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Elevational Variation in the Thermal Constraints on and Microhabitat Preferences of the Greater Earless Lizard *Cophosaurus texanus*

FARRAH BASHEY AND ARTHUR E. DUNHAM

We compared the intensity of thermal constraints on the activity of the lizard *Cophosaurus texanus* found in two populations in Big Bend National Park, Texas. The low elevation site was known to be hotter than the high elevation site; we asked whether this coarse-grain environmental difference was relevant to *C. texanus*. We used hollow-bodied copper models and transect sampling to measure the operative environmental temperatures and relative availability of microhabitats at both sites. Based on laboratory measures of the critical thermal extrema and the range of field-active body temperatures of lizards in each population, we estimated the percent of the environment thermally acceptable to *C. texanus*. We found that the high elevation site had on average more than 70% of operative environmental temperatures thermally acceptable during midday, whereas the low elevation site had less than 20%. Thus, we concluded that the activity of *C. texanus* should be more constrained by the thermal environment at the low elevation site. To verify this result, we compared the actual microhabitat use patterns of lizards at each site with a null model of random use of thermally acceptable microhabitats. Predicted preferences more closely matched the observed behavior of lizards from the low elevation site, demonstrating that the activity of lizards at this site was more greatly influenced by the thermal environment than at the high elevation site.

INDIVIDUAL growth rates and survival probabilities of lizards are directly influenced by their body temperatures (Huey, 1982). The physiological effects of body temperature on prey capture success and handling time can affect gross energy intake (Avery et al., 1982), whereas net assimilation of this energy is affected by temperature through its effect on metabolic rate (Beaupre et al., 1993a) and digestive efficiency (Beaupre et al., 1993b). Similarly, the thermal dependence of sprint speed and stamina in lizards may affect their ability to avoid predators (Bennett, 1980).

Because of the thermal sensitivity of physiological processes, lizards have a well-defined range of temperatures where their performance is maximized (Huey, 1982). To keep their body temperatures in this favorable range, many lizards thermoregulate by selecting microhabitats that allow them to achieve these temperatures. The success of behavioral thermoregulation depends on the distribution of these microhabitats in the environment (Dewitt, 1967). If few appropriate microhabitats are available, then lizards could be forced to be active in suboptimal thermal conditions (Huey and Bennett, 1987; Autumn et al., 1994) or, alternatively, to forgo activity altogether (Grant and Dunham, 1988, 1990; Hertz et al., 1988). Available activity time affects lizard life-history traits by modifying individual energy budgets, social status, and risks of predation (Dunham et al., 1989). Moreover,

the combined effects of environmental temperature on body temperature and activity time may cause phenotypic differences in life-history patterns equivalent to those predicted from evolutionary models (Adolph and Porter, 1993). Thus, geographic variation in the distribution of thermal microhabitats has a potentially large influence on the life-history patterns and local abundances of lizard species (Grant and Dunham, 1990).

Variation in the distribution of thermal microhabitats over the course of the day forms the basis for influences of environmental temperatures seen on geographic scales. Because of the low thermal inertia of small ectotherms, body temperature can change rapidly with changes in microhabitat. Therefore, if the distribution of thermal microhabitats is such that the requirements of temperature regulation take precedence over requirements of other activities (e.g., foraging, mating), then the thermal environment can be viewed as constraining (Dunham et al., 1989). When thermal constraints vary among populations, the thermal environment has the greatest opportunity to cause variation in life-history phenotypes (Grant and Dunham, 1990; Beaupre, 1995). Therefore, examining the relationship among the environmental distribution of thermal microhabitats, the requirements for thermoregulation, and patterns of lizard microhabitat use between populations is necessary to quantify thermal

constraints and to verify potential mechanisms of populational differences.

We characterized the thermal environment and activity patterns for two populations of the greater earless lizard *Cophosaurus texanus* found along an elevational gradient. We asked whether temperature differences between sites resulted in differences in thermal constraints faced by the two populations and whether this potential constraint affected microhabitat use. Using the distribution of operative environmental temperatures (Bakken, 1976) and estimates of the thermal requirements of *C. texanus*, we found the proportion of the environment thermally acceptable to *C. texanus* varied markedly between the two sites over the course of a day, such that lizard activity at the low elevation site was potentially more constrained by the thermal environment. To test whether lizard activity was more constrained by the thermal environment at the low versus high elevation site, we predicted hourly microhabitat preferences of lizards at each site based on a null model of random use (i.e., in proportion to availability) of thermally acceptable microhabitats. Observed microhabitat preferences matched the predicted preferences at the low elevation site better than at the high elevation site, providing support for greater thermal constraints on activity at the low elevation site.

MATERIALS AND METHODS

System.—The greater earless lizard (*C. texanus*: Iguanidae) is a small insectivorous sand lizard which inhabits sandy or rocky desert flats (Clarke, 1965). It maintains a higher active body temperature (mean $T_b = 38.3$ C, range = 31.8–40.9 C, $n = 60$) and a delayed activity period when compared with sympatric lizard species (Milstead, 1959; Clarke, 1965).

We conducted this study at two elevations in Big Bend National Park, Texas, during the summer of 1991. The high elevation site, Grapevine Hills (1036 m), consisted of a sandy wash which constitutes the main drainage area of the hills, and the flats surrounding the wash. The low elevation site, Boquillas Canyon (560m), was hotter (average July air temperature = 31 vs 27 C), drier (average annual rainfall = 24 vs 34 cm), and more sparsely vegetated (percent cover = 15.1 vs 23.2) than the Grapevine site (Grant and Dunham, 1990).

