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## TRADE-OFFS IN ACTIVITY TIME AND PHYSIOLOGICAL PERFORMANCE FOR THERMOREGULATING DESERT LIZARDS, *SCELOPORUS MERRIAMII*<sup>1</sup>

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**Abstract.** Average body temperatures ( $T_b$ ) of summer-active *Sceloporus merriami* were lower in the morning (33.3°C) than in the evening (37.0°) at an arid locality in Big Bend National Park, Texas. During midafternoon, lizards were inactive and retreated to deep crevices and caves. According to a multivariate analysis, overall rates of lizard activities (movements, feeding, and social displays) were similar between morning and evening activity, indicating that lizards were behaving similarly during the different activity periods. However, at 37°, estimated rates of metabolism and water loss were greater and sprint speed was lower relative to these rates at 33°, suggesting that substantial resource and performance costs may have been imposed by the observed higher evening activity  $T_b$ .

To investigate this unusual pattern of body temperature variation, I compared the morning and evening distributions of available operative environmental temperatures ( $T_e$ ) as estimated by an array of randomly deployed and oriented copper models of *S. merriami* placed on rock and ground surfaces within lizard home ranges. In the morning, lizards had access to a wide range of  $T_e$  (30°–60°), and a large fraction of the  $T_e$  distribution was below 36° at the time of peak morning activity. During the morning, a hypothetical increase in  $T_b$  to within the interval 36°–38° would have allowed lizards to occupy <10% more of the available thermal microclimates. But in the evening, most of the available microclimates were in the interval 36°–38° (>90% depending on the exact time), and microclimates below 36° were unavailable until just before dark. The available  $T_e$  distributions in the evening forced lizards to accept a higher activity  $T_b$ , and concomitantly higher metabolic and water loss rates, and lower locomotor performance, or remain inactive in crevices and caves. Thus in the evening, and not in the morning, the gain in usable home range due to accepting a higher  $T_b$  was great, and the lizards exploited this fraction at an increased  $T_b$  only in the evening. These data suggest that the distribution of available  $T_e$  can directly influence the cost/benefit economics of lizard body temperature selection.

**Key words:** activity; biophysical constraints; body temperature; Chihuahuan Desert; desert lizard; operative environmental temperature; performance; *Sceloporus merriami*; thermal constraints; thermoregulation.

### INTRODUCTION

Small lizards regulate their body temperatures ( $T_b$ ) by behaviorally selecting appropriate thermal microclimates (e.g., Cowles and Bogert 1944). Costs and benefits of regulating a particular  $T_b$ , within the available distribution of operative environmental temperatures,  $T_e$  (Porter et al. 1973, Bakken and Gates 1975, Bakken 1976), derive from two principal sources (Huey and Slatkin 1976, Huey 1982, Beuchat and Ellner 1987). The first source involves the temperature dependence of physiological performance such as locomotor ability (Huey and Stevenson 1979, Bennett 1980, Huey 1982, Huey and Hertz 1982, 1984, Hertz et al. 1983, Waldschmidt and Tracy 1983), food processing capacity (Dawson 1975, Windell and Sarokon 1976, Waldschmidt et al. 1986), and expenditure of assimilated

energy and water resources on physiological maintenance (Porter and James 1979, Congdon et al. 1982, Crowder and Magnuson 1983, Porter and Tracy 1983). This source of costs and benefits has received a great deal of attention in a variety of lizard systems (reviewed by Huey and Stevenson 1979, Huey 1982).

The second source of costs and benefits relates to how spatiotemporal variation in  $T_e$  availability constrains activity and home range use (DeWitt 1967, Huey 1974b, Huey and Slatkin 1976, Tracy 1982, Christian et al. 1983, Tracy and Christian 1986, Grant and Dunham 1988). For small lizards with low thermal inertia, constraints on activity may be quantified for a particular time and  $T_b$  by measuring the frequency distribution of available thermal microclimates and determining the fraction in which this particular  $T_b$  may be attained (Grant and Dunham 1988). If this fraction is low, then activity is highly constrained at this time for this  $T_b$ , and a lizard may have to expend energy and risk exposure to predation in locating a suitable thermal microclimate (Huey 1974a, b, 1982), or become

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inactive. If all available microclimates exhibit a suitable  $T_e$  at a given time, then activity is unconstrained by temperature at that time.

Body temperatures of active lizards are known to vary among species in syntopy (Bogert 1949, Brattstrom 1965, Vitt 1974, Huey and Pianka 1977, 1983, Hertz 1979, Roughgarden et al. 1981, Avery 1982, Bowker 1984), among populations of the same species that differ altitudinally or geographically (Burns 1970, Clark and Kroll 1974, Hertz 1981, Hertz and Huey 1981, Grant and Dunham 1990), among seasons for the same population (Ballinger et al. 1969, 1970, Case 1976, Huey and Pianka 1977, Christian et al. 1983), and among individuals that differ in reproductive condition (Stewart 1984, Beuchat 1986). However, the above sources of variation have yet to be codified in a synthetic theory that views temperature selection as a result of ecological compromises between constraints on individual activity and physiological performance (Huey and Slatkin 1976, Beuchat and Ellner 1987). Since few studies have simultaneously estimated covariation in individual activity constraints and performance, it has proven difficult to develop a rigorous cost/benefit theory (but see McFarland 1976, Waldschmidt and Tracy 1983). An aim of the present study was to provide such a database.

