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Behavioural plasticity in an ecological generalist: microhabitat use by western fence lizards

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ABSTRACT

Question: What is the basis for geographic variation in microhabitat use in fence lizards?

Hypothesis: Population differences in microhabitat use reflect behavioural plasticity rather than genetic or experiential differences.

Organisms: Western fence lizards (*Sceloporus occidentalis*).

Field site: Three sites (desert, valley, and mountain) in southern California, USA.

Methods: We compared habitat use by free-ranging lizards in three field populations. We also collected lizards from these three populations and studied their microhabitat use in experimental enclosures at a single field site.

Results: In the wild, lizards chose higher and shadier perches at the hottest (desert) site, lower and sunnier perches at the coolest (mountain) site, and intermediate perches at the thermally intermediate valley site. However, lizards collected from the three source populations did not differ in microhabitat use in experimental enclosures at a common field site, supporting our hypothesis. Microhabitat choice is an important thermoregulatory mechanism in this species.

Keywords: field experiment, geographic variation, habitat shift, microclimate, nature vs. nurture, thermal biology.

INTRODUCTION

Animal species whose habitat use varies geographically provide excellent opportunities for examining the relative roles of genetic differences and behavioural plasticity, and for understanding the ecological factors that influence habitat choice. However, relatively few studies have examined whether genetic differences among populations contribute to intraspecific geographic variation in habitat use (Thompson, 1999). In contrast, interspecific differences in habitat use have been extensively documented, especially in the context of interspecific competition and resource partitioning (e.g. MacArthur, 1958; Rosenzweig, 1973; Schoener, 1977; Roughgarden, 1995).

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Lizards are important model organisms for studying intraspecific geographic variation in numerous characteristics, including life-history traits (Niewiarowski, 1994), sexual selection (Kwiatkowski and Sullivan, 2002), anti-predator behaviour (Downes and Adams, 2001), display behaviour (Martins *et al.*, 1998), thermal physiology (Crowley, 1985; Tsuji, 1988), and ecomorphology (Sinervo and Losos, 1991). Geographic variation in habitat or microhabitat use has been described in several lizard species (e.g. Parker and Pianka, 1973; Schoener, 1975; Hertz and Huey, 1981; Irschick *et al.*, 2005). These intraspecific shifts in habitat use could reflect genetic differentiation among populations, differences in experience (Davis and Stamps, 2004), and/or behavioural plasticity (Wecker, 1963; Hildén, 1965); however, the roles of these factors in determining habitat use are essentially unexplored in lizards (Heatwole, 1977; Adolph, 1990b).

The western fence lizard, *Sceloporus occidentalis* (Phrynosomatidae), is an excellent candidate for examining geographic variation in habitat use. *Sceloporus occidentalis* is an ecological generalist, found across a wide variety of habitats and elevations in the western United States, including grassland, chaparral, woodland, coniferous forest, and high desert (Marcellini and Mackey, 1970; Rose, 1976; Stebbins, 2003). Previous work on this species has documented geographic shifts in microhabitat use – in particular, fence lizards in a desert population are highly arboreal and usually perch in the shade, whereas lizards from a cooler mountain site tend to perch in full sunlight closer to the ground (Adolph, 1990a; Sinervo and Losos, 1991). However, previous studies did not determine whether geographical variation in habitat use reflected genetic or experiential differences between populations or was simply due to behavioural plasticity.

In this study, we examined microhabitat use by free-living *S. occidentalis* at an inland valley site in southern California and compared these data with those of a previous study of mountain and desert populations (Adolph, 1990a). We then conducted microhabitat choice experiments in which lizards native to these three field populations were tested in field enclosures at a single location. This experiment tested whether lizards from populations that differ in arboreality in their native environments also show these differences in a common environment. We also measured the thermal microclimates within the enclosures so that we could evaluate the role of thermoregulation in microhabitat selection (Adolph, 1990a).