Range of lizard body temperatures.—We assessed the ranges of body temperatures (T_b) acceptable to *C. texanus* with two metrics: the critical thermal extrema (Lowe and Vance, 1955) and

field activity limits. For the critical thermal maxima (CTMax), we placed a lizard in a plastic bucket and gradually moved the bucket from the shade into the full midday sun resulting in a heating rate of approximately 1–2 C per minute. As T_b increased, the lizard increased its rate of panting until its motion abruptly ceased and it was unable to move. We determined CTMax at this sudden onset of rigor by measuring the cloacal T_b with a fast-reading Schultheis thermometer. We determined the critical thermal minima (CTMin) by placing a lizard in a container and adding ice to the bath surrounding the container; this resulted in a cooling rate of approximately 1 C per minute. As T_b decreased, locomotor activity became increasingly uncoordinated, and we measured CTMin at the onset of rigor using the same criteria and method as CTMax. We determined the critical thermal extrema of eight lizards from Grapevine and four lizards from Boquillas within one to two days of field capture. Because of difficulty in obtaining Boquillas lizards, we measured both extremes on the same individuals. For these animals, we measured CTMin first because it appeared less stressful and then determined CTMax after waiting one day. All lizards used appeared to recover fully after the extrema were measured.

Field activity limits were determined from the range of body temperatures observed at both sites. We collected lizards in the field by noosing them and then taking the cloacal T_b immediately with a Schultheis thermometer. Body temperatures were obtained from 22 lizards at Boquillas and 97 lizards from Grapevine under a range of weather conditions, times of day, and microhabitat classes.

Operative environmental temperatures.—We used hollow-body copper models fitted with copper-constantan thermocouples to estimate the temporal pattern of operative environmental temperatures (T_e) available to *C. texanus* (Grant and Dunham, 1988). We designed the models to duplicate the external heat transfer properties of *C. texanus* by using a museum specimen of *C. texanus* to create the mold and by painting the models to match the coloration of *C. texanus* from Big Bend National Park. In addition, we made the distal portion of the legs out of a flexible plastic, so we could vary the posture of the models to mimic *C. texanus* behavior.

We calibrated the models by comparing the model temperature (T_e) to the equilibrium body temperature of a lizard tethered next to the model in the same solar microhabitat. The calibration runs ranged in T_b from 30–42 C and were conducted in shade to full sun under vari-

able wind speeds. The agreement between the models and lizards was high ($r^2 = 0.99$, $P < 0.0001$, $df = 7$) and $T_b = 4.25 + (0.89) T_e$. Within the observed activity range of *C. texanus*, body temperatures were within 1 C of T_e ; thus we assumed the model temperatures accurately represented heat load of the environment for a *C. texanus*. The models thereby provided a simplified method of obtaining a description of the thermal environment as it is actually perceived by the lizards (Bakken, 1976, 1992).

We deployed 32 models at each site to quantify the availability of environmental temperatures. We placed models on a variety of substrates and in various postures to accurately sample *C. texanus*' ability to utilize available microhabitats. A data logger (Campbell Scientific 21X Micrologger) scanned the thermocouples of the models every minute and averaged the temperature of each model at 15-min intervals. We calculated the mean, minimum, and maximum T_e for each hour by averaging several typical, nonovercast days in midsummer. The potential constraint the thermal environment placed on lizard activity throughout the day was calculated as the proportion of the model locations that yielded an acceptable thermal environment. Acceptable T_e s were those within the limits demarcated by the critical thermal extrema and the temperature extremes exhibited by field active lizards.

We examined fine-scale spatial heterogeneity by classifying the microhabitat of each model into three solar radiation categories: (1) SUN represented direct solar radiation striking the substrate; (2) PARTIAL resulted from sunlight filtering through vegetation; and (3) SHADE indicated the complete absence of direct radiation resulting from interception by vegetation, rocks, clouds, or time of day (i.e., before local sunrise or after local sunset). More detailed categories based on the angle of incident solar radiation (Grant and Dunham, 1988) were redundant because most substrates were flat, and thus the angle correlated with the time of day. We determined the hourly mean T_e for each solar microhabitat as well as the fraction of each microhabitat that was thermally acceptable to *C. texanus*. We viewed the fraction of each microhabitat acceptable to *C. texanus* at any given time of day as a measure of its usability or thermal quality.

Microhabitat availability.—We estimated microhabitat availability (i.e., the temporal occurrence of SUN, PARTIAL, and SHADE) via transect sampling. In each study site, we deployed a 30-m transect line at a location chosen random-

ly at each site. We placed sample points every meter along the transect line and at one meter perpendicular to the line on either side, such that there were 93 points in all. We walked transects at 15–30 min intervals from local sunrise to sunset. To obtain the temporal distribution of microhabitat availability, we calculated the proportion of observations within the three solar microhabitats for each hour.

Predicted lizard behavior.—We developed a conceptual model for predicting the microhabitat use pattern of a lizard whose behavior was based solely on an assessment of thermal quality. We assumed that, if a microhabitat was thermally acceptable to *C. texanus*, it was used at random (i.e., in proportion to availability). Thus, we predicted that *C. texanus* would use microhabitat m in a given hour according to the following relationship: $predicted\ use_m = acceptability_m \cdot availability_m$. The *acceptability* of microhabitat m was the proportion of copper lizard models in that microhabitat in a given hour whose T_e was in the acceptable range, whereas the *availability* of microhabitat m was determined as described above. We defined the acceptable range based on two sets of data on body temperature extremes. This resulted in two sets of predictions, one based on the critical thermal extrema (which we refer to as the critical limits model) and one based on the extremes of field-active lizards (which we refer to as the activity limits model). To isolate lizard behavior from site-to-site differences in the availability of a given microhabitat and to facilitate comparisons with observed behavior, we standardized the predicted use of a microhabitat by its relative availability using the Chesson-Manly Preference Index (see Lizard microhabitat use below).

Lizard microhabitat use.—To determine the pattern of microhabitat use at each site, we recorded the microhabitat of the perch (as well as time of day and weather) for lizards that we saw as we walked through the study sites. If the lizard was actively moving about the environment, then we took multiple sightings of the same individual as it stopped at different perches; otherwise, we did not record the same lizard twice during the same pass of the study site. We used only observations of adult lizards from nonovercast days which resulted in 193 observations from Boquillas and 487 from Grapevine Hills. We pooled observations from 1300–1700 h at Boquillas, because we recorded fewer than five observations in each hour. To determine the temporal distribution of microhabitat utiliza-

tion, we used the relative frequency of lizards in each solar microhabitat at each hour of day.