I studied thermal constraints on activity as a source of costs and benefits of temperature regulation to the desert lizard *Sceloporus merriami* at an arid locality, Boquillas, in Big Bend National Park, Texas. I show that these lizards had lower body temperatures during activity in the morning than in the evening (averaging 33.3° and 37.0°C, respectively). Despite differences in  $T_b$ , overall rates of activity relating to feeding and social biology were indistinguishable during the morning and evening activity periods. Previous studies at higher elevation sites in Big Bend and at Boquillas during the fall and spring showed that the lower average of 33° is typical for active *S. merriami* (Grant and Dunham 1988, 1990, Dunham et al. 1989, B. W. Grant and S. R. Waldschmidt, *personal observation*). Further, increasing  $T_b$  from 33° to 37° substantially reduces locomotor ability and increases resource expenditure (Huey and Dunham 1987, P. Niewiarowski and S. R. Waldschmidt, *unpublished manuscript*).

DeWitt (1967) suggested that allowing above normal body temperatures should benefit a lizard if this results in increased daily activity time, or in other words, if a higher  $T_b$  reduces the constraint on its activity. Thus, the benefit of accepting a higher  $T_b$  and extending daily activity time for foraging and social interactions must be weighed against the performance costs and resource expenditures that result from higher  $T_b$  (Huey 1982). A critical determinant of this trade-off is the increase in the fraction of usable habitat due to accepting microclimates in which the warmer  $T_b$  may be obtained, or alternatively, by the decrease in the amount by which activity is constrained. The observed difference in  $T_b$

is hypothesized to arise if the corresponding marginal increase in usable habitat is large only in the evening. To test this hypothesis, I used arrays of painted copper models of *S. merriami* to estimate the temporal distribution of  $T_e$ , and compared the fraction of model temperatures near the observed averages of  $T_b$  in the morning and evening. These fractions are a direct measure of thermal constraints on activity as a function of  $T_b$  and time.

#### MATERIALS AND METHODS

*Study system.*—The Boquillas study site is a narrow north-south oriented canyon 180 m in length, from 20 to 60 m in width, and at an elevation of 560 m in Big Bend National Park, Texas. This site has grid stakes at 10-m intervals. Plant cover is sparse, and species composition is characteristic of the lowland Chihuahuan desert biome (Wauer 1971). Limestone outcrops containing numerous cracks and solution caves line the sides of the canyon.

The canyon lizard, *Sceloporus merriami*, is a small ( $\approx 50$  mm snout-vent length) rock-dwelling iguanid, and is limited in its distribution to the Big Bend region of Texas in the United States, and Coahuila and north-eastern Chihuahua in Mexico. A long-term mark-recapture study of life history variation has been conducted on this site since 1981 (Ruby and Dunham 1987, Grant and Dunham 1990). At Boquillas, lizard home ranges were on outcrops and terraces on the east or west side of the canyon. No home range spanned the arroyo (dry stream bed) bisecting the site, although occasionally in early morning or near twilight, some marked individuals were found in the arroyo or outside of the canyon on the exposed flats to the east and west.

Densities of *S. merriami* at the Boquillas locality were greater, and home range sizes and nearest neighbor distances were smaller than for other higher elevation populations in Big Bend (Ruby and Dunham 1987, Dunham et al. 1989). Adult males were highly territorial during midsummer, and frequently engaged in courtships of females and challenges with other males.

*Lizard body temperature and activity.*—Body temperatures ( $T_b$ ) of active lizards (i.e., found on exposed surfaces, Grant and Dunham 1988) were measured during the summers of 1982–1986. Lizards were located by walking through the study site. If a lizard was captured within the first few noosing attempts ( $\approx 30$  s), its cloacal temperature was measured ( $\pm 0.1^\circ\text{C}$ ) within 20 s using a fast-reading mercury thermometer. Time and weather conditions were also noted (all times are reported in Central Daylight Time [CDT]). Most captures of lizards occurred in the morning because the activity period is longer in the morning (see *Results: Lizard activity and body temperature*), and sampling effort was more intense.

To estimate the timing of daily activity, observers walked fixed transect paths along each side of the can-

yon (about halfway up) and recorded the individual paint marks and total number of lizards seen, excluding hatchlings. Observations were made during July 1986, under sunny conditions, and consecutive transects on the same day were always >30 min apart. These transects crossed the home ranges of 60–80% of the resident lizards (A. E. Dunham, *personal communication*). The times that maximal numbers of lizards were seen were assumed to be similar to the times at which peak rates of activity occurred (Huey 1974a, 1983), and were estimated for each canyon side (east vs. west) and time period (morning vs. evening).

Rates of individual activity were estimated using 30-min observations of eight randomly selected adult lizards from the resident population (two males and two females each from the east and west sides). An observer continuously viewed one of these lizards at a time through binoculars from a sufficient distance ( $\geq 10$  m) to avoid disturbance, and recorded the number and distances of movements, and the number of feeding strikes and social displays (Grant and Dunham 1988, 1990). All observations were timed to coincide with the peak in the number of lizards seen per side per time period (see *Results: Lizard activity and body temperature* for times) in an attempt to insure that rates of individual activity were comparably estimated among sides of the canyon and for the morning and evening activity periods. Each 30-min observation contributed one datum to a two-way MANOVA (SAS 1982) to test for differences in activity rate by sex and time period (morning vs. evening). Small sample sizes of observations per lizard per time period necessitated pooling data among different individuals.

*Microclimate use and availability.*—I estimated the temporal pattern of microclimate use by lizards with techniques similar to Grant and Dunham (1988). Lizards were located by walking arbitrarily through the study site. If a lizard was not moving when first seen, then its perch substrate was classified as being either in full sun (substrate nearly perpendicular to direct solar radiation), oblique sun (substrate normal vector differed from the vector to the sun by  $\approx 20^\circ$ – $70^\circ$ ), tangent sun (substrate nearly parallel to direct solar radiation), sunlight filtering through vegetation, full shade and open to the sky, or full shade in a crevice or cave. Hourly frequencies for each of the possible states were calculated for data on lizards ( $\equiv$  microclimate use) and on randomly selected points along line transects ( $\equiv$  microclimate availability, transect methods described in next section).