METHODS

Field observations of free-ranging lizards

We observed microhabitat use by free-ranging *S. occidentalis* at the Bernard Biological Field Station ('valley' site) in Claremont, California, USA (elevation 1325 m; 34°07′N, 117°42′W). The habitat at the valley site consists primarily of coastal sage scrub interspersed with native trees, including coast live oak (*Quercus agrifolia*), canyon live oak (*Quercus chrysolepis*), California laurel (*Umbellularia californica*), and blue elderberry (*Sambucus mexicana*). We searched for active lizards from June through September 2002 and 2003. We noted each lizard's perch position including substrate (e.g. tree, ground), sun/shade condition (full sun, partial sun, full shade), and body orientation (horizontal or vertical). We then captured the lizard by noosing and recorded air temperature (shaded bulb, 1 m above ground), time of day, sex, snout-to-vent length (SVL), mass, perch height and perch circumference (for off-ground perches). For some lizards we measured cloacal body temperature using a quick-reading mercury thermometer. Before release, lizards were marked with non-toxic white paint to avoid recapture.

We compared habitat use of free-ranging valley *S. occidentalis* with data from Adolph's (1990a) previous study at two other sites in southern California (summer 1983). The 'mountain' site is in open pine/oak woodland forest (mean elevation 2230 m; 34°23′N, 117°40′W; known as Table Mountain). The 'desert' site is a high-desert Joshua tree woodland environment (mean elevation 1250 m; 34°27′N, 117°45′W; known as Joshua). Pairwise map distances between these three sites range from 11 to 39 km.

We compared distributions of field perch heights and sun/shade frequencies among populations using chi-square tests. We combined data for male and female lizards because a preliminary statistical analysis showed no significant difference in field perch heights between the sexes.

Perch choice experiments

We conducted field experiments in individual enclosures to determine whether *S. occidentalis* from different source populations exhibited differences in habitat use when placed in a common structural and thermal environment. We constructed seven enclosures in unshaded habitat at the valley site with adequate spacing to prevent interaction between lizards. Enclosures were 3.7 m in diameter, with sheet metal walls 50 cm high. The centre of each enclosure had a simple arrangement of potential perches including a section of tree stump as a base, a horizontal branch, and a vertical branch. Branches and stumps had bark or a rough surface that lizards could easily climb. The bases ranged in height from 36 to 56 cm, topped with a vertical branch, for a total height of 186–235 cm, and a horizontal branch 121–181 cm in length. Circumferences ranged from 138 to 220 cm for the tree stumps, 28 to 47 cm for the vertical branches, and 27 to 40 cm for the horizontal branches.

We measured the surface area available for perching in each enclosure and averaged these values for each perch surface across the six enclosures, yielding availability measures. We compared the frequency with which lizards perched on each object to their availabilities to determine how perch use compared with relative abundance (Adolph, 1990a).

Six of the enclosures were used for lizards, and the seventh was equipped with operative temperature models [T_e (Bakken, 1989)] to measure microclimates. Our models were copper tubes (70 mm long, 15 mm diameter) painted grey to approximate the reflectivity of *S. occidentalis* (Peterson *et al.*, 1993), and sealed with corks. Model internal temperatures were recorded with type T thermocouples and an electronic thermometer (Bailey model BAT-12). Pairs of models were placed (one in full sun and one in full shade) in five locations: at heights of 2 m and 1 m on the vertical perch, on one end of the horizontal branch, horizontally on the surface of the stump, and horizontally on the ground. Air temperature was also taken at 1 m above the ground with a shaded thermocouple. We repositioned the models frequently so that they remained in full sun or full shade throughout the day, to bracket the range of T_e available in each perch location. These data provided information on the temporal changes and spatial distributions of microclimates available for the lizards.

We conducted habitat selection trials on 18 separate days during July–September 2002 and 2003 during normal summer weather. For each day's experiment, adult lizards (>59 mm SVL) collected from each source population (mountain, desert, and valley) were placed in individual enclosures the preceding evening. Lizards were randomly assigned to enclosures with respect to sex and source population. On the day of the experiment, we observed lizards and recorded T_e at 50-min intervals from 09.00 to 16.30 h Pacific Standard

Time (ten observations per lizard per day). We initially examined enclosures from a distance with binoculars to determine whether the lizard was readily visible. If not, we slowly approached the enclosure to locate the lizard. We marked perch heights on photographs of the enclosures, and noted the lizard's sun/shade condition (sun, partial sun, shade) and body orientation (horizontal, vertical, diagonal). We later estimated perch heights with a tape measure, using the marked photograph for reference. If we could not locate an individual within 5 min, it was assumed to be on the ground or burrowed under the topsoil; in this case, it was assigned a perch height of zero. After the final survey, we captured each lizard and returned it to its original capture site within 3 days. Each lizard was only used for one trial.