Microhabitat utilization was adjusted for variation in microhabitat availability with the Chesson-Manly Preference Index (Manly, 1974; Chesson, 1978, 1983):

$$\beta_m = \frac{\frac{use_m}{availability_m}}{\sum_m \frac{use_m}{availability_m}}$$

where β_m represents the lizards' selectivity for microhabitat m , use_m , the proportion of behavioral observations in microhabitat m in a given hour, and $availability_m$, the relative availability of microhabitat m in that hour. The β_m for the three microhabitats sum to one: if $\beta_m = 0.33$, the lizards used the microhabitat at random (i.e., in proportion to its availability); if $\beta_m > 0.33$, the lizards used the microhabitat more often than expected based on its availability, and if a $\beta_m < 0.33$, the lizards underutilized the microhabitat. Because this index standardized for the relative availability of each microhabitat, it was possible to compare lizard behavior across times of day and between sites where the availabilities of the solar microhabitats were changing. Furthermore, because both observed and predicted use were standardized by the Chesson-Manly index, it was possible to compare the observed and predicted (β) preferences to assess the degree to which behavior was dictated by the thermal environment at the two sites.

We compared the fit of our behavioral model with the behavior of *C. texanus* by examining the functional relationship between predicted and observed preferences at the two sites. Because the preferences for a given hour sum to one, we were concerned about nonindependence of data points. Therefore, we created 10,000 random datasets with this structure (i.e., having the β and β for the third microhabitat in each hour equal one minus the values for the first two microhabitats) and examined the resulting correlation coefficients and slopes. Because these random datasets gave unbiased statistics, we feel confident in using standard hypothesis testing to interpret our results.

RESULTS

Range of lizard body temperatures.—Critical thermal extrema did not vary significantly between sites (CTMin: $F_{1,10} = 0.42$, $P = 0.53$, CTMax: $F_{1,10} = 0.08$, $P = 0.78$) or sexes (CTMin: $F_{1,10} = 2.65$, $P = 0.13$, CTMax: $F_{1,10} = 1.53$, $P = 0.24$), nor was any correlation found with snout-vent

length. Thus the data were pooled, and we used one measure of critical limits for all lizards at both sites. The CTMax for *C. texanus* was 44.4 ± 1.5 C, and the minimum was 15.4 ± 1.9 C (mean \pm SE, $n = 12$).

There was no significant difference between the daytime body temperatures found in the two populations ($F_{1,117} = 0.03$, $P > 0.87$). T_b did not vary significantly with hour of day at Grapevine ($F_{9,87} = 1.14$, $P = 0.35$). At Boquillas, body temperatures were significantly lower in the afternoon ($F_{6,15} = 20.17$, $P < 0.001$), but because weather and time were confounded as a result of the low sample size at this site, we decided to use a single measure for activity limits for all lizards at both sites. The overall mean body temperature was 38.6 ± 2.5 C (mean \pm SD, $n = 119$) and ranged from 23.5–42.1 C. Because 23.5 C was a major outlier (Grubbs and Beck, 1972: (mean-outlier)/SD = 6.0, $P < 0.001$), the next lowest record of $T_b = 31.0$ C was used as a more accurate reflection of the minimum body temperature (T_{bmin}) of an active lizard.

Operative environmental temperatures.—The hourly mean temperature at Boquillas was 4.6 C hotter than at Grapevine (Fig. 1). At both sites, the maximum T_e exceeded CTMax for several hours of the day. Additionally, the mean T_e exceeded CTMax at Boquillas. Minimum temperatures at both sites indicate refugia from the heat were available on the surface at all hours of the day.

Based on the critical thermal limits (15.4–44.4 C), the profile of the fraction of the environment acceptable followed a U-shaped curve over the course of the day (Fig. 2). Both sites started and ended the day with 100% of the environment acceptable, with an increasing part of the environment becoming unacceptable around midday as T_e s exceeded CTMax. The T_e never dropped below CTMin at either site. At Boquillas, more than 80% of the environment from 1300–1600 h was unacceptable (i.e., lethal to a *C. texanus* at thermal equilibrium). In contrast, during this same time interval at Grapevine, no more than 40% was unacceptable. This difference in percentage of the environment that was unacceptable can be viewed as a difference in the magnitude of the thermally imposed constraints on activity existing at the two sites.

Using the range of observed body temperatures of field-active lizards (31.0–42.1 C) to delimit acceptable environmental conditions indicated an even more restrictive thermal environment (Fig. 2). At Boquillas, not only did the

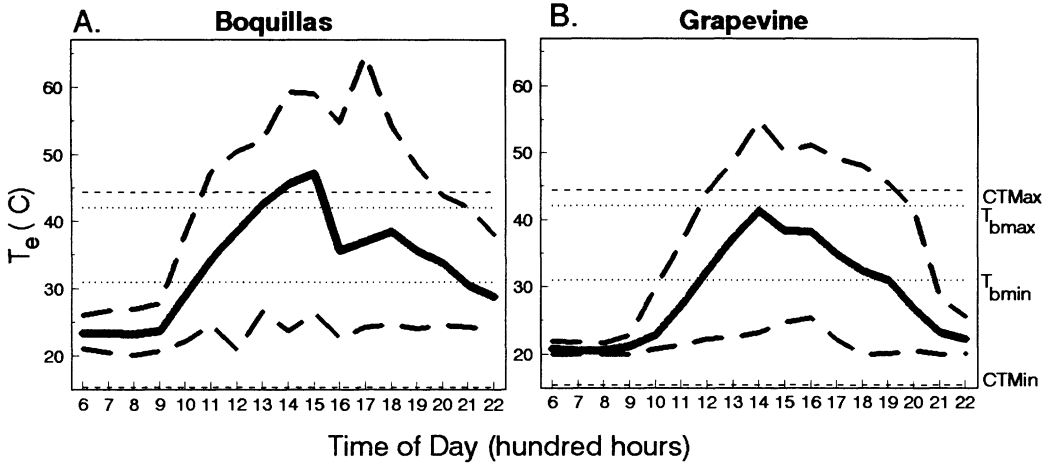


Fig. 1. Hourly mean (solid line), minimum and maximum (dashed lines) operative environmental temperatures (T_e) for *Cophosaurus texanus* at Boquillas (A) and Grapevine (B) sites in Big Bend National Park in the summer of 1991. Activity limits (T_{bmax} and T_{bmin}) and critical limits (CTMax and CTMin) are indicated, respectively, by dotted and dashed lines.

level of acceptable habitat drop to less than 10% during the 1300–1600 interval, but a constraint on activity arose before 1000 h as a result of temperatures falling below T_{bmin} as well. At Grapevine, the level of acceptable habitat remained above 50%, but activity was potentially constrained by cold temperatures throughout the day. Thus, during midday, lizards were constrained potentially by the environment being too hot in some microhabitats and too cold in others. Constraints at Grapevine solely resulting from low temperatures were restricted to early morning (before 1000 h) and late evening (after 1800 h).