*Environmental temperature availability and thermal constraints.*—I estimated the distribution of available environmental temperatures ( $T_e$ ) by deploying 45 painted hollow-body copper models of *S. merriami*, each containing a thermocouple. Copper model construction and painting techniques were described in Grant and Dunham (1988), and model temperatures were not significantly different from the body temper-

atures of perching lizards (average differences were  $\leq 0.5^\circ$ , Grant and Dunham 1988, Grant 1988). Thus, these models are an accurate estimate of  $T_e$  for these lizards.

One model was placed per metre along three 15 m long transects that enwrapped ground and rock surfaces in areas known to be within lizard home ranges. The three transects were parallel and 0.5 m apart, and the orientation of each model was randomly determined. The thermocouples of each model were connected to a data logger (Campbell Scientific, CR5), which scanned all 45 models at 10-min intervals. For each logger scan, the quartiles and extrema of model temperatures were determined (quartiles 1–3 enclose 50% of the data symmetric about the median). Data were collected during late June and July 1986, on 22 dates of sunny and dry weather, and average values of the above statistics were calculated for 10-min intervals for the west and east sides.

This contour-hugging transect scheme samples microclimates in the exposed habitat on an equal surface area basis, and thereby provides a direct estimate of the distribution of available microclimate temperatures to active *S. merriami* (i.e., found on exposed surfaces, Grant and Dunham 1988). Thus, thermal constraints on lizard activity can be directly calculated as a function of time and temperature from the copper model  $T_e$  data. If few models in the array exhibit a  $T_e$  within a specified temperature interval, then the thermal constraint on activity would be high for a lizard attempting to regulate its  $T_b$  within this interval.

## RESULTS

*Lizard activity and body temperature.*—During the summer, activity was bimodal with distinct morning and evening activity periods (Fig. 1). On the west side, peaks in activity (i.e., the number of lizards seen) occurred at about  $\approx 0900$  and  $2000$  (Fig. 1A). Lizards retreated into deep caves and crevices in midafternoon and were inactive (i.e., they were immobile and had closed their eyes). Lizards were never observed (with the aid of flashlights) on the surface after darkness at  $\approx 2115$ . The activity pattern for the east side of the canyon was similar except that the morning activity peak was delayed by  $\approx 2$  h and the evening emergence of lizards from crevices was delayed by  $\approx 1$  h (Fig. 1B).

Similar maximal numbers of lizards were seen for each activity peak (14 individuals in the morning for both west and east, and 11–12 in the evening for the west and east, respectively). These numbers correspond to only about a third of the resident lizards whose home ranges were crossed by the transect paths (Ruby and Dunham 1987, A. E. Dunham, *personal communication*), which suggests that the actual number of lizards seen underestimated the number active.

Note on the east side that a relatively large number of lizards were seen in late morning after 1200. This is somewhat deceptive since many of these lizards (11

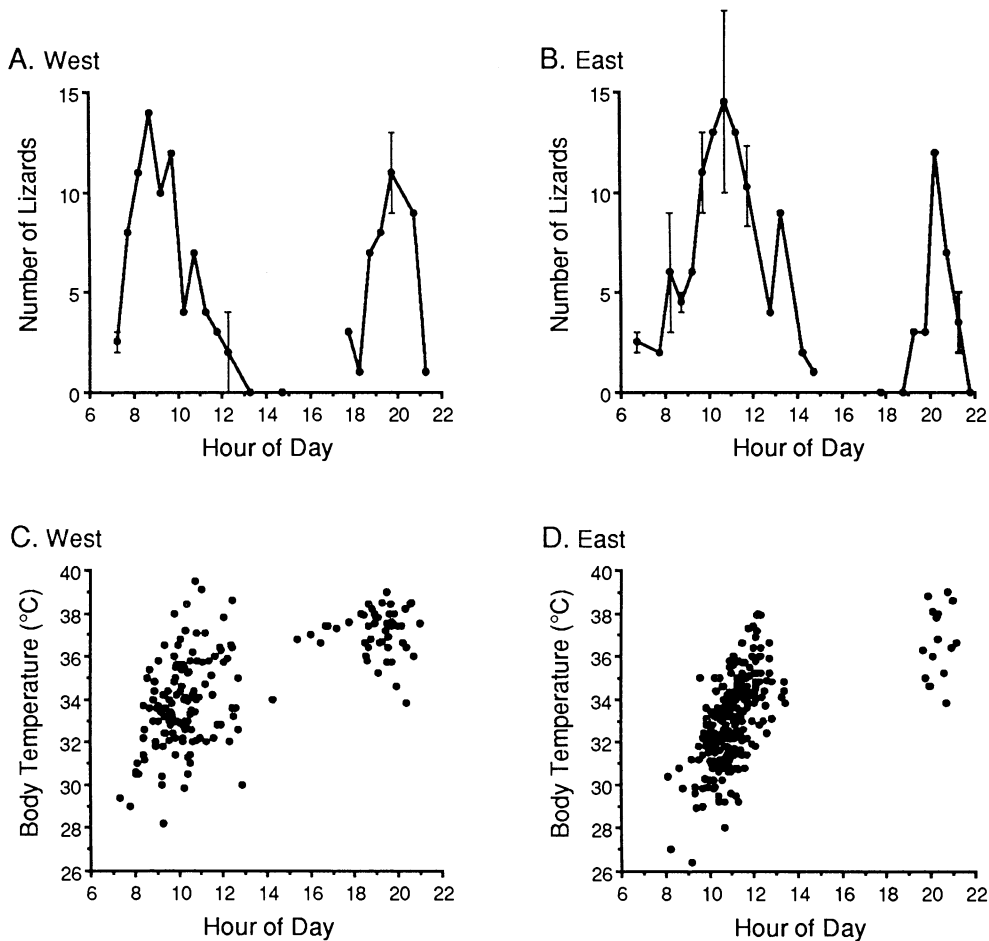


FIG. 1. The number of *Sceloporus merriami* (excluding hatchlings) seen by walking fixed transect paths along the west (A) and east (B) sides of the Boquillas study plot for sunny and dry dates in July 1986. Replicate transects on different dates during the same half-hour were averaged, and error bars represent the range. No transects occurred on the same day and canyon side <30 min apart. All times are Central Daylight Time. Body temperature measurements,  $T_b$ , for active *S. merriami* are plotted for the west (C) and east (D) sides of Boquillas for sunny and dry days during the summers of 1982–1986. Differences in sample sizes between morning and evening activity periods reflect collecting effort.