We tried to have a balanced design with one male and one female from each of the three source populations each day. Although this was not always feasible, on 17 of the 18 experimental days we had at least one individual from all three source populations. To verify that source population and sex were not confounded by covariation with environmental conditions, we used two-way analyses of variance to compare T_e for both the full shade and full sun models on the stump top. Operative temperature did not differ significantly among populations or between males and females (all P-values > 0.5). Similarly, individuals from different source populations did not differ significantly in body size (either SVL or mass; two-way analyses of variance; Table 1).

We analysed perch heights using a repeated-measures analysis of variance (ANOVA), with sex and source population as factors and the ten observations as the repeated measure. We calculated repeatabilities for females and males separately as a measure of the individual consistency of perch height. Because perch height varied with time of day, we adjusted each perch height by subtracting the mean of all perch heights for lizards of the same sex at the same sampling time (across all days of the experiment). We used these residual values to calculate intra-class correlation coefficients (Sokal and Rohlf, 1981) and their standard errors (Becker, 1984).

We used randomization tests to analyse sun/shade frequencies of the lizards. This allowed us to use all of the observations for each individual without assuming independence of observations within individuals. We pooled the data for lizards from a given source population to obtain an overall distribution of observations in full sunlight, partial sunlight, and shade for each population (omitting observations during overcast skies). Then we calculated a chi-square statistic using the observed data and the expected data under the null hypothesis of no difference in sun/shade frequencies between populations. We compared our observed chi-square statistic to the null distribution obtained by randomly reassigning each individual (including all 10 observations) to a source population and recalculating a chi-square value from the randomized data ($N = 1000$ replicates; custom C program). We used similar randomization tests for diel changes in sun/shade frequency, sex differences in sun/shade frequency, and population differences in perch substrate choice.

Table 1. Sizes of adult western fence lizards (*Sceloporus occidentalis*) used in perch experiment (mean ± s)

Source population	Mass (g)	SVL (mm)	N (females, males)
Valley	11.18 ± 2.99	67.0 ± 5.1	38 (22, 16)
Mountain	11.21 ± 3.01	68.0 ± 5.3	35 (21, 14)
Desert	12.00 ± 3.55	69.2 ± 6.0	34 (20, 14)

RESULTS

Habitat use by lizards in the wild

Mean body temperature of active lizards at the valley site was 34.1°C (standard deviation [s] = 1.9, N = 20), verifying that the thermal biology of lizards in this population is similar to that in previously studied field populations, including the mountain and desert sites (Adolph, 1990a).

Valley lizards perched most frequently on trees, but were also observed on a wide range of other substrates, including logs and other wooden debris, rocks, and the ground. Mean perch height was 84.4 cm (s = 72.1, N = 140) and mean perch circumference was 73.3 cm (s = 55.6, N = 113). Valley lizards chose intermediate perch heights compared with the perch heights chosen by mountain and desert lizards (χ^2 = 122.402, d.f. = 10, P < 0.0001; Fig. 1) (Adolph, 1990a). In pairwise comparisons, valley lizards perched significantly lower than desert lizards (χ^2 = 44.267, d.f. = 5, P < 0.0001), but significantly higher than mountain lizards (χ^2 = 28.183, d.f. = 5, P < 0.0001). Because Adolph (1990a) did not report perch circumferences, we compared field data collected from the lizards used as our experimental subjects. In this smaller sample (N = 92), mean perch circumference ($\pm s$) of valley lizards