To get a measure of microhabitat quality in terms of the thermal constraints faced by *C. tex-*

anus, we calculated the proportion of each microhabitat acceptable over the course of the day (Fig. 3). With the critical limits, all Boquillas microhabitats had an approximately U-shaped distribution of fraction acceptable over time of day (Fig. 3A). They each started and ended the day fully acceptable and became partially unacceptable in midday; the magnitude and duration of this effect increased from SHADE to PARTIAL to SUN. In contrast, at Grapevine (Fig. 3B), virtually all of the SHADE and PARTIAL microhabitats were acceptable throughout the day, whereas SUN dipped in acceptability from 1200–1600 h. Note however, that the dip in acceptability of the SUN microhabitats at Grapevine was much less than that at Boquillas, and

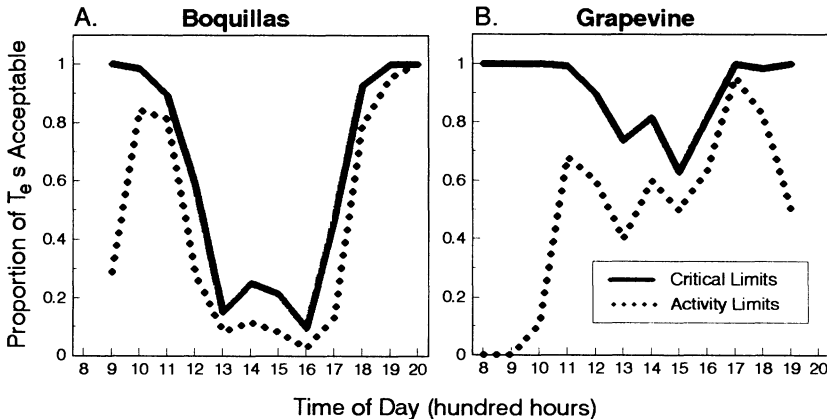


Fig. 2. Proportion of operative environmental temperatures (T_e) within either the critical limits (solid line) or activity limits (dotted line) for *Cophosaurus texanus* at each hour. T_e measurements were taken over several days in the summer of 1991 at two sites in Big Bend National Park, Texas: (A) Boquillas and (B) Grapevine.

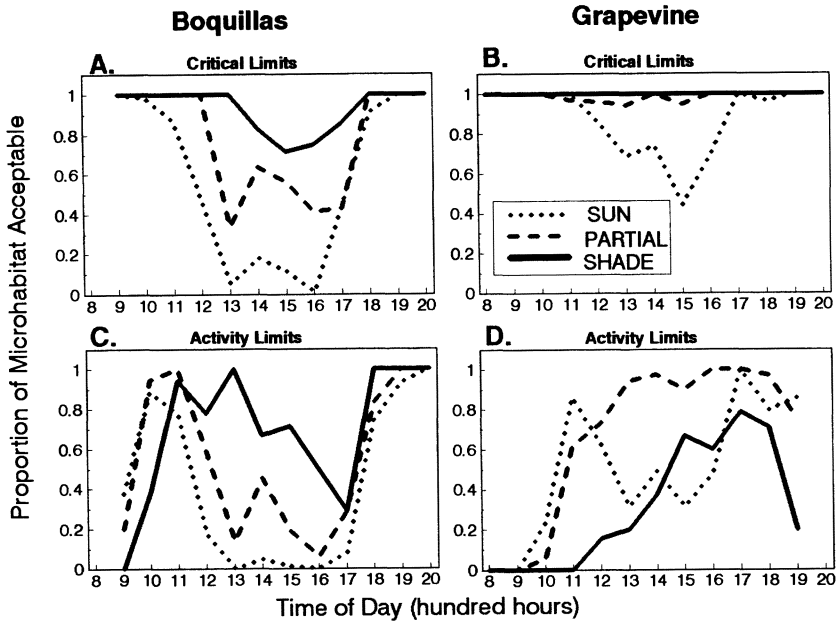


Fig. 3. Proportion of each microhabitat thermally acceptable at each hour for *Cophosaurus texanus* at two sites in Big Bend National Park in the summer of 1991. For plots Boquillas (A) and Grapevine (B), acceptability is based on the fraction of T_s s in each microhabitat that was within the critical limits. In plots Boquillas (C) and Grapevine (D), acceptability is based on the fraction of T_s s in each microhabitat that was within the activity limits.

thus during midday, SUN at Grapevine can be considered of higher thermal quality than SUN at Boquillas.

With activity limits as the measure of quality, Boquillas (Fig. 3C) showed a more severe version of the pattern afforded by the critical limits, with the added feature of microhabitats being too cold before 1000, 1100, and 1200 h, for SUN, PARTIAL, and SHADE, respectively. At Grapevine (Fig. 3D), the SUN and PARTIAL habitats were too cold before 1100 h and after 1900 h and too hot between these times, whereas the SHADE microhabitat was partially unacceptable because of cold temperatures throughout the entire day.

Comparisons of sites and times are based on the fraction of the models in a given microhabitat that were in the acceptable range. Because not all microhabitats were available at the same level throughout the day, the reliability of this measure of thermal quality is variable (i.e., sample sizes ranged from 4–100 models per hour). However, given the general consistency of this pattern across times of day, we feel that percentage of models with acceptable T_s s is a good indicator of microhabitat quality.