of 13) were observed in the same location when seen on the previous transect 30–45 min earlier, whereas significantly fewer lizards (19 of 58) were within 2 m of their previous location for sequential transects at midmorning ( $\chi^2 = 11.70$ ,  $df = 1$ ,  $P < .05$ ,  $n = 71$ ). Even though these lizards were on the surface, they were immobile and simply had not yet retreated into nearby crevices. Too few lizards were seen on sequential transects on the west side in late morning for comparison with the east.

Pooled observations (transect + census data) of the marked population of Boquillas *S. merriami* from 1986 suggested that similar proportions of each sex and the same individuals were active in morning and evening (1986 had the most complete census records in both the morning and evening). Although male *S. merriami* behaved more conspicuously and were  $\approx 1.5$  times as frequently observed as were females, the sex ratio of observations did not differ in the morning, 822  $\delta$  and

581  $\text{♀}$ , when compared with the ratio in the evening, 607  $\delta$  and 402  $\text{♀}$  ( $\chi^2 = 0.599$ ,  $df = 1$ ,  $P > .05$ ,  $n = 2412$ ). Also for 1986, all 101 individuals with six or more observations were seen at least once in both the morning and evening, which rules out the possibility of morning or evening specialist lizards.

Average rates of behaviors (movements, feeding, and displays) during the morning and evening activity periods for the eight lizards randomly chosen for continuous observations appear in Table 1. The daily activities of males were different from those of females, principally due to a higher display rate for males, and the effects of sex and time period did not interact (two-way MANOVA, Table 1). Despite a significant tendency for lizards to have moved farther in the evening (see *Discussion*), the MANOVA indicated that overall lizard activity rates were indistinguishable between the morning and evening time periods (Table 1).

Body temperatures of active lizards on sunny days

TABLE 1. Rates of behaviors from continuously observed focal lizards. "Time" refers to the morning vs. evening time periods. Multivariate tests are Wilks' lambda (SAS 1982).

Behavior	Sex	Morning						Evening						Univariate tests (ANOVA) for time and sex					
		Sex	$\bar{X}$		2 SE	n	$\bar{X}$		2 SE	n	Time		Sex		Time × sex				
			$\bar{X}$	2 SE			$\bar{X}$	2 SE			$F_{1,41}$	P	$F_{1,41}$	P	$F_{1,41}$	P			
Moves (no./30 min)	♂	12.84	6.86	16	15.60	9.46	10	1.31	NS	0.47	NS	0.22	NS						
	♀	8.16	4.78	11	14.70	10.97	8												
Total distance (m/30 min)	♂	5.39	2.50	16	7.42	3.91	10	4.22	<.05	1.55	NS	0.62	NS						
	♀	2.12	1.37	11	6.69	4.87	8												
Feeding strikes (no./30 min)	♂	2.00	2.11	16	2.20	1.97	10	0.16	NS	0.59	NS	0.06	NS						
	♀	2.67	1.71	11	3.47	4.27	8												
Displays (no./30 min)	♂	5.46	1.59	16	5.80	2.50	10	0.12	NS	15.79	<.001	0.01	NS						
	♀	0.18	0.36	11	0.76	1.04	8												
Time without motion (min/30 min)	♂	20.65	3.25	16	19.50	4.74	10	0.84	NS	2.44	NS	0.12	NS						
	♀	24.55	2.54	11	21.96	5.84	8												

Multivariate test (MANOVA) for time and sex					
Time		Sex		Time × sex	
$F_{5,37}$	P	$F_{5,37}$	P	$F_{5,37}$	P
1.33	NS	4.07	<.01	0.22	NS

during the summer averaged almost 4°C higher in the evening than in the morning activity periods (Table 2). Despite differences in the timing of peak activity, average  $T_b$ 's on the east and west sides differed only slightly (0.7° in the morning and 0.6° in the evening, Table 2). No interactions among main effects of canyon side, sex, and time period were significant. Although the upper extremes for observed  $T_b$  were similar in the morning and evening, only a small fraction of  $T_b$  data was above 36° in the morning, whereas most data were above 36° in the evening (see Fig. 1C, D).

*Microclimate use and availability.*—On the west side early in the morning (0800–0900), lizards used perches in the sun that were commonly available at this time since this side faces the rising sun (Fig. 2A, C). However, after 1000, > 80% of the lizards were perched only in shady microclimates, which were rare ( $\leq 10\%$  of the habitat) throughout the morning. Lizard activity declined dramatically after 1000 when lizards restricted their perching to rare shaded microclimates (Fig. 1A). When activity resumed in the evening (>1900), lizards perched almost exclusively in the shade, which was the most commonly available microclimate type.

On the east side in contrast to the west, lizards rarely used the scarcely available sunlit perches in early and midmorning (0900–1200). Instead, east-side lizards used commonly available shaded microclimates (Fig. 2B, D). Toward late morning (>1200) shade availability declined, and the number of active lizards declined (Fig. 1B). When activity resumed in the evening, lizards perched almost exclusively in the shade, similar to the west side in the evening.