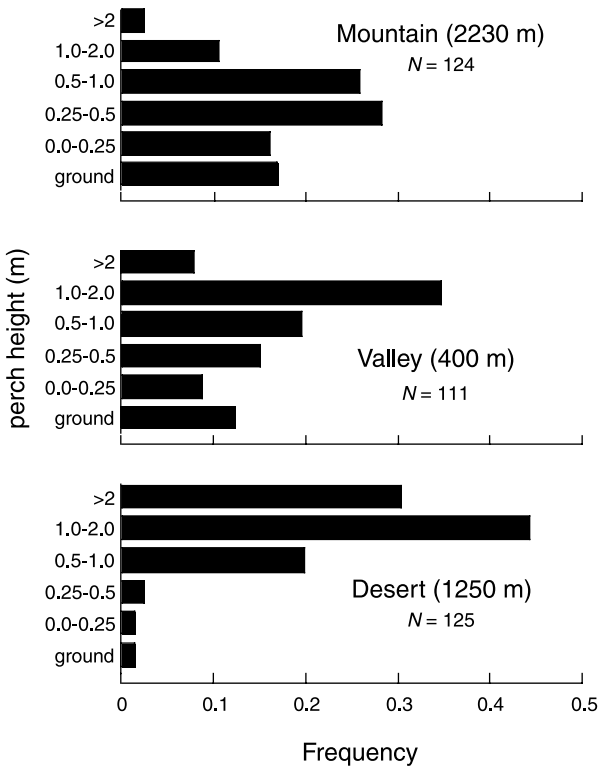

Fig. 1. Perch height distribution of free-ranging western fence lizards (*Sceloporus occidentalis*) at three field sites in southern California. Data for mountain and desert sites are from Adolph (1990a). Panels are arranged in order of summertime temperatures from the coolest site (mountain) to the warmest site (desert).

(84.8 ± 49.8 cm) was intermediate to that of desert (54.1 ± 11.9 cm) and mountain (158.11 ± 144.8 cm) lizards ($F_{2,86} = 9.582$, $P = 0.0002$). Pairwise differences in perch circumference were significant for valley versus mountain and for desert versus mountain, but not for valley versus desert (Fisher's PLSD *post hoc* tests).

Similarly, sun/shade frequencies of valley lizards were intermediate to those of the desert and mountain populations ($\chi^2 = 67.952$, d.f. = 4, $P < 0.0001$; Fig. 2). Lizards at the valley site perched significantly more often in full sunlight, and less often in shade, than those at the desert site ($\chi^2 = 34.045$, d.f. = 2, $P < 0.0001$). Although valley lizards perched more often in shade and less often in full sun than mountain lizards, this pairwise comparison was not significant ($\chi^2 = 4.711$, d.f. = 2, $P = 0.095$). We omitted observations of lizards under overcast skies, which included 4 valley, 17 mountain, and 6 desert observations.

Males and females at the valley site did not differ in either perch circumference ($F_{1,86} = 0.005$, $P = 0.9467$) or sun/shade frequency ($\chi^2 = 1.283$, d.f. = 2, $P = 0.5266$). Males perched somewhat higher than females (mean ± *s*: 93.8 ± 78.4 cm for males, 75.6 ± 65.0 cm for females), but the difference was not significant ($F_{1,138} = 2.235$, $P = 0.1372$). Lizards perched more frequently in the shade as air temperature increased; mean air temperature (± standard error) for lizards in the shade was 29.4 ± 0.54°C, for lizards in partial sun 27.7 ± 0.50°C, and for lizards in full sun 27.0 ± 0.46°C (ANOVA $F_{2,103} = 5.15$, $P = 0.0074$). Perch height was not correlated with air temperature measured at the time of capture ($r = 0.021$, $P > 0.5$).

Microclimates in experimental enclosures

On all substrates, T_e increased until mid-afternoon, and then declined slightly during the last few hours of the experiment (Fig. 3). While T_e in the sun exceeded T_e in the shade for all substrates, the magnitude of this difference was greater on the ground and the stump top than on the horizontal and vertical poles. All substrates offered temperatures within the lizards' preferred temperature range [34.2–36.5°C (Adolph, 1990a)] for at least part of the day.

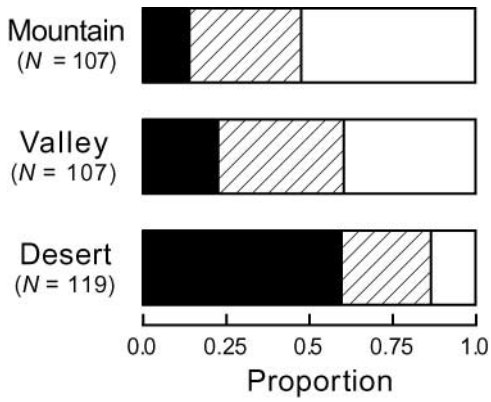

Fig. 2. Proportion of free-ranging western fence lizards (*Sceloporus occidentalis*) in full shade (black bar), partial or filtered sunlight (hatched bar), and full sunlight (open bar) microhabitats at three field sites in southern California. Data for mountain and desert sites are from Adolph (1990a). Observations during overcast weather were omitted. Panels are arranged in order of summertime temperatures from the coolest site (mountain) to the warmest site (desert).

