Journal of Herpetology, Vol. 32, No. 1, pp. 51-50, 1998

Habitat Relationships of Amphibians and Reptiles in California Oak Woodlands

WILLIAM M. BLOCK[1] AND MICHAEL L. MORRISON[2,3]

[1]*USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 2500 S. Pine Knoll Dr., Flagstaff; Arizona 86001, USA*
[2]*Wildlife and Fisheries Resources, School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721, USA*

ABSTRACT.—We, used pitfall traps and time-constrained searches to sample amphibians and reptiles and to describe their habitats in oak woodlands at three areas in California. We captured 766 individuals representing 15 species during pitfall trapping and 333 animals representing 15 species during the time-constrained searches. A total of 19 species were sampled. Across all study areas, several positive relationships were found between animal abundance and the cover of specific tree species. At Tejon Ranch, two salamanders—*Batrachoseps* nigriventris and Ensatina eschscholtzii croceater—were associated with canyon live oak (Quercus *chrysolepis*) and two lizards—Sceloporus *occidentalis* and *Eumeces* gilberti—were associated with California black oak (*Q. kelloggii*). At San Joaquin, *B.* nigriventris was associated with foothill pine (*Pinus* sabiniana), as was B. attenuatus at Sierra Foothill. Generally, salamanders were found in live oak woodlands on north-facing slopes at Tejon Ranch, or on north-facing woodlands dominated by foothill pine and interior live oak (*Q. wislizenii*) at Sierra Foothill and San Joaquin. In contrast, lizards used more xeric and open habitats dominated by California black oak, blue oak (*Q. douglasii*), and valley oak (*Q. lobata*). As would be expected for terrestrial and fossorial animals, litter depth, the development of grasses and forbs, and cover by downed woody debris and rocks were important in the habitat models. At Sierra Foothill and San Joaquin, these latter variables, in addition to slope, were of primary importance in the habitat models.

Oak woodlands encompass over 2.5 million ha in California. These woodlands range from open savanna to dense montane forests and include 18 species of oaks and numerous hybrids (Allen, 1990). Historically, oak woodlands have been used as rangelands and for firewood production. Although extensive research has been conducted on various species of amphibians and reptiles (Marcellini and Mackey, 1970; Rose, 1970; Davis and Verbeek, 1972), few papers address habitat relationships in oak woodlands. Less is known of the effects of habitat-altering land use, particularly cattle grazing and firewood harvest, on reptiles and amphibians in oak woodlands.

Vertebrates select habitats at several spatial and temporal scales (Johnson, 1980; Morrison et al., 1992; Block and Brennan, 1993). Johnson (1980) established a framework that considered four spatial levels of habitat selection increasing in specificity from the geographic range of the species to substrates or resources used for specific needs. Understanding patterns of habitat selection at different scales is paramount to providing appropriate management for the conservation of the species. For example, it may be insufficient simply to maintain an oak woodland for a species if required fine-grained habitat components—plant species composition, dead woody material, vertical structure—are not provided within the woodland.

In this paper, we describe distributions and habitats of herpetofauna in three California oak woodlands based on pitfall trapping and time-constrained searches. We examine habitat use at two scales: general macrohabitat associations and microhabitat patterns. We define macrohabitat as stand-level features that are correlated to the distribution and abundance of a species or group of species (Block and Brennan, 1993). Microhabitat refers to within-stand correlates of a species' distribution and abundance (Block and Brennan, 1993). We also present microhabitat models based on logistic regression to provide multivariate descriptions of the habitats of the more common species.

MATERIALS AND METHODS

Study Areas—The study areas were: (1) San Joaquin Experimental Range, Madera County; (2) Sierra Foothill Range Field Station, Yuba County; and (3) Tejon Ranch, Kern County. Both San Joaquin and Sierra Foothill are in the foothills of the Sierra Nevada, with Sierra Foothill lying northeast of Marysville and San Joaquin north of Fresno. Tejon Ranch is located in the Tehachapi Mountains east of the town of Lebec. San Joaquin is characterized by a relatively flat

[3] Present Address: Department of Biological Sciences, California State University, Sacramento, California 95819, USA.