*$T_e$  availability and comparisons with lizard activity and  $T_b$ .*—On the west side (Fig. 3A) immediately fol-

lowing sunrise at 0745, most of the habitat was exposed to direct sunlight and environmental temperatures increased rapidly. By 0900, 75% of the models were above 38° (see curve for the first quartile in Fig. 3A). This was about the time that lizard activity began to decline (see Fig. 1A). On average <20% of the available  $T_e$ 's were in the interval 36°–38° in the morning (Fig. 3C), and relatively few lizards exhibited body temperatures in this interval (Fig. 1C). Although  $T_e$ 's of 36°–38° were available in late morning between 1000 and 1200, these perches represented <5% of the available habitat (Fig. 3C), consisted of rare patches of shade (Fig. 2C), and were surrounded by thermally stressful (i.e.,  $T_e > 38^\circ$ ) sunlit perches. In the morning, lizards did not extend activity time to use these rare microclimates, and instead ceased activity and retreated to crevices and caves (Figs. 1A and 2A).

On the west side at the time of evening activity, the frequency distribution of available  $T_e$  was very different from that in the morning. By  $\approx 1900$ , all of the exposed habitat was shaded (Fig. 2C) and uniformly hot (90% within 37°–42°, Fig. 3A). As the habitat cooled, an average of 70% (up to >90%) of the available microclimates were within 36°–38° (Fig. 3C), and at this time lizards accepted an elevated  $T_b$  and became active (Fig. 1A, C). If lizards had not accepted an elevated  $T_b$  in the evening (crevice temperatures averaged 31.5°, Grant and Dunham 1990), they could not have initiated activity until after 2030 and would have had less than half as much time for evening activity (Fig. 3A).

The spatiotemporal pattern of available temperatures on the east side was basically similar to the west except for effects due to the orientation of these slopes (Fig. 3B, D). On the east side, local sunrise was more

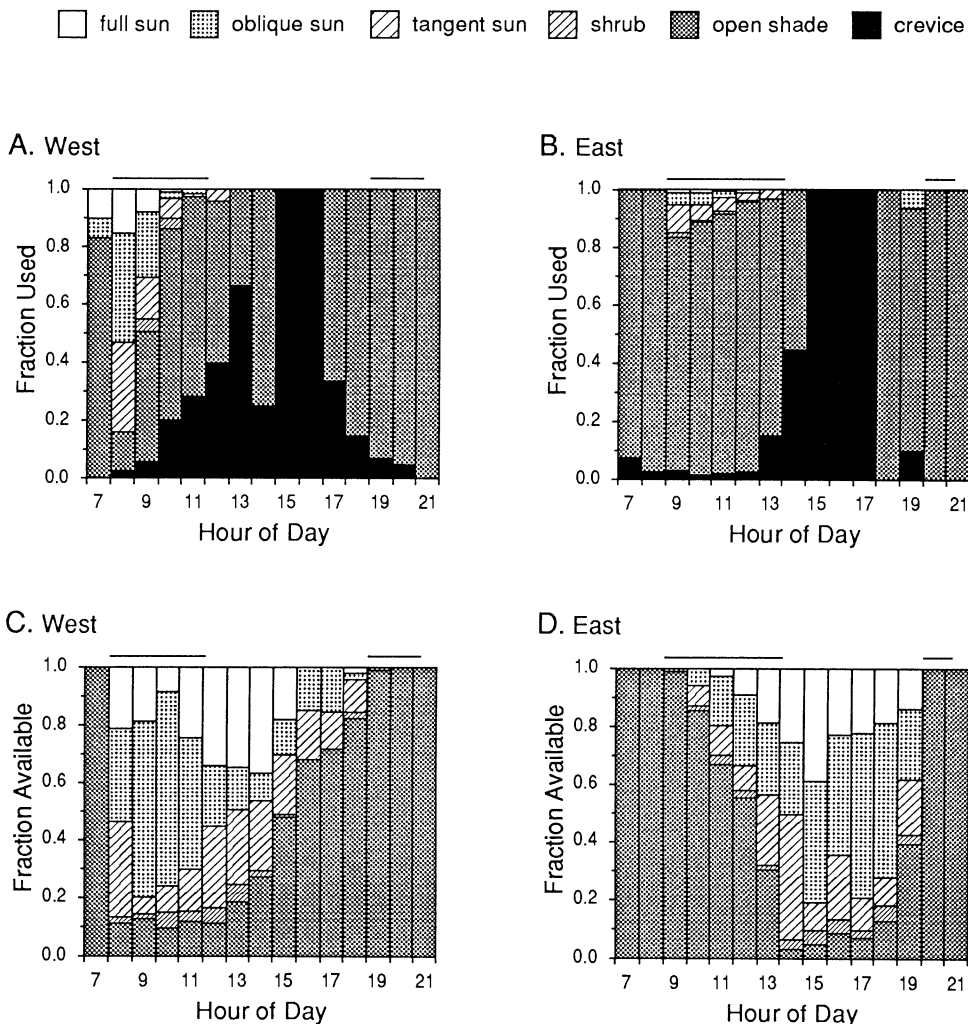


FIG. 2. Upper graphs: Hourly fractions of microclimates used by perching *Sceloporus merriami* for the west (A) and east (B) sides of the Boquillas study plot. The microclimate types are defined in *Materials and methods: Microclimate use and availability*. Lines across the top indicate the general times for morning and evening lizard activity and sample sizes for hours beneath these lines were  $>25$ , but were generally  $<10$  for other hours when few lizards could be found. Lower graphs: Hourly fractions of microclimates available to surface active *S. merriami* for the west (C) and east (D). Data were recorded by scoring the perch substrate types of randomly deployed copper models ( $n = 45$  for all time intervals).

