HABITAT SELECTION BY THE LIZARD LACERTA LEPIDA IN A MEDITERRANEAN OAK FOREST

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ABSTRACT

We studied habitat selection by Lacerta lepida in an open, degraded Mediterranean Quercus ilex-forest using two different methods. First, the frequency of lizard observations in distinct habitat types was compared with habitat availability. Although lizards were seen in a wide range of habitats, a preference for sites with a complex vertical vegetation structure was evident. We also quantified structural features of the habitat at sighting spots of adult lizards. Both univariate and multivariate analyses indicated that lizards preferred sites with a relatively high coverage of high (>2 m) vegetation, but with some low (<50 cm) vegetation, and where some rocks were present.

INTRODUCTION

Lacerta lepida, the largest European lacertid lizard (adult SVL: 140-230 mm), is distributed throughout most of Spain and Portugal, southern France and extreme north-west Italy (Bischoff et al., 1984). It is a diurnal, heliothermic, ground-dwelling lizard that forages actively on a large variety of mainly arthropod prey (Castilla et al., 1991). This lizard occurs from sea-level up to ca. 2000 m (Seva, 1982; Filella, 1983), and is found in a wide variety of both uncultivated and manmade habitats, including coastal sand-plains and dunes, arable land, olive groves, orchards, vineyards, grassland, shrubland, etc. (Arnold & Burton, 1976; Seva, 1982; Bischoff et al., 1984; Barbadillo, 1987). Due to its seemingly ubiquitous presence in different habitats, it is generally considered as not exhibiting strong habitat preferences. However, quantitative data on habitat use are very scarce. Only Busack & Visnaw (1989) provide quantitative information on the presence of L. lepida in different habitats within the province of Cádiz (southern Spain). These authors concluded that lizards inhabited different habitat types in direct proportion to their availability (but see Discussion).

We here report on a study of the habitat selection patterns of *L. lepida* in an open Mediterranean oak woodland in central Spain. Very high densities are usually attained in this macrohabitat, which is often composed of distinct habitat types. We combine two complementary approaches to the study of habitat preference. First, we examine lizard sighting frequency in the different habitat categories in relation to their availability. Second, we attempt to identify the cues that guide habitat occupation through a comparison of quantitative features of the habitat structure between sites occupied by lizards and available habitats.

MATERIALS AND METHODS

The study was conducted between March and September 1985-1986 in an area of degraded oak woodland ("encinar adehesado") near Navas del Rey (40°23'N, 4°15'W, province of Madrid, Spain). The study site consists of several well-recognisable habitats, shaped mainly through varying degrees of past and current human exploitation (sheep and cattle grazing, burning).

HABITAT CATEGORIES

Observations on habitat utilisation were made while one of us walked along a fixed 3700 m transect, which crossed all habitat categories. The route was walked 125 times between 07.00-22.00 hr (Mean European Time), covering the entire daily activity period of lizards. Upon sighting of a lizard, we recorded: date, time, size (≈ age) class [juvenile: ≤ 70 mm snout-vent length (SVL); subadult: 71-139 mm SVL; adult: SVL ≥ 140 mm], and habitat category.

We established 12 representative habitat categories: 1) Dry, homogeneous grassland; 2) low (<50 cm), mixed shrubland with young oak (Quercus ilex), dwarf-shrubs and grasses; 3) dry areas with a patchy covering of dwarf-shrubs (mainly Lavandula stoechas); 4) moist areas with abundant cover of rushes (Juncus sp.); 5) sites with a patchy covering of broom bushes (Lygos sphaerocarpa); 6) dense bushes of brambles (Rubus sp.); 7) almond (Prunus dulcis) orchard; 8) riverside areas with ashes (Fraxinus angustifolia); 9) riverside areas with willows (Salix atrocinerea); 10) isolated Juniperus oxycedrus trees with dense grassy undergrowth; 11) open, degraded oak forest (Quercus ilex) with grassy undergrowth; 12) open evergreen forest of mixed composition (Quercus ilex, oxycedrus) and with a heterogeneous undergrowth of shrubs and grasses.