Microhabitat availability and predicted preferences.—SUN comprised the greatest proportion of the

microhabitats at Boquillas (Fig. 4A). There it constituted more than 80% of the environment from 1100–1800 h, whereas at Grapevine (Fig. 4B), SUN barely exceeded 60% at its maximum abundance. Not surprisingly, SHADE microhabitats were the most common microhabitat class at both sites early and late in the day. The effect of the sparse vegetation at the Boquillas site was reflected dramatically in the relative availability (an average of 3% at Boquillas vs 20% at Grapevine) of PARTIAL microhabitats.

Predicted microhabitat preferences based on the critical limits model anticipate that lizards whose behavior was based solely on staying within their critical thermal extrema should have used all microhabitats at random (i.e., in proportion to availability) in the morning and evening at both sites (Fig. 5A–B). At the Boquillas site during midday (Fig. 5A), our model predicted that SHADE should have been preferred, PARTIAL used randomly, and SUN relatively avoided. During this same interval at Grapevine (Fig. 5B), the critical limits model predicted that lizards should have preferred PARTIAL and SHADE equally and slightly more than random, whereas SUN should have been slightly avoided.

The activity limits model at Boquillas (Fig. 5C) predicted that SUN should have been high-

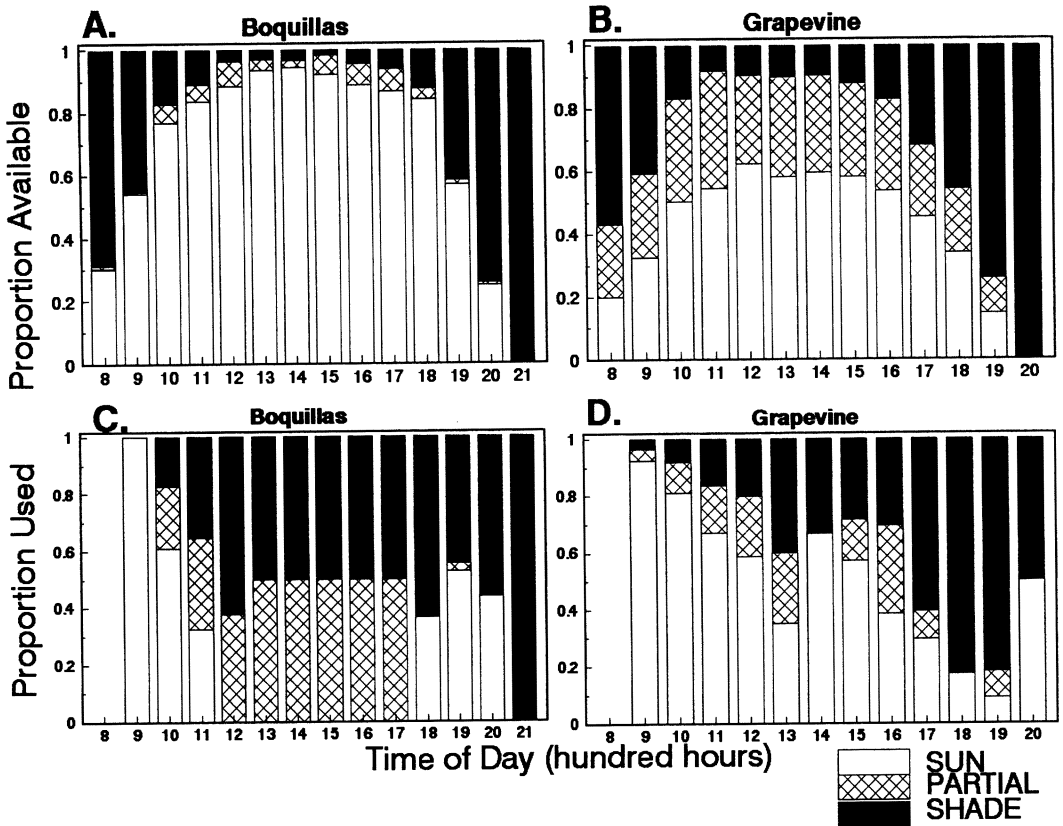


Fig. 4. Relative availability of microhabitats at each hour as determined by transect sampling at Boquillas (A) and Grapevine (B) sites in Big Bend National Park during the summer of 1991. Relative use of microhabitats by *Cophosaurus texanus* at each hour as determined by behavioral observations at Boquillas (C) and Grapevine (D) in the summer 1991.

ly preferred early in the morning ($\beta_{Sun} = 0.62$) then have dropped to zero by 1300 h. SHADE was predicted to show the opposite pattern, starting at zero and rising above 0.8 at 1300 h. Predicted preference for PARTIAL fluctuated around random but on average was predicted to be avoided at midday. Predicted preferences for all three microhabitats became random by the evening. At Grapevine, predicted preferences for SUN started at about 0.8, dropped to 0.2 at midday, and rose to 0.5 by evening (Fig. 5D). The predicted preference for SHADE never increased above random, most likely because of its being too cold, and, unlike Boquillas, PARTIAL was predicted to be preferred during midday.

Microhabitat use and observed preferences.—At Boquillas, lizards were only observed to use SUN before 1200 h and after 1800 h (Fig. 4C). Taking into account availability, SUN was only used more often than random before 1000 h and after 2000 h (Fig. 5E). Preference for PARTIAL

started low but rose to be the most preferred from 1000–1200 h as use of SUN dropped. From 1200–1900 h, SHADE was the most preferred habitat at Boquillas.

At Grapevine, SUN was used during all daylight hours (Fig. 4D) but only used more often than random before 1100 h and after 2000 h (Fig. 5F). Use of SHADE at Grapevine increased throughout the day until the last hour of sunlight, which resulted in its preference (above random use) from 1100 h to 2000 h. PARTIAL was used during almost all of the hours of the day, but this use never exceeded random.