gradual and cooler shaded perches were far more available during lizard activity. On some days, up to 50% of the available microclimates were between  $36^{\circ}$  and  $38^{\circ}$  at midmorning (see curve for "max" in Fig. 3D), but during late morning  $<10\%$  more home range would have been gained by an elevated  $T_b$ . Lizards abandoned activity and sought crevices rather than elevate  $T_b$  to use these scarce microclimates (Figs. 1B, D, and 2B). During the evening on the east side relative to the west, local sunset was later and more abrupt, and habitat cooling was more rapid (Figs. 2C, D, and 3A, B). But similarly with the west, east-side lizards initiated activity as soon as a large fraction of the habitat cooled to within  $36^{\circ}$ – $38^{\circ}$ , which forced an elevated  $T_b$  (Figs. 1B, D, and 3B, D).

The higher cooling rate of the east side, compared to the west, resulted in a narrower time interval ( $<1$  h, Fig. 3B) during which lizards were forced to accept an elevated  $T_b$ . The lower evening average fractions of models within  $36^{\circ}$ – $38^{\circ}$  for the east, compared with the west, are due to differences among days in the time of day when most model temperatures passed through the  $36^{\circ}$ – $38^{\circ}$  interval (Fig. 3D). Note that the fraction of models within  $36^{\circ}$ – $38^{\circ}$  peaked on some days as early as 1900 and as late as 2200 (Fig. 3D). Some evenings were so hot that lizards could not be active at all without an elevated  $T_b$ , but on other evenings lizards had access to cooler perches ( $34^{\circ}$ – $36^{\circ}$ ) before darkness. Nonetheless, on both sides of Boquillas, body temperatures were higher in the evening than in the morning

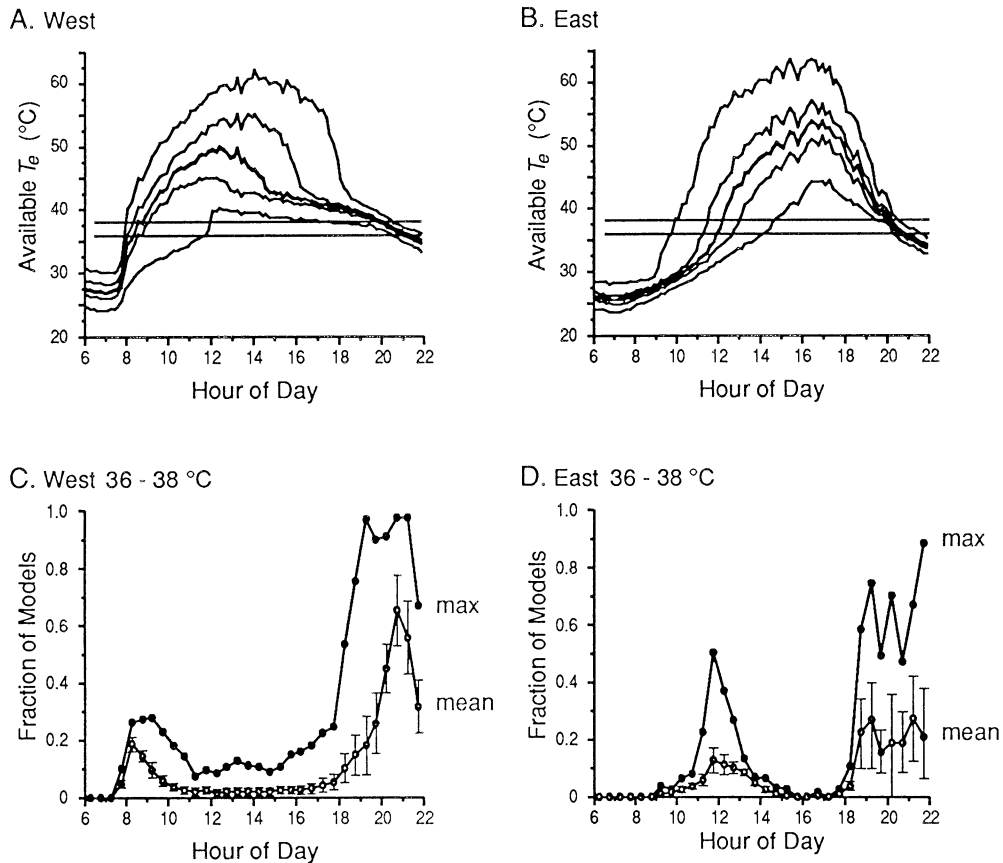


FIG. 3. Nonparametric descriptive statistics of the distribution of environmental temperatures,  $T_e$ , available to surface-active *Sceloporus merriami* for the west (A) and east (B) sides of Boquillas. Curves are the average maximum (highest curve), third quartile (next highest), median (second quartile = middle curve), first quartile (next lowest), and minimum (lowest curve) model temperatures for 22 dates of sunny and dry weather during midsummer, 1986. Average values of the above statistics were calculated for 10-min intervals among dates. Quartiles 1–3 enclose 50% of the  $T_e$  data for each time interval. The horizontal lines enclose the interval 36°–38°C. The mean and maximum fraction of copper models ( $\pm 1$  SE) of *S. merriami* exhibiting  $T_e$  in the interval 36°–38° vs. time for the west (C) and east (D) sides of Boquillas. Values were calculated at 30-min intervals from the same 22 dates summarized in A and B. When a high fraction of the model  $T_e$ 's were within the 36°–38° interval, then the activity of lizards accepting an elevated  $T_b$  was unconstrained by temperature.

(Table 2) due to the absence of cool microclimates (Fig. 3A, B), and the acceptance of hot microclimates by thermoregulating lizards, only in the evening.