terrain with rolling hills on a general southwest facing slope; elevation ranges from 200 to 500 m. The overstory is dominated by blue oak (*Quercus* douglasii), interior live oak (Q. *wislizenii*), and foothill pine (*Pinus* sabiniana), with buckbrush (Ceanothus cuneatus), chaparral whitethorn (C. leucodermis), redberry (*Rhamnus* crocea), coffeeberry (R. californicus), and poison oak (*Toxicodendron* diversiloba) comprising the woody understory. Annual grasses and forbs dominate the herbaceous layer. Topography is steeper at Sierra Foothill with moderate slopes facing in a general westerly direction; elevation ranges from 200 to 700 m. Dominant overstory trees include blue oak, interior live oak, foothill pine, California black oak (Q. *kelloggii*), valley oak (Q. lobata), and ponderosa pine (P. ponderosa). Major shrubs are buckbrush, coffeeberry, toyon (*Heteromeles* arbutifolia), and poison oak; annual and perennial grasses and forbs comprise the herbaceous layer. Terrain at Tejon Ranch is more mountainous than at Sierra Foothill or San Joaquin, consisting of steep slopes facing in all directions. Elevation of Tejon Ranch ranges from 1100 to 1700 m. This topography contributes to a more diverse flora in which blue oak, interior live oak, canyon live oak (Q. chrysolepis), California black oak, valley oak, and Brewer's oak (Q. garryana var. *breweri*) dominate the overstory. The woody understory consists of buckbrush, redberry, chamise (Adenostoma *fasciculatum*), bigberry manzanita (*Arctostaphylos glauca*), and mountain mahogany (Cercocarpus betuloides). Annual and perennial grasses and forbs comprise the herbaceous understory.

Sampling intensity for amphibians and reptiles was greater at Tejon Ranch than at San Joaquin or Sierra Foothill. Because San Joaquin and Sierra Foothill were relatively small in total area (1800–2200 ha), we were limited in the placement of spatially-independent sampling grids and surveys. Sampling units (i.e., pitfall grids or time-constrained sampling areas) were separated by at least 800 m. This distance minimized the probability of individuals occurring within two sampling units. In contrast, oak woodlands covered about 40,000 ha at Tejon Ranch; consequently, we had a greater area to place grids and conduct surveys. Moreover, stands of major oak species at Tejon Ranch were often monotypic, providing an opportunity to test for differences among these distinct stand types.

Pitfall Sampling and Data Analysis.—Pitfall trapping (Corn, 1994) was used to capture active amphibians and reptiles and to describe general habitat associations and microhabitats. Pitfall traps consisted of 3.8-1 buckets that were sunk to ground level and covered with a square piece of plywood elevated 5–10 cm above the lip of the bucket (Block et al., 1988, provide a more detailed discussion of the methods). Traps were arrayed in 6 $\times$ 6 grids with 20-meter spacing between buckets. We placed 13 grids at Tejon Ranch (N = 452 traps), and four each at Sierra Foothill (N = 144) and San Joaquin (N = 144) for a total of 740 traps (16 traps destroyed by cattle at Tejon Ranch were omitted from analyses). Traps were monitored at Tejon Ranch from 4 January to 20 May 1987, 10 December 1987 to 20 June 1988, and 10 November 1988 to 30 April 1989; traps were monitored at Sierra Foothill and San Joaquin from 10 January to 17 March 1988, and from 10 November 1988 to 15 January 1989. All traps in a grid were open simultaneously; 4-5 grids were sampled at the same time at Tejon Ranch, whereas 2 4 grids were sampled during the same dates at Sierra Foothill and San Joaquin. Traps were left open for 30 to 65 consecutive days; all traps were monitored during each of the trapping periods listed above. The total trapping effort encompassed 98,592 trap days, which included 65,850, 17,280, and 15,462 trap days at Tejon Ranch, San Joaquin, and Sierra Foothill, respectively. Traps were checked every 2 4 d for captured animals. Captures were identified and removed from the trapping grid.

Habitat characteristics were measured within a 5 m radius circular plot centered on each trapping station. We estimated cover by woody vegetation using the point intercept method (Heady et al., 1959). We placed a 10 meter long intercept, centered on the trap, along a random bearing with 1-meter spacings between points. Cover by woody vegetation was recorded by species at four height strata: <1 m, 1–2 m, >2–5 m, and >5 m. Ground cover by grasses, forbs, rocks, lichens, dead woody debris of three diameter classes (<1 cm, 1–10 cm, and >10 cm), leaf litter, moss, and exposed soil was estimated as the percent of the 10 points intercepted. Shrub height was measured with a meter stick and tree height with a clinometer. Average shrub height and average tree height were calculated by averaging the heights of up to five randomly sampled shrubs and trees, if that many occurred in the plot. Average litter depth and herbaceous plant (herbaceous defined as grass or forb) height were calculated by averaging five measurements taken every 2 m along the intercept. Slope was measured in degrees with a clinometer, and aspect in degrees with a compass. Used habitat for a species consisted of the set of plots where the species was captured at least once. We defined all other plots to be unused habitat, although we acknowledge that these areas could have been used. Defining plots as used or unused was necessary to meet statistical requirements for application of logistic regression. Using traps as indications of habitat use or nonuse requires the assumption that the species will enter the trap. Thus, data such as ours are likely biased to some unknown degree by trapability of the different species.