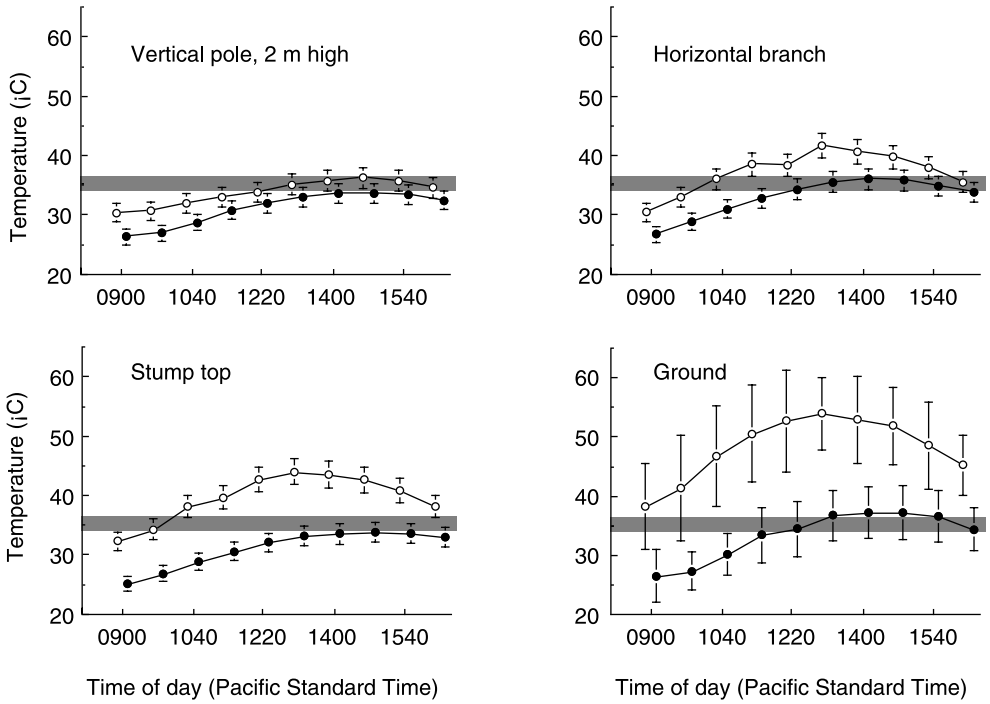

Fig. 3. Summary of operative temperatures (mean ± standard error) of copper models on different substrates during perch choice experiments. ○ = model in full sunlight, ● = model in full shade. Horizontal grey bar indicates the central 50% of body temperatures recorded for free-ranging *Sceloporus occidentalis* [34.2–36.5°C (data from Adolph, 1990a)].

Operative temperatures were hottest on the ground and coolest on the vertical pole. During the morning, pole T_e frequently fell below the lizard's preferred temperature range; during the afternoon, ground temperatures often exceeded this range.

Microhabitat choice in experimental enclosures

Fence lizards perched most frequently on the stump top and ground but also used all other perch locations (vertical branch, horizontal branch, stump side). Lizards from the three source populations chose perch substrates in similar proportions (Fig. 4). Substrate use was marginally significantly different among populations (randomization test, $\chi^2 = 49.96$, $P = 0.054$); desert natives perched on the ground and on the vertical pole more often, and on stump tops less often, than valley and mountain natives. Overall, lizards perched off the ground more often (59.1% of observations) than expected based on the relative availability of off-ground (19.7%) versus ground surface area (80.3%) in the enclosures. Electivity indices (not shown) indicated that lizards preferentially chose stump tops, used horizontal branches approximately in proportion to availability, and tended to use stump sides and vertical poles less than their relative availability.

Lizards perched higher during the middle of the day (Fig. 5, Table 2). However, lizards from the three source populations did not differ in perch height (Table 2). Males perched