#### DISCUSSION

During the summer, *S. merriami* were active at similar rates during their morning and evening activity periods but averaged a 4°C higher  $T_b$  in the evening than in the morning. This degree of daily variation in activity  $T_b$  suggests that the thermal biology of *S. merriami* is very unusual among diurnal desert lizards; however, this pattern could be more common than has been previously reported since bimodality in daily activity is well known (DeWitt 1967, Mayhew 1968, Huey 1982), and the types of data necessary to elucidate this pattern are only infrequently taken (Porter et al. 1973, Christian et al. 1983, Porter and Tracy 1983, Waldschmidt and Tracy 1983). Grant and Dunham (1990), using similar techniques as described here, report that

bimodally active *S. merriami* at a higher elevation locality in Big Bend, Grapevine (elevation 1036 m), also exhibit a low morning average  $T_b$  of 32.2° and emerge at an elevated  $T_b$  averaging 36.2° for evening activity (see also Grant and Dunham 1988). Slightly cooler microclimate temperatures at Grapevine, especially in the evening, relative to Boquillas, are sufficient to account for the slightly lower average  $T_b$ 's of lizards at Grapevine.

At a high elevation site, Maple Canyon (elevation 1609 m), the cool thermal environment allows *S. merriami* to be active throughout the day, and their body temperatures do not rise in late afternoon since cooler microclimates ( $<36^\circ$ ) are amply available at this time (average  $T_b$  of 32.3° for data before 1400, and 32.2° after 1400, Grant and Dunham 1990). Since the Boquillas environment in late fall and early spring is thermally similar to Maple Canyon at midsummer, it should be no surprise that *S. merriami* are also unimodally



active in spring and fall at Boquillas with an average  $T_b$  of  $\approx 32^\circ\text{--}33^\circ$  (B. W. Grant and S. R. Waldschmidt, *personal observation*).

The prevalence of the lower body temperature value of  $\approx 33^\circ$  at higher elevations, and during cooler seasons, suggests that *S. merriami* may have been forced to compromise their optimal or preferred activity  $T_b$  at lower elevations in order to be active in the evening. Several lines of evidence corroborate this suggestion.

Firstly, according to Huey and Dunham (1987), sprint speeds of Boquillas *S. merriami* ranked fastest at a  $T_b$  of  $33.5^\circ$  relative to sprinting at either  $37.0^\circ$  or  $28.0^\circ$  ( $n = 11$ ). On average, sprint speeds declined by 25.7% (range 2.2–60.1%) at  $37.0^\circ$  relative to  $33.5^\circ$ . This decline in locomotor performance for only a  $4^\circ$  higher  $T_b$  is typical for iguanids (Huey 1982, 1983, Huey and Bennett 1987) and is potentially important to a variety of ecologically relevant activities including predator escape, prey capture, and performance in social interactions (Huey 1982).

Secondly, according to regressions in Bennett and Dawson (1976), a  $4^\circ$  higher  $T_b$  will increase the resting metabolic rate of a small iguanid (e.g., a 50-mm snout-to-vent *S. merriami*) by over 40%. Data for fasted male *S. merriami* (P. Niewiarowski and S. R. Waldschmidt, *unpublished manuscript*) corroborate this trend. However, the relevant comparison is between an inactive *S. merriami* with its  $T_b$  equal to the  $T_e$  in deep crevices ( $31.5^\circ$ , Grant and Dunham 1990) and an active *S. merriami* with its  $T_b$  elevated to  $37^\circ$ . Using values for activity scope (fractional increase in metabolic rate due to activity, Bennett and Dawson 1976) that span the range suggested for iguanids (1.8–3.0, Congdon et al. 1982), I calculated that *S. merriami* metabolic expenditure is 191–385% higher by being active at the elevated  $T_b$ . This amounts to 6–10% of the total daily energy expenditure for each hour of activity at  $37^\circ$  relative to inactivity in crevices at  $31.5^\circ$ .

Finally, evaporative water loss in iguanid lizards increases rapidly with increased  $T_b$  (Mautz 1982, Tracy 1982). Laboratory experiments on *Uta stansburiana* (Waldschmidt and Porter 1987), from a desert grassland population in Texas, indicate that total evaporative water loss increases at a rate of  $\approx 0.1$  mg/(gm $\cdot$ h $\cdot$ °C) for  $T_b$ 's between  $30^\circ$  and  $38^\circ$  (low wind speed, eyes open, see their Fig. 1, p. 683). This results in a predicted 22% increase in water loss rate between  $33^\circ$  and  $37^\circ$ . Comparable data for *S. merriami* (A. E. Dunham and M. Fusco, *unpublished manuscript*) indicate a 37% increase in water loss rate for a rise in  $T_b$  from  $33^\circ$  to  $37^\circ$ . Also, since the relative humidity is much lower in the evening than in the morning at Boquillas (B. W. Grant, *personal observation*), by emerging for activity at an elevated  $T_b$  in the evening, lizards may incur a higher cost in water loss than by allowing a higher  $T_b$  in the morning.

Since thermal acclimation typically requires several days to weeks in iguanids (Huey 1982), the functional

TABLE 2. Body temperatures at Boquillas. Data for summers 1982–1986, cloudless weather, all lizards were captured on surface. "Side" refers to the east or west side of the canyon. "Time" refers to time block, morning or evening.