The preference for SUN at Grapevine was initially less intense than at Boquillas, but lizards at Grapevine preferred the SUN for almost two hours longer than did Boquillas animals (Fig. 5E–5F). Moreover, lizards at Grapevine never avoided SUN to the extent that animals at Boquillas did (β_{Sun} averaged 0.2 vs 0.0). In the evening, lizards at Boquillas and Grapevine had similar preferences for SUN. Preference for SHADE at the two sites was of similar magni-

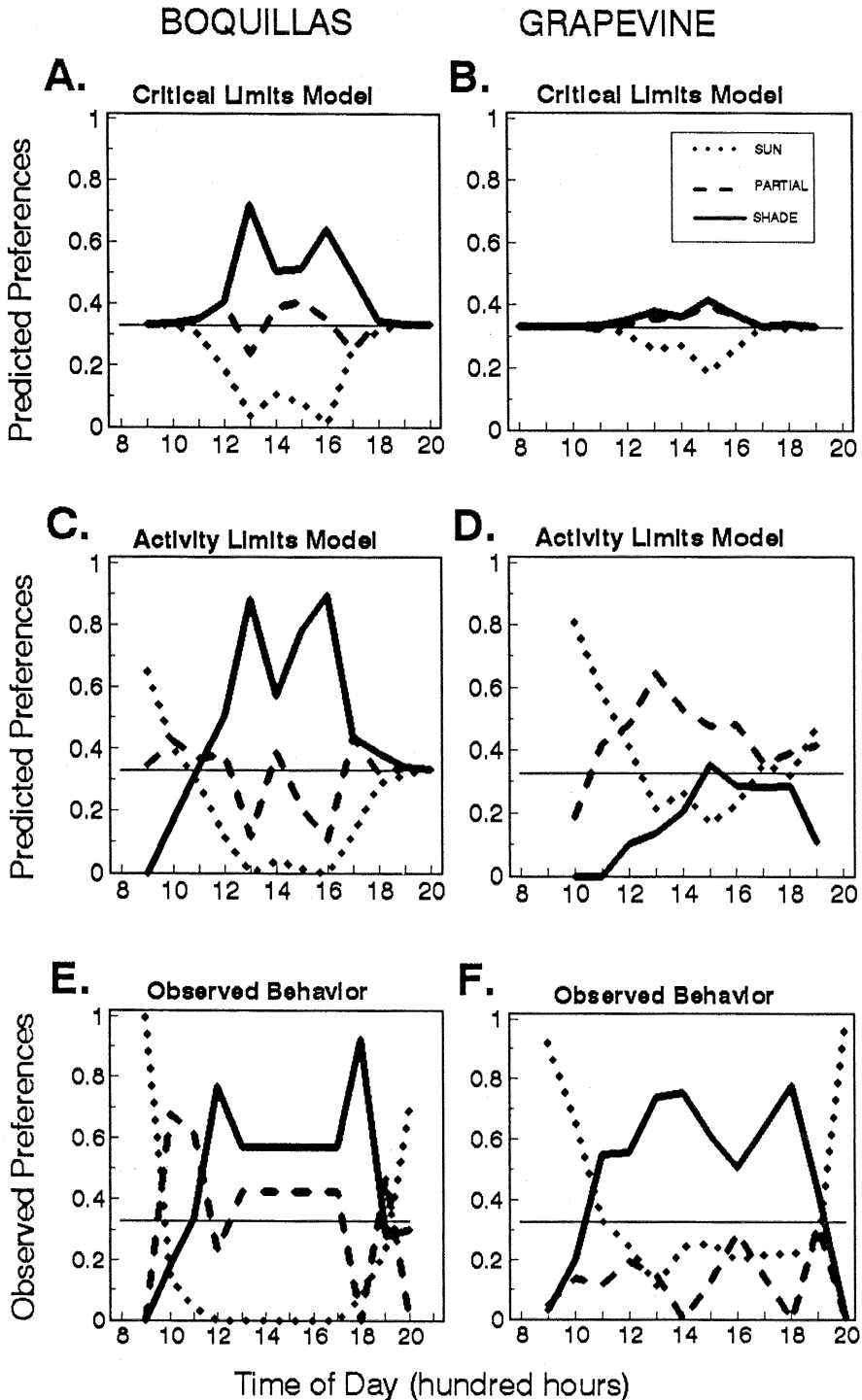


Fig. 5. Predicted hourly microhabitat preferences of *Cophosaurus texanus* determined from the critical limits model at Boquillas (A) and Grapevine (B) sites in Big Bend National Park, Texas, during the summer of 1991. Predicted hourly microhabitat preferences from the activity limits model for Boquillas (C) and Grapevine (D). Both models assumed random use of microhabitats that were thermally acceptable to *C. texanus* (as shown in Fig. 3). *Cophosaurus texanus* microhabitat preferences determined for each hour from observational data at Boquillas (E) and Grapevine (F) during the summer of 1991. Both predicted and observed microhabitat preferences are standardized by the relative availability of microhabitats (as shown in Fig. 4A–B).

tudes and duration. One surprising difference in preferences at the two sites was that, despite the greater availability of PARTIAL at Grapevine, it was never preferred, whereas Boquillas animals preferred this microhabitat to the others from 1000–1200 h and at 1900 h.

Comparison of observed and predicted preferences.—We found a significant correlation between observed and predicted preferences at Boquillas (activity limits model $r = 0.64$, $P = 0.0001$; critical limits model $r = 0.53$, $P = 0.0009$) but not at Grapevine (activity limits model $r = -0.22$, $P = 0.23$; critical limits model $r = 0.21$, $P = 0.20$). We interpret this to mean that the thermal environment dictates behavior to a greater extent at Boquillas, i.e., that lizards at Boquillas do experience a greater thermal constraint. Although the slope of the relationship between observed and predicted preferences at Boquillas for both the activity limits model and critical limits model are not significantly different from one, the activity limits model explains considerably more of the variation in the observed preferences than does the critical limits model.