We estimated the availability of the distinct habitat categories by recording their presence at 25 m intervals along the transect line. These frequency counts were converted to the expected number of lizard observations under the null-hypothesis that sighting frequency in each habitat was directly proportional to its availability.

SELECTION OF HABITAT FEATURES

We quantified structural features of the habitat at sighting spots of 66 adult lizards. Habitat availability was estimated through sampling 51 sites that were situated at 70 m intervals along the transect line.

For each habitat sample we located 5 points: the spot where the lizard was first sighted, and the endpoints of two orthogonal 6 m lines that intersected at the sighting spot. The direction of these lines was determined haphazardly by throwing a pen on the ground. Each of these points served as the centre of a circle with 1 m radius. Within each circle we estimated the following 11 variables: 1-3) percentage cover at ground level of rock/ stone, sand and litter; 4-8) percentage cover of the vegetation layers with heights <25 cm, 25-50 cm, 50-100 cm, 100-200 cm and >200cm; 9) maximum height of the vegetation; 10) distance towards the nearest rock and 11) distance towards the nearest patch of vegetation that would potentially provide shelter to predators. Three additional variables were calculated; 12) total vegetation cover: summation of the vegetation cover over the 5 layers; 13) vertical diversity: calculated over the 5 vegetation layers with the Shannon-Wiener formula; 14) horizontal diversity: calculated over the habitat variables that cover the ground (rock/stone, sand, litter, vegetation <25 cm) with the Shannon-Wiener formula.

We calculated the mean value for each variable in the 5 sampling points. This value estimates the average habitat structure within a circular area with 4 m radius, surrounding the spot where the lizard was seen. Our data hence provide a description of habitat structure for an area, rather than for a particular point, that is a portion of the lizard's home range.

We performed a principal component analysis on the correlation matrix of the habitat variables to reduce the dimensionality of the habitat space. We use F-tests, and t-tests (equal variances) or Mann-Whitney U-tests (unequal variances) to evaluate the statistical significance of differences in variances and means among lizard observation sites and availability samples, both for the original variables and the scores on the principal components.

RESULTS

HABITAT CATEGORIES

Lizard size classes did not differ in sighting frequency in the distinct habitat categories ($X^2 = 14.99$, 22 df, P > 0.80). We did not detect seasonal differences in habitat occupation ($X^2 = 29.07$, 33 df, P > 0.10), and therefore lumped all data for further analysis.

Lizards were observed in all habitats. Sighting frequency in the distinct habitat categories was not directly proportional to their availability ($X^2 = 327.97$, 11 df, P < 0.001; Fig. 1). We saw more lizards than expected in the mixed forest, in mixed shrubland, and near bramble bushes. Lizards seemed to avoid grasslands and, to a lesser extent, vegetations dominated by rushes, patches of broom bushes, and oak forests (Fig. 1).

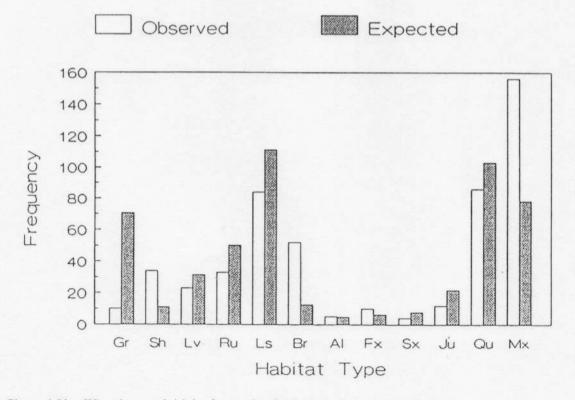


Fig. 1. Observed (N = 509) and expected sighting frequencies of *L. lepida* in distinct habitat categories.

Gr. grassland; Sh. mixed shrubland; Lv. vegetations with *Lavandula stoechas*; Ru: moist areas with rushes; Ls. sites with *Lygos sphaerocarpa*; Br. dense bushes of brambles; Al: almond orchard; Fx: riverside areas with ashes; Sx: riverside areas with willows; Ju: isolated *Juniperus oxycedrus*-trees with dense grassy undergrowth; Qu: open oak forest; Mx: mixed evergreen forest.

