50% of all Tb records. LSR refers to local sunrise.

randomly selected rock edges rather than rock faces whereas females used faces and edges at random. There were no differences in  $T_e$  averages during the morning between rock faces and rock edges in full shade, and only slight and inconsistent differences in the sun (for which there was a trend for operative temperatures for rock faces to exceed those of rock edges). However, male body temperatures equal those of females, thus the greater use of rock edges by males seems unlikely to be due to temperature. Alternatively, the greater use of edges by males could be due to the polygynous social system of *S. merriami*. Larger males are territorial and aggressively defend their territories against intruding males and actively approach and engage in courtship displays at nearby females (Ruby and Dunham 1987 and A. E. Dunham *personal observation*). Rock edges may afford increased visibility to surrounding rock surfaces for detecting potential reproductive competitors or mates. Some support for this suggestion comes from a significant correlation between male display rates (Fig. 3) and the proportions of rock edges used by males through time ( $R^2 = 0.8232$ ,  $n = 6$ ,  $P < .05$ ).

As another example, the avoidance of gravel and stones by lizards cannot be explained by temperature availability. Because gravel operative temperatures in the shade were only  $\approx 2^\circ$  cooler than operative temperatures on rocks in open shade, and because shaded gravel was as common as shaded rock throughout the

morning, lizards should not discriminate between shaded gravel and rock on the basis of temperature. Gravel in sun was first cooler (at LSR), then hotter (after 1100), than rock in sun. Thus, during activity in the early morning, lizards should not discriminate between sunlit gravel and sunlit rock on the basis of temperature. We suspect that similar statements could be made about stones, and yet lizards only perch on rocks. An alternative explanation is that this pattern is due to predation. Avoiding gravel may decrease exposure to predators, including several species of rattlesnakes and whipsnakes (Dunham 1981), which are typically found on or near the ground (B. W. Grant and A. E. Dunham, *personal observation*). These counterexamples clearly indicate that temperature availability is not the only constraint on lizard microclimate selection. Nonetheless, the observed patterns of temperature availability account for the majority of observed variation in lizard activity and home range use.

The narrowness of the activity window for *S. merriami* suggests that these lizards may be severely time constrained by the limited availability of favorable operative temperatures on this site because of their low average activity temperature. In Brattstrom's (1965) extensive review of reptile body temperatures, there are  $\approx 20$  iguanids that could be classified as inhabiting low to midelevation deserts in North America. The average Tb for this group is  $>4^\circ$  above the value we

report here. In fact, *S. merriami* exhibits the lowest body temperature in this group and exhibits a Tb that is comparable to many Central American and the Caribbean iguanids (Avery 1982). If *S. merriami* were to allow a Tb more comparable to other desert iguanids (raise the line at 32.2° in Fig. 6 by 4°), *S. merriami* could occupy open shade microhabitats until well after 1400 and greatly increase the time available for daily activity. However, open shade is infrequent in the habitat at this time (Fig. 3B); and an increased Tb may not reduce thermal constraints on activity and home range use as much as would be predicted by examining only the range of available operative temperatures (Fig. 6). The important consideration in delineating thermal constraints on lizards may well be the actual distribution of available operative temperatures to lizards and not just the range.

The observation that lizards were moving about their home ranges (Fig. 2) and feeding (Fig. 3) prior to local sunrise at body temperatures 5° cooler than after sunrise (Fig. 1) is consistent with the above suggestion. Since the habitat is uniformly shaded, all available operative temperatures are similar and ≈5°–6° cooler than the average Tb for *S. merriami* after LSR. Thus, a lizard tolerating a 5° lower Tb could move about in its home range and feed unconstrained by temperature availability at this time.

Accepting a higher, or lower, Tb to attain an increase in activity time could benefit a lizard in several ways. During activity, lizards allocate time to meet requirements of foraging and social interactions. Increased activity time may translate into greater daily food consumption, and/or increased courtships and territorial encounters. When integrated over a breeding season, foraging time and environmental resource availability will influence the total amount of energy and water for allocation to the competing functions of growth, maintenance, storage, and reproduction in a life history (Congdon et al. 1982). Further, time spent in social interactions (especially for males) along with local population parameters, such as density of potential mates and reproductive competitors, will determine encounter and courtship rates, mating success, social status, territory size, and other factors relating to the conversion of energy allocated to reproduction into offspring. An individual *S. merriami* that regulated a higher, or lower, Tb could benefit from an increase in activity time if more food could be eaten or more matings could be obtained per day. However, costs could be incurred due to decreased physiological performance (e.g., in terms of locomotion, digestion, etc.) and concomitant increase in mortality, or, for the case of higher Tb, lizards will incur increased metabolic and water loss rates possibly resulting in resource demands in excess of environmental supply. Elucidating the costs and benefits of regulating a particular body temperature in a particular environment, requires an understanding of the Tb dependence of environmental thermal con-

straints on activities, such as foraging and social interactions, as well as of the Tb dependence of physiological performance.

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