DISCUSSION

We examined the consequences of maintaining body temperature in a given range on microhabitat use patterns in two populations of *C. texanus*. Examination of the distribution of operative environmental temperatures led us to believe that lizards at Boquillas faced a much greater thermal constraint than did lizards at Grapevine. By comparing the degree to which lizard microhabitat use could be predicted by a purely thermal model at the two sites, we hoped to test the hypothesis that the Boquillas population was more constrained by its thermal environment. If thermal requirements dictate behavior, then other requirements, such as social interactions, foraging success, and predator avoidance, might be constrained to microhabitats of poor quality (but of appropriate thermal conditions). In such cases, the thermal environment potentially influences individual growth, survival, and reproductive success and could cause differences in population parameters at the two sites (Dunham et al., 1989). Conversely, if thermal requirements do not dictate behavior, then other requirements such as those mentioned above would be more influential in dictating microhabitat use. Assessment of the importance of thermal constraints requires closer evaluation of our model and the data.

The aim of our model was to see whether knowledge of the T_c distributions of three sim-

ple microhabitat classes was sufficient to predict lizard microhabitat use. The value of this technique is that these microhabitats can be assessed easily and uniformly across sites and times of day, without an immediate measurement of T_c . We predicted that *C. texanus*' use of a microhabitat was equivalent to the product of the thermal acceptability of that microhabitat and its relative availability. The fit of our model could be improved with knowledge of preferred T_b s or the range of optimal performance (Hertz et al., 1993), which would allow us to weigh the use of microhabitats differentially.

The Chesson-Manly Preference Index was an important tool for presenting our model and observations. If we evaluated our model by comparing predicted and observed usages rather than preferences, we would need to continually refer to the microhabitat availabilities to interpret the observed behavior, because changes in availabilities could obscure changes in behavior brought about by differences in thermal acceptability. Using a standardized preference index enabled us to focus solely on the lizards' selection of a microhabitat, isolating thermal acceptability from availability, so that this preference could be compared across times of day and between sites. Although other standardized indices have been used before in studies of the effect of the thermal environment on microhabitat use (Roughgarden et al., 1981; Waldschmidt and Tracy, 1983), these studies calculated T_c rather than directly measuring T_c s of available microhabitats and were thus unable to measure fine-scale microhabitat acceptability (Bakken, 1992).

The activity limits model predicted the temporal pattern of microhabitat preferences at both sites more successfully than the critical limits model (Fig. 5). The critical limits model was only useful at resolving differences in microhabitat use at midday, when operative environmental temperatures approached and exceeded CTMax. The critical limits model also provided insight into emergence time. At Grapevine, the activity limits model did not predict activity until after 1000 h because none of the microhabitats affords T_c s in the activity range (Fig. 5D). Nevertheless, lizards were active in the previous hour (Fig. 5F). The critical limits model (Fig. 5B) allowed for activity after 0800 h but that predicted all microhabitats should be used at random. Although both models predicted activity after local sunrise at Boquillas, again the critical limits model did not predict differential microhabitat preferences. According to the critical limits model, temperatures were sufficiently warm in all three microhabitats in the morning

for lizards to be mobile on the surface; in contrast at midday, certain microhabitats must be avoided for *C. texanus* to be active. These results conform to the standard interpretation of the critical thermal limits; they set a template of possible activity, but lizards confine their activity to a narrower range of T_b s (Pough and Gans, 1982). Thus, the influence of the thermal environment must be considered even when temperatures are not approaching lethal levels.

We now examine the activity limits model in detail to gain insight into these more subtle thermal constraints. Despite its overall better fit, the activity limits model failed to accurately predict lizard microhabitat use in three instances. First, predicted preferences for SUN were lower than observed at both sites in the morning and evening. Second, lizards avoided SUN earlier than expected at both sites. And finally at Grapevine, lizards overwhelmingly preferred SHADE in the afternoon, whereas the model predicted that PARTIAL would be preferred. We will discuss each of these discrepancies in turn with the aim of determining whether these cases reflect errors in model construction or differences in thermally imposed constraints on microhabitat use.

One reason why preference for SUN is underestimated in the morning at both sites might be that lizards were better at finding microhabitats with high T_e s than we were at sampling them. The SUN that we sampled during 0900 h at both sites was exclusively comprised of microhabitats where the angle of incident solar radiation was either tangent or oblique to the substrate; these sites on average have a lower T_e than microhabitats where the sun is striking the substrate in a perpendicular fashion, (i.e., "full sun": Grant and Dunham, 1988; Bashey, 1992), with "tangent sun" microhabitats being cooler than "oblique sun." At Boquillas, lizards used 100% oblique sun, and of the SUN microhabitats that lizards used during this hour at Grapevine, 28% were full sun and 72% were oblique sun. No tangent sun was used at either site during 0900 h. Therefore our sampling underestimated the T_e of SUN microhabitats relative to the lizards, and thus we did not recognize its relatively high thermal quality in the morning. The converse of this argument does not explain why preference for SUN was underestimated in the evening at Boquillas where the majority of our T_e sampling and lizard sightings were in tangent sun. In contrast, at Grapevine after 2000 h, all of the T_e s sampled were SHADE microhabitats, but lizards were still able to find SUN (Fig. 4B,D).

Another consideration not included in our

thermal model is that lizards potentially were better able to warm in sun than were our copper models because of darkening of pigment (Norris and Lowe, 1964; Norris, 1967). We simulated changes in pigmentation with the program TBLIZ (Grant and Dunham, 1988; available from AED). Depending on the intensity of solar radiation and wind speed, a 10% change in pigmentation can alter the T_b of a *C. texanus* in Big Bend National Park by maximum of approximately 2 C.

Another factor to consider is that the activity limits model predicted random use of microhabitats if the microhabitats were between 31.0 and 42.1 C. However, work on the canyon lizard *Sceloporus merriami* has demonstrated that this species maintains a higher mean T_b in the evening (Grant, 1990). Although we did not find any evidence of an increase in mean active body temperature in the afternoon for *C. texanus*, perhaps more extensive sampling would show this to be the case. If the range of acceptable T_b was in fact narrower or higher in the evening, then we would predict a higher preference for SUN, more closely matching that observed at Boquillas at 2000 h.