We calculated product-moment correlations (Sokal and Rohlf, 1969) to measure associations of species of amphibians and reptiles with tree species. Similar analyses were done to evaluate relationships of amphibians and reptiles as taxonomic classes with cover by tree species. For common amphibian or reptile species (i.e., those captured at >30 trapping stations), one-way analysis of variance (ANOVA) was used to compare variables between used and unused trap stations within study areas, and one-way ANOVA was also used to compare habitat variables between or among study areas (Sokal and Rohlf, 1969:204–252).

We used stepwise logistic regression on common species to develop multivariate models contrasting used and unused plots within study areas (Hosmer and Lemeshew, 1989). These models can be used to predict habitat in lieu of sampling animals directly. Variables were entered into the model based on the significance of the Wald statistic. Some variables that were significantly different by ANOVA were not included in the model if they did not contribute significantly to the model. Multivariate analyses were restricted to species with >30 capture stations to ensure an adequate sample-t;-variable ratio for analysis (Williams et al., 1990). Prior to these multivariate analyses, we reduced the number of habitat variables by using only variables that had significant ($P < 0.05$) differences by ANOVA and retaining only one of any pair of variables with a product-moment correlation of $r > 0.5$ (Morrison et al., 1987, 1992). Square-root and log transformations (Sokal and Rohlf, 1969) were used on variables with highly skewed distributions to strive for more normal distributions.

Time-constrained Sampling.—Time-constrained searches (Scott, 1994) were conducted during spring and fall, 1986–1988, to locate amphibians and reptiles. We conducted 28 searches at Tejon Ranch, nine at Sierra Foothill, and seven at San Joaquin. We pooled results within each study area for a general description of the herpetofauna present. The time-constrained method consisted of searching on all possible substrates, and in and under possible cover items where an animal might be found. The amount of time devoted to searching was constrained to four person-hours. Because of biases inherent to time-constrained sampling related to observer variation, environmental heterogeneity, and temporal variation in habitat use (Scott, 1994; Crump and Scott, 1994), we present only descriptive information on species' capture numbers.

Results

Macrohabitat Patterns.—We captured 766 individuals representing 15 species during pitfall trapping, including three salamander, one newt, one frog, two toad, seven lizard, and one snake species (Table 1). Because snakes, frogs, toads, and some lizards (e.g., Anniella, Uta) were not adequately sampled by pitfall traps, we included them only in analyses of taxonomic groups.

Western fence lizards (Sceloporus occidentalis) and Gilbert's skinks (Eumeces *gilberti*) were the most frequently captured animals accounting for about 67% of all captures. Amphibians were most closely associated with canyon live oak ($r = 0.67$, $P < 0.01$), which occurred only at Tejon Ranch. Black-bellied slender salamanders (*Batrachoseps* nigriventris) ($r = 0.66$, $P < 0.01$) and yellow-blotched ensatinas (Ensatina eschscholtzii *croceater*) ($r = 0.69$, $P < 0.01$) were both positively associated with cover by canyon live oak. At San Joaquin and Sierra Foothill, slender salamanders were positively associated ($r = 0.72$, $P < 0.01$) with foothill pine cover. We found no significant associations of reptiles as a group with stand type or species of tree. Western fence lizards ($r = 0.69$) and western skinks (*E.* skiltonianus) ($r = 0.59$), however, showed positive associations ($P < 0.01$) with cover by California black oak. No other species analyzed was significantly positively or negatively correlated with specific tree species.

General Microhabitat Patterns.—At Tejon Ranch, vegetation cover at all heights except between 2–5 m was greater at the habitats of the salamanders than the lizards (Fig. 1). At San Joaquin, habitats of two species captured with adequate samples (Eumeces, Sceloporus) did not differ significantly ($P < 0.05$) in any structural habitat feature. Within Sierra Foothill, Eumeces, Sceloporus, and Elgaria overlapped extensively in habitat characteristics. The only significant differences found was that Eumeces used areas of greater slope ($F = 5.88$, $df = 2, 42$, $P = 0.006$); more small (<1 cm diameter) woody debris was found in Sceloporus habitat ($F = 3.59$, $df = 2, 42$, $P = 0.036$); and more large (>10 cm diameter) woody debris ($F = 5.18$, $df = 2, 42$, $P = 0.0098$) was found in Elgaria habitat than in the habitats of the other species.

Species Microhabitat Patterns.—We captured Ensatina eschscholtzii croceater only at Tejon Ranch, where it occurred in 13% of the 452 pitfall traps. Within pitfall grids, 11 of 23 habitat variables differed ($P < 0.05$) between used and unused habitat (Table 2). Used plots had greater slope, taller herbs, less grass and forb cover, greater rock cover, taller trees, greater litter depth, greater canyon live oak cover, and less blue oak cover than unused plots. In addition,

TABLE 1. Relative abundances of amphibians and reptiles captured in pitfall traps and during time-constrained searches at three California oak woodlands—Tejon Ranch, San Joaquin Experimental Range, and Sierra Foothill Range Field Station—from 1987 through 1990. Pitfall abundances are reported as the number of captures per 1000 trap days. Search abundances are reported as the number of captures per search hour.