SELECTION OF HABITAT FEATURES

Structural features of sites occupied by adult lizards and of available microhabitats are summarised in Table 1. Note that for many variables the observation sites had a higher variance, but a similar mean value than the availability samples. This indicates that lizards were seen more often than expected at sites with low values, and at places with high scores for these habitat characteristics.

	Observed	Available	P	P
			var	means
% cover sand	21.1±15.2	27.5+15.4	NS	NS
rock	21.1 ± 16.8	15.5+12.6	**	NS
litter	8.7 ± 15.1	5.8+11.1	**	NS
% cover veg. <25cm	49.0 ± 21.3	50.9+17.2		NS
25-50cm	29.1 ± 18.1	30.8 + 13.8		NS
50-100cm	13.1 ± 11.1	11.8+8.9	*	NS
100-200cm	7.4 ± 6.6	7.1+7.9	NS	NS
>200cm	16.2 ± 21.6	8.5±9.7	***	NS
tot. veg. cover	114.9 + 43.4	109.2+39.4	NS	NS
max. veg. height (cm)	246.2±171.5	158.3 ± 90.0	***	**
distance veg. (cm)	146.1 ± 94.8	249.0±172.4	***	***
distance rock (cm)	238.3±250.4	329.2+241.9	NS	*
vertical div.	0.84 ± 0.22	0.79 ± 0.21	NS	NS
horizontal div.	0.59 <u>+</u> 0.18	0.61 ± 0.14	*	NS
PC1	-0.09+2.44	0.12+1.75	**	NS
PC2	0.48 + 1.93	-0.63 + 1.64	NS	**
PC3	0.19 + 1.27	-0.25 ± 1.19	NS	=0.06

TABLE 1. Summary (mean \pm 1 SD) of structural habitat features at lizard observation sites and availability samples, and probability of differences between their variances (*F*-test) and means (*t*-test or Mann-Whitney *U*-test). N = 66 for lizard observation sites; N = 51 for availability samples. *: P < 0.05; **: P < 0.01; ***: P > 0.001; NS: P > 0.05.

A principal component analysis was used to obtain a more integrated picture of the habitat attributes. The first three principal components accounted respectively for 31, 24 and 10% of the total variance of the raw data. The first principal component (PC1) was strongly positively correlated with percent cover of the vegetation layers <25 cm, 25-50 cm and 50-100 cm, total vegetation cover, vertical diversity, and distance to the nearest rock.

	PC1	PC2	PC3	
% cover sand	-0.052	-0.667	-0.314	
rock	-0.566	0.303	0.605	
litter	-0.514	0.627	-0.333	
% cover veg. <25cm	0.845	-0.135	0.013	
25-50cm	0.896	0.105	0.013	
50-100cm	0.785	0.323	0.100	
100-200cm	0.332	0.489	-0.084	
>200cm	-0.357	0.795	-0.250	
tot. veg. cover	0.844	0.480	-0.085	
max. veg. height (cm)	-0.331	0.821	-0.280	
distance veg. (cm)	-0.185	-0.489	-0.481	
distance rock (cm)	0.507	-0.403	-0.438	
vertical div.	0.599	0.550	-0.185	
horizontal div.	-0.465	0.001	-0.412	

TABLE 2. Correlations between habitat characteristics and the first three principal components. Only correlation coefficients significant at $\alpha = 0.001$ and higher than 0.50 were considered in the interpretation of the principal axes, and are shown in boldface.

It was negatively correlated with percent cover by stones/rocks and by litter at ground level (Table 2). This represents a gradient from habitats with extensive cover by stones/rocks and litter, and sparse vegetation near the ground towards sites with abundant vegetation at <100 cm above ground level. The second principal axis was positively correlated with percent cover by vegetation >200 cm high, maximum vegetation height, vertical diversity and percent cover of litter, and exhibited a strong negative correlation with percent cover by sand at ground level. Thus, PC2 describes a gradient from open, sandy sites to locations with upright bushes or trees. The third principal component showed a strong positive correlation with percent cover by rocks (Table 2).