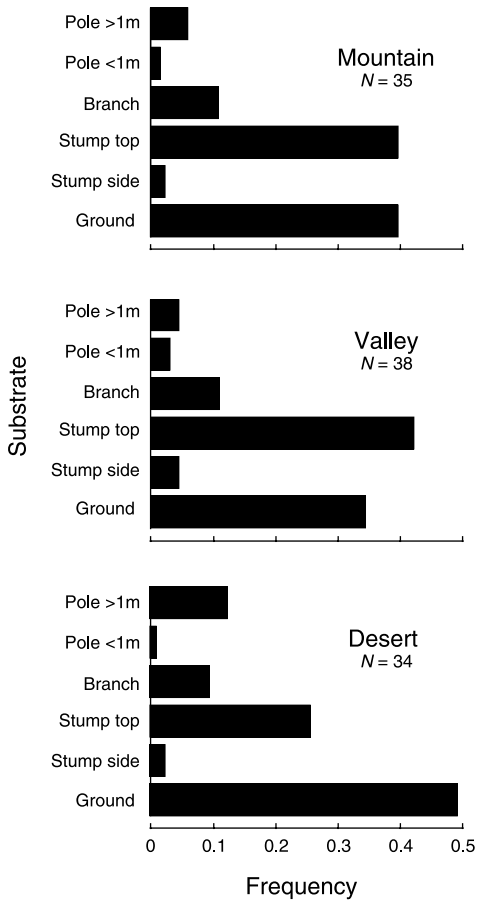

Fig. 4. Perch locations chosen by western fence lizards (*Sceloporus occidentalis*) from three different source populations within field enclosures at a common site (valley). Sample sizes show numbers of individual subjects; we made 10 observations per subject.

higher than females during most of the day; this difference was greatest during late morning and midday (Fig. 5, Table 2).

Sunlight levels chosen by lizards did not vary with source population (randomization test, $\chi^2 = 5.124$, $P = 0.559$). Males perched in full sunlight more often than females (randomization test, $\chi^2 = 11.648$, $P = 0.033$). Lizards basked in full sun more frequently in the morning than they did later in the day (randomization test, $\chi^2 = 138.8$, $P < 0.001$).

Individual lizards chose moderately consistent perch heights over the 10 successive observations: intra-class correlation coefficients (± standard error) were 0.345 ± 0.051 for females and 0.511 ± 0.062 for males (ANOVA, $P < 0.0001$ in both cases). In contrast, we did not observe a consistent relationship between the average perch height chosen by each individual lizard in the enclosure experiment and the perch height where it had been observed when it was collected from the wild 1–2 days before the experiment. Pooling all lizards, wild versus experimental perch height choices were not correlated ($r = -0.0006$). Analysed separately, desert and mountain natives showed no relationship between perch

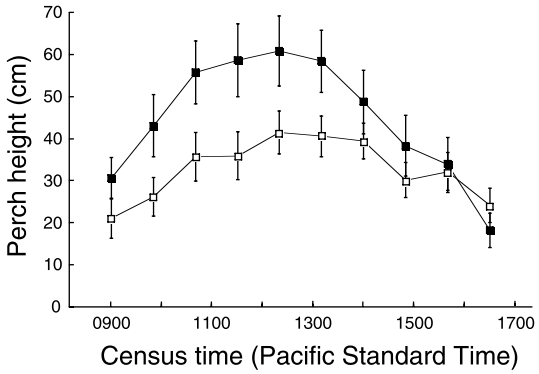

Fig. 5. Perch heights (mean ± standard error) chosen by western fence lizards (*Sceloporus occidentalis*) in experimental enclosures over the course of the day. ■ = males, □ = females. We combined data from the three source populations because they did not differ significantly (Table 2).

Table 2. Results of repeated-measures ANOVA for perch heights chosen by western fence lizards (*Sceloporus occidentalis*) in experimental enclosures over the course of the day

Source	d.f.	Sum of squares	Mean square	*F*	*P*
Population (= A)	2	812.7	406.4	0.047	0.954
Sex (= B)	1	37540.9	37540.9	4.319	0.040
A × B	2	16178.4	8089.2	0.931	0.398
Subjects within groups	101	877891.0	8692.0		
Repeated measure (height = C)	9	102742.5	11415.8	11.120	<0.0001
A × C	18	13264.3	736.9	0.718	0.795
B × C	9	20589.6	2287.7	2.229	0.018
A × B × C	18	14869.5	826.1	0.805	0.696
C × subjects within groups	909	933146.6	1026.6		

heights in the wild and in enclosures ($r = 0.123$, $P > 0.2$ and $r = 0.037$, $P > 0.5$ respectively), whereas valley natives surprisingly showed a negative correlation ($r = -0.324$, $P < 0.05$). The negative correlation for valley natives was mainly attributable to males ($r = -0.525$, $P = 0.035$, $N = 16$) rather than females ($r = -0.181$, $P = 0.425$, $N = 22$). Thus, this negative relationship occurred in only one of six sex/population subgroups.