Side of canyon	Morning			Evening		
	$\bar{X}$	2 SE	$n$	$\bar{X}$	2 SE	$n$
West	33.8	0.4	138	37.2	0.3	50
East	33.1	0.2	254	36.6	0.8	16
Combined	33.3	0.2	392	37.0	0.3	66

Three-way ANOVA on body temperatures

Source	df	Mean square	F value	P
Side	1	16.58	4.71	<.05
Sex	1	0.01	0.00	NS
Time	1	483.47	137.31	<.001
Side $\times$ sex	1	0.26	0.07	NS
Side $\times$ time	1	0.80	0.23	NS
Sex $\times$ time	1	1.91	0.54	NS
Side $\times$ sex $\times$ time	1	2.77	0.79	NS
Error	450	3.52		

relationships between body temperature and locomotion, metabolic and water loss rates, or other processes were probably identical for the morning and evening activity periods. To a first approximation, the physiological costs described above of a  $4^\circ$  higher  $T_b$  were likely to have been identical in the morning and in the evening. Therefore, observed differences in thermoregulation cannot be attributed to different metabolic or evaporative costs, or locomotor performance between morning and evening activity periods.

At the time of the observed initiation of evening activity ( $\approx 1900$  for the west and  $2000$  for the east), there was a substantial increase in the fraction of microclimates within the interval  $36^\circ\text{--}38^\circ$  (ranging to above 90%, Fig. 3). Thus, the constraint on activity was greatly decreased at this time, and lizards accepted a higher  $T_b$  and higher associated physiological costs (Huey 1974b) and became active. In contrast, an elevated  $T_b$  in late morning (after  $\approx 1100$  on the west, and after  $\approx 1300$  on the east) would have failed to decrease the constraint on their activity by more than  $\approx 10\%$  (Fig. 3), and lizards would have had to pay all of the physiological costs described above. Instead, lizards became inactive in late morning rather than accept a higher  $T_b$ .

I suggest that lizards directly responded to differences in the distribution of available temperatures by accepting the costs of a higher  $T_b$  and initiating activity in the evening because they could move about in their home ranges relatively unconstrained by temperature in the evening. Lizards accepted substantially reduced sprint capacity and higher metabolic and water loss rates in the evening when a higher  $T_b$  allowed them to be active throughout most of their home range (high benefit/cost). Whereas, in the morning few thermal microclimates could be used for activity with an elevated  $T_b$  (low benefit/cost) and lizards abandoned activity in late morning instead of accepting these higher physi-

ological costs. In other words, the net ecological benefit of increased activity time resulting from an elevated  $T_b$  is small in the morning, but great in the evening. In fact, the significantly higher movement rates of individuals in the evening suggests that peak lizard activity was even less constrained in the evening (when >70% of the surface was acceptable) than at peak activity in the morning (Table 1, Fig. 3).

Data in this paper support previous observations (e.g., DeWitt 1967, Grant and Dunham 1988) that the thermal constraint on ectotherm activity is directly related to the distribution of available  $T_e$ . Moreover, in thermally heterogeneous habitats, such as deserts, the range of available  $T_e$  is obviously an inadequate descriptor of the commonness or rarity of usable microclimates and may lead to overestimates of total activity time for mobile thermoregulating lizards such as *S. merriami*. However, for larger ectotherms, with greater thermal inertia, shuttling between thermal extremes may be a critical component of temperature regulation, and transient  $T_e$  modeling of these extremes may offer a better estimate of thermal availability (C. R. Peterson, *personal communication*).

Several observations suggest that increased total daily activity time may be important to Boquillas lizards. Despite the observed higher evening  $T_b$  and associated increased activity time, the daily total at Boquillas is still lower by several hours than for other higher elevation populations of *S. merriami* in Big Bend (Grant and Dunham 1990). Since arthropod food abundance is also lower at Boquillas (Ruby and Dunham 1987), foraging time in the evening may be critical to meeting energy needs during the breeding season. However, an increased rate of depletion of assimilated energy and water may result in resource demands in excess of environmental supply. This may account for the observed mass loss by adult lizards at Boquillas during midsummer (Grant 1988, Dunham et al. 1989, Grant and Dunham 1990). Also, because population densities and average home range overlap are highest at Boquillas relative to other populations in Big Bend (Ruby and Dunham 1987, Grant 1988), maximizing time spent in social interactions (territory defense and courtships) may improve an individual's chance of obtaining a mating, especially for males. Thus, a higher  $T_b$  to extend daily activity time and concomitantly higher metabolic and water loss rates and potentially lower capacity to escape a predator could be viewed as intrinsic costs of reproduction for these lizards.

Several other considerations could also be affecting this cost/benefit relationship. Firstly, higher food availability in the evening could potentially result in increased prey capture rates sufficient to offset increased resource costs. Although no data are available on temporal differences in food availability at Boquillas, it seems unlikely that higher food availability in the evening could account for lizard activity at this time since individual feeding rates were indistinguishable be-

tween morning and evening (Table 1). An additional consideration involves risk of overheating (C. R. Peterson, *personal communication*). Since extremely hot microclimates were abundant in the morning (Fig. 3), an elevated  $T_b$  at this time would have placed a lizard at greater risk of approaching lethal thermal stress ( $\approx 41^\circ$ , B. W. Grant, *personal observation*). In contrast, during the evening activity period, no  $T_e$ 's exceeded  $40^\circ$ , and despite the observed elevated  $T_b$  there was no risk of lethal thermal stress to these lizards. (I thank C. R. Peterson for this intriguing suggestion.)

These considerations underscore the complexity of the interaction between thermal constraints, activity time, physiological performance, and social/demographic factors (related to transducing energy and mass resources into offspring, Grant 1988, Dunham et al. 1989) that potentially influence the costs and benefits of lizard body temperature regulation. Empirical investigations of lizard thermal biology should therefore be of sufficient resolution to assess these interactions. I suggest that a synthetic cost/benefit theory of lizard body temperature selection must realistically incorporate the effects of these influences and treat body temperature as a variable. Fitness differences associated with particular body temperatures should result from the effect of  $T_b$  on expected rates of resource and mate acquisition, risk of predation, and resource processing and allocation to maintenance or production in a particular thermal environment.

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