We examined habitat occupation by considering the projections (= scores) of the different samples on the component axes. The range of the scores for lizard sighting spots was similar to that of the available sites on the three first principal components. Comparison of the distribution of scores on PC1 reveals a higher variance, but a similar average, for lizard sighting spots than for available sites (Table 1). This indicates that more lizards than expected were seen at both extremes of the gradient represented by PC1, i.e. at sites with few low vegetation and many rocks on the one hand, and at places with much low vegetation on the other hand. Scores on PC2 were significantly higher for observation sites (Table 1), indicating that lizards preferred habitats with upright trees or bushes, and that they avoided open, sandy areas. Lizard sighting spots had a marginally non-significant higher average score on PC3, suggesting a tendency for lizards to select sites with much cover by rocks at ground level.

DISCUSSION

Our data, collected within a restricted area of degraded Mediterranean woodland, indicate that L. lepida used the entire range of available habitats. Nevertheless, lizards exhibited a preference for certain habitat types. They were observed more often than expected in the mixed forest, in mixed shrubland and near bramble bushes, and they avoided grasslands. Busack & Visnaw (1989) reported data on habitat use collected in a large geographical area (province of Cádiz, Spain), and distinguished between several broad habitat categories, based on their type of land use. L. lepida was found in most of these biotopes and it was concluded that it did not exhibit any habitat preference (Busack & Visnaw, 1989). Reanalysis of their data, using appropriate frequency-dependent statistical procedure, indicates that lizards do not inhabit the different habitat types proportionally to their abundance $(X^2 = 76.32, 12 df, P < 0.001)$. More lizards than expected were seen in sclerophyllous shrub and grassland, whereas sighting frequency was lower than expected in agriculturally unproductive areas [see Table 4 in Busack & Visnaw (1989)]. Hence, although L. lepida should be considered as a habitat generalist, its preference for certain biotopes is evident both on a local and a regional scale.

Our study of the quantitative features of habitat structure indicates that lizards were seen throughout the range of available sites. This again shows that lizards occupied all structural habitats that were available in the study area. However, sighting frequency was higher than expected at sites with upright (>2 m) trees and bushes, at places with many stones or rocks and at habitats with much low (<1 m) vegetation. Lizards tended to avoid open, sandy areas with little vegetation. These results point to a preference for sites with a rather complex habitat structure, although lizards are definitely not restricted to such places.

Several factors might invoke a preference for habitats with a high structural diversity. The presence of trees or bushes creates a sun-shade gradient. This should facilitate the shuttling between sunlit and shaded sites, a conspicuous aspect of the thermoregulatory behaviour of Lacertid lizards (Avery, 1976; Arnold, 1987; Van Damme et al., 1987). Rocks and/or stones might also serve a thermoregulatory function. On repeated occasions we observed lizards basking on rocks or stones near abundant low vegetation. The variable orientation of stony surfaces should facilitate postural adjustments that increase net radiation intake, and a close contact with their sun-warmed substrates enhances heat gain through conduction. At the same time, rockcrevices and holes between piled stones provide shelter to predators. In addition, it might be hypothesised that the number of invertebrate prey might be highest in structurally complex habitats (Strijbosch, 1988).

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The broad range of habitat types occupied by L. lepida might, at least partly, reflect the large size of their home range and their high mobility. Average home range size for adult males and adult females in our study population was 1324 and 1699 m2, respectively (Castilla, 1989). Corresponding estimates for home range size, obtained by the equations in Christian & Waldschmidt (1984) are 3200 m2 for a 200 g male, and 2000 m2 for a 160 g female. It is not unlikely that some areas within the home range are used more extensively that others (Stamps, 1977; Christian et al., 1986). Our samples might therefore include observations of lizards that were moving through "suboptimal" habitats that separate distinct core areas within the home range. An additional possibility is that lizards use distinct types of habitat for different activities. Such changes in habitat use might be the result of diel or spatial variation in the constraints imposed by the thermal environment (e.g. Huey & Pianka, 1977; Grant & Dunham, 1988), and/or by variation in food availability.

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