The activity limits model predicted that Grapevine lizards should prefer SUN for an hour longer than the Boquillas animals. Although this prediction was borne out, lizards at both sites began to avoid SUN an hour earlier than expected. We can pinpoint no specific problem in our model construction that explains this early avoidance of SUN, except that this discrepancy is perhaps representative of the limited power of our T_e sampling to distinguish temporal shifts in thermal acceptability. Alternatively, if this early avoidance of SUN accurately represents the behavior of *C. texanus*, the shift could represent the response of *C. texanus* to a thermally induced change in microhabitat use of an associated species (Porter and James, 1979). Because of the high CTMax of *C. texanus*, the shift is more likely tracking the retreat of a prey species, rather than avoidance of a predator found in SUN, although the feeding ecology of *C. texanus* is unstudied.

Unlike these first two discrepancies, which concern differences in the magnitude of the observed and predicted preferences, the following case represents a severe disparity in ordering. At Grapevine, the activity limits model predicted that PARTIAL should be preferred from 1300–1700 h, whereas SHADE proved to be overwhelmingly preferred from 1200–1900 h. There are several possible reasons why the model proved inaccurate. As above, first we discuss problems in constructing the model and then

consider the implications of this discrepancy between the model and our observations.

Our assessment of microhabitat quality was perhaps compromised at certain times of the day (see Results). During midday, SHADE T_c s were less well sampled than PARTIAL and SUN, because SHADE microhabitats were rarer. These SHADE T_c s included copper models which were placed deep in vegetation, whereas most of the SHADE lizards used at Grapevine was more transient, at the edges of vegetation. The potential influence of deep vegetation SHADE on our measure of thermal acceptability would be greatest during midday because during this period, they comprised the majority of the few SHADE T_c s measured, most of the T_c probes being in other microhabitats. If this did lead to an underestimation of SHADE T_c s relative to PARTIAL, then this would explain why preference for SHADE is higher than predicted at Grapevine.

Alternatively, if our assessment of SHADE being of low thermal quality is correct, one reason its use was underestimated could be shuttling between microhabitats. Our assessment of microhabitat quality and prediction of preferences was based on equilibrium T_c s; however, many of the behavioral observations of microhabitat use did not last the three minutes needed to ensure the lizards had equilibrated. Thus lizards might avoid SHADE if their use of this microhabitat required that their T_b dropped below their activity range, but if they could shuttle to and from this habitat as they needed to cool down, then their preference for SHADE would be higher.

If, despite the above arguments, we accept that our model adequately represents the thermoregulatory behavior of *C. texanus*, then we can view the relative fit of the model predictions to Boquillas lizard observations ($r = 0.64$) as evidence that the thermal environment is important in explaining behavior at that site and the discrepancy between the model predictions and observed microhabitat preferences at Grapevine ($r = -0.22$ ns) as indicative of the thermal environment being less important. If there are nonthermal reasons for lizards at Grapevine to choose SHADE over PARTIAL and they can bear the cost of responding to these factors over thermal considerations, then the thermal environment is not constraining. However, if nonthermal factors cause a conflict with thermally determined microhabitat preferences which cannot be resolved in favor of the nonthermal factors, then the thermal environment is constraining.

The high preference for SHADE that we ob-

served, but did not predict, at Grapevine suggests that SHADE might offer enhanced foraging or social success and/or lower risk of predation. We have observations of foraging strikes and social interactions (push-ups, shutterbobs, chasing) from both sites. Although we did not correct for availability because of the small sample size, the pattern is striking. Of the 31 observations of social interactions from Grapevine, 74% occurred in SUN, 23% in SHADE, and only 3% in PARTIAL. Similarly of 35 social observations made at Boquillas, 74% occurred in SUN, 17% in SHADE, and only 9% in PARTIAL. Although these numbers could be an artifact demonstrating difficulty in observing lizards not in the open, Degenhardt (1974) suggested that a high density of vegetation was detrimental to *C. texanus* population growth because of this species' need of high visibility for social interactions. In agreement with the low social quality of PARTIAL, of the 11 foraging strikes observed at Grapevine, seven occurred in SUN, three in SHADE, and only one in PARTIAL. So potentially Grapevine lizards, although largely excluded from the socially best habitat (SUN) by thermal considerations, are forgoing the thermally optimal and readily available habitat (PARTIAL) in favor of a more profitable habitat socially and nutritionally (SHADE).

In contrast, at Boquillas, not only were the thermally optimal habitats preferred, but the thermal environment was so extreme that occupying these microhabitats essentially precluded social or foraging activity. During midday, SHADE comprised less than 5% of the Boquillas environment which essentially caused this microhabitat to form isolated refuges from the heat. In fact, the lower than predicted preference for SHADE and the higher than predicted preference for PARTIAL during this time (compare Fig. 5C with Fig. 5E) was due to observations of a single lizard found uncharacteristically up a bush. This heavily influenced the data because of the low number of total observations. Because this behavior was previously unobserved, no T_c measurements had been made of this arboreal habitat. And, although it was classified as PARTIAL, most likely the T_c was similar to SHADE at that hour because of increased convection. Because so few lizards were observed at Boquillas during midday and those that were observed appeared to be confined to their current perch, we conclude that the severity of the thermal environment during midday at Boquillas served to restrict the activity of *C. texanus* to thermoregulatory behavior.

Thus, the relative fit of the activity limits mod-

el at the two sites helped us to confirm that midday was the time of differential thermal constraints. During midday, the activity of Boquillas lizards was extremely limited, whereas Grapevine lizards underused a thermally optimal habitat. By limiting the activity of Boquillas lizards to thermoregulation, thermal constraints potentially lessened the foraging and mating opportunities of this population relative to Grapevine. This result of greater thermal constraints on the Boquillas population is in concordance with studies of the canyon lizard *S. merriami* (Grant and Dunham, 1990) and the mottled rock rattlesnake *Crotalus lepidus* (Beaupre, 1995), which also inhabit these sites. These studies concluded that the thermal environment limited the energy budgets of Boquillas populations to an extent that could account for lower individual growth rates and adult body sizes relative to the Grapevine populations. Because of this and lower population densities of *C. texanus* at the Boquillas site (FB, pers. obs.), we suggest that an examination of differences in growth rates and fecundity in these two populations of *C. texanus* is warranted.

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