DISCUSSION

Behavioural plasticity and geographic variation in microhabitat use

Our field observations confirmed that microhabitat use by *Sceloporus occidentalis* varies geographically, as several authors have noted previously (e.g. Stebbins, 2003). Specifically, lizards chose higher, shadier perches at the hottest (desert) site, lower, sunnier perches at the coolest (mountain) site, and intermediate perches at the thermally intermediate (valley) site (Figs. 1 and 2). In contrast, adult lizards from these three sites chose very similar perches when

tested in a common environment. The experimental findings imply that geographic habitat shifts are due to behavioural plasticity rather than genetic differentiation in microhabitat preference. This conclusion is consistent with experiments involving laboratory-reared juvenile *S. occidentalis*, which revealed no differences in climbing tendencies between desert and mountain natives (Adolph, 1990b). The apparent lack of genetic differentiation in microhabitat preference is consistent with the high rates of gene flow estimated among populations of *S. occidentalis* in southern California, including the desert and mountain sites (C.S. McFadden and S.C. Adolph, unpublished manuscript). High rates of gene flow between populations could impede genetic differentiation in habitat preferences, while facilitating the evolution of phenotypic plasticity (Sultan and Spencer, 2002). Furthermore, daily and seasonal changes in thermal environments within sites should also favour behavioural plasticity (e.g. Huey and Pianka, 1977).

Our experiments also found no evidence that lizards have particular perch height preferences as a result of individual experience or genetic predisposition. This is suggested by the lack of among-population differences in perch heights in enclosure experiments (Table 2) and the absence of a positive correlation between (1) the height chosen by individuals in enclosures and (2) the height at which they had been observed in the wild. On the other hand, individuals chose moderately consistent perch heights over the 7.5 h of the experiment. This short-term consistency may simply reflect fence lizards' sedentary nature (Schall and Sarni, 1987); individuals often occupied the same perch on successive censuses.

Sceloporus occidentalis is, ecologically, very generalized; Stebbins (2003) notes that it can be found in a wide variety of habitats, including grassland, chaparral, sagebrush, woodland, open coniferous forest, and farmland. In addition, we have observed this species in rocky riparian zones, Joshua tree woodland, oceanside scrub, and suburban neighbourhoods. Many authors have documented microhabitat use in *S. occidentalis* (Bartlett and Gates, 1967; Marcellini and Mackey, 1970; Davis and Verbeek, 1972; Fuentes, 1976; Rose, 1976; Schall and Sarni, 1987; Adolph, 1990a; Grover, 1996; Zani, 2001; Covill, 2002); these studies collectively show that perch heights and substrates vary substantially among populations. Our experiment suggests that these geographic differences may be largely due to behavioural flexibility rather than genetic differences; plasticity of habitat use undoubtedly facilitates ecological generalization.

Thermal biology and the adaptive significance of behavioural plasticity

The behaviour of lizards in the field enclosures indicates that microhabitat use is intimately related to temperature. Lizards preferentially used the most thermally favourable perches overall (Figs. 4 and 5), and also chose higher, shadier perches during the hotter periods of the day (Fig. 3). Although we did not measure cloacal body temperature in our experiments, Adolph (1987) found that *S. occidentalis* maintain a mean cloacal body temperature of 35.7°C in enclosures, and McGinnis (1970) reported similar temperatures for *S. occidentalis* in enclosures. These studies indicate that *S. occidentalis* behaviourally thermoregulate in simple field enclosures as they do in the wild. The between-site differences in microhabitat use similarly suggest that thermal characteristics are a primary factor governing perch choice in *S. occidentalis* (Figs. 1 and 2) (Adolph, 1990a). Bartlett and Gates (1967) and Grover (1996) noted similar microhabitat shifts by *S. occidentalis* across seasons.

Both biophysical models and empirical measurements have demonstrated that the microclimates of higher perches are often cooler (Geiger, 1965; Bartlett and Gates, 1967; Porter *et al.*, 1973;

Bakken, 1989; Adolph, 1990a), although in some cases the relationship between perch height and T_e can be decoupled or even reversed (Roughgarden *et al.*, 1981; Hertz *et al.*, 1994). Climbing to thermoregulate has been observed in other lizards (Bradshaw and Main, 1968; Heatwole, 1970; Porter *et al.*, 1973; Huey and Pianka, 1977; Melville and Schulte, 2001), as well as in snakes (Shine *et al.*, 2005), snails (McBride *et al.*, 1989), and grasshoppers (Whitman, 1987).

Fence lizards also modified their exposure to sunlight as a thermoregulatory mechanism, as indicated both by among-site and within-site variation in sun/shade frequency in response to ambient temperatures. The choice of sunny versus shady microhabitats is undoubtedly the most common thermoregulatory behaviour in lizards (e.g. Cowles and Bogert, 1944; Heath, 1965; Huey and Pianka, 1977; Muth, 1977; Hertz and Huey, 1981; Waldschmidt and Tracy, 1983). Experiments have demonstrated that some lizards use sunlight and light intensity as cues for choosing habitats (Hertz *et al.*, 1994; Tiebout and Anderson, 2001).

Ideally, habitat use should be evaluated in terms of how it affects individual performance and fitness (Waldschmidt and Tracy, 1983; Irschick and Losos, 1999; Misenhelter and Rotenberry, 2000). The connection between microhabitat use, thermoregulation, and physiological performance clearly suggests the adaptive value of flexible habitat use by *S. occidentalis*. Fence lizards thermoregulate to maintain a narrow range of body temperatures (32–36°C) both in the wild and in laboratory thermal gradients (Bogert, 1949; Wilhoft and Anderson, 1960; Brattstrom, 1965; McGinnis, 1966, 1970; Mayhew, 1968; Adolph, 1990a; Wang and Adolph, 1995; Covill, 2002). This temperature range is optimal for many physiological traits in *S. occidentalis* (Werner, 1972; Bennett and Gleeson, 1976; Harwood, 1979; Bennett, 1980; Huey, 1982). Flexible microhabitat use, because it facilitates careful thermoregulation, ensures that fence lizards are capable of high levels of physiological performance in the face of daily, seasonal, and geographic variation in thermal environments.

Microhabitat choice by females versus males

Males perched higher than females in both free-ranging and experimental conditions at the valley site, although the difference was not statistically significant for free-ranging lizards. Male lizards commonly perch higher than females (e.g. Fleming and Hooker, 1975), a difference usually attributed to a greater degree of territoriality in males. In the enclosure experiment, lizards were introduced into a novel environment, which could elicit enhanced territoriality. This effect could be particularly pronounced in male *S. occidentalis*, which are highly territorial during the summer (Davis and Ford, 1983; Sheldahl and Martins, 2000); however, our experiments were conducted after the breeding season, which could have reduced the intensity of territorial behaviour. Interestingly, females chose shadier perches than did the males in the enclosures. In this environment, a lower shady perch will offer a similar microclimate as a higher sunny perch. Adolph (1990a) found no differences in the field cloacal body temperatures of male and female *S. occidentalis*, suggesting that males and females do not differ in their thermal preferences. Therefore, differences in habitat use between males and females must be due to something other than thermal physiology. Differences in microhabitat use between the sexes are not always observed in *S. occidentalis*: Adolph (1990a) found that free-ranging females and males did not differ in perch height or sun/shade frequency at the desert and mountain sites.

CONCLUSION

Our study further documents geographic variation in microhabitat use in western fence lizards, and our results suggest that this is due to behavioural plasticity rather than to genetic differentiation. Plasticity of microhabitat choice undoubtedly facilitates behavioural thermoregulation in *S. occidentalis*. Plasticity of habitat use could also have evolutionary consequences: behavioural shifts could either buffer or drive natural selection on physiological and morphological traits (Huey *et al.*, 2003). *Sceloporus occidentalis* appears to exemplify both of these phenomena. On the one hand, the cloacal body temperature of active fence lizards varies little among populations inhabiting different thermal environments (Bogert, 1949; Brattstrom, 1965; Mayhew, 1968; Adolph, 1990a; Covill, 2002), so that selection for geographic differentiation in thermal physiology is likely to be weak (Huey *et al.*, 2003). On the other hand, geographic variation in microhabitat use appears to be responsible for the evolution of differences in limb proportions and arboreal locomotor performance between northern and southern populations of *S. occidentalis* (Sinervo and Losos, 1991). These observations demonstrate the utility of species that show behavioural plasticity in habitat use, such as *S. occidentalis*, as candidates for exploring the importance of behavioural drive and behavioural inertia in evolution (Huey *et al.*, 2003).

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