	Pitfall			Search		
Species	Tejon Ranch	San Joaquin	Sierra Foothill	Tejon Ranch	San Joaquin	Sierra Foothill
Trap days/Search hours	65,850	17,280	15,462	112	28	36
Amphibians						
Taricha torosa		0.06				
Ensatina eschscholtzii	1.59			0.68		
Batrachoseps nigriventris	0.61	0.75		0.23	0.11	
Batrachoseps attenuatus			0.13			0.33
Scaphiopus hammondii		0.17				
Bufo boreas	0.02	0.06				
Hyla regilla	0.03					0.08
Reptiles						
Uta stansburiana		0.06			0.04	
Sceloporus occidentalis	2.66	2.66	7.89	0.44	1.07	1.36
Eumeces gilberti	1.78	3.24		0.22	0.57	
Eumeces skiltonianus			1.16			0.19
Elgaria multicarinatus	0.08		0.65	0.04		0.61
Anniella pulchra	0.02			0.03		
Cnemidophorus tigris		2.66				
Coluber constrictor						0.03
Masticophis lateralis						0.03
Diadophis punctatus	0.02					0.03
Pituophis melanoleucus				0.01	0.04	
Crotalus viridis						0.03

cover values for all three size classes of downed woody cover were greater in used habitat, although differences were not significant within any category. Overall classification success from the logistic regression was 72.3% of all trapping stations (Table 3). Cover by canyon live oak was positively related with capture sites, whereas cover by blue oak was negatively related.

We captured *Eumeces gilberti* in 15% of the pitfall traps at Tejon Ranch. Habitat characteristics from pitfall sampling were significantly different ($P < 0.05$) for 11 of the 23 variables exam-

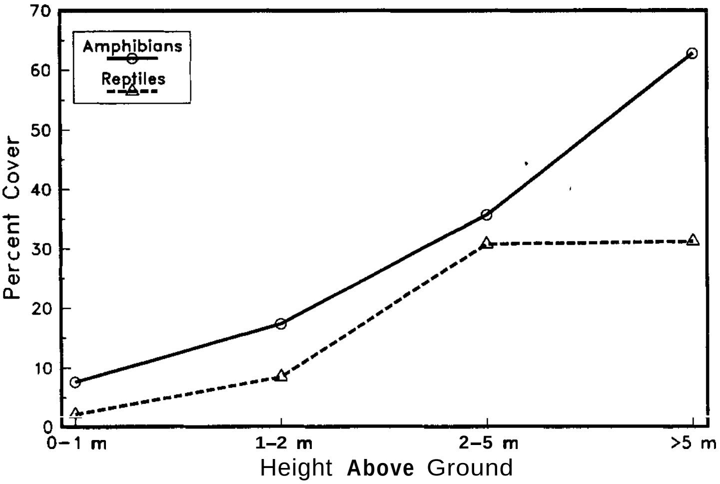

FIG. 1. Comparison of vegetation structure between reptiles and amphibians from Tejon Ranch, Kern County, California, 1986–1988.

TABLE 2. Habitat characteristics for selected amphibians and reptiles captured in pitfall traps at Tejon Ranch (452 traps), San Joaquin Experimental Range (144 traps), and Sierra Foothill Range Field Station (144 traps). Only species captured in >30 pitfall traps are reported. Values are for trap stations where the species was captured at least once; N is the number of traps where at least one individual was captured; numbers presented are means (SE); >, the variable was significantly greater ($P < 0.05$) at used plots than unused plots; < variable was significantly less ($P < 0.05$) at used than at unused plots; *, the variable was significantly different ($P < 0.05$) between/among study areas.

	Ensatina eschscholtzii	*Eumeces gilberti*		*Sceloporus occidentalis*		
Variable	Tejon Ranch ($N = 60$)	Tejon Ranch ($N = 69$)	San Joaquin ($N = 33$)	Tejon Ranch ($N = 87$)	San Joaquin ($N = 34$)	Sierra Foothill ($N = 37$)
Slope (degrees)	55.2 (2.5)>	32.0 (2.3)<	10.6 (1.0) *	30.0 (1.6)<	11.6 (1.1)	16.1 (1.2) *
Grass cover (%)	20.5 (4.1)<	56.8 (3.2)>	69.7 (3.9) *	41.5 (3.8)>	72.3 (3.5)	65.9 (3.1) *
Forb cover (%)	11.2 (2.1)<	19.6 (2.8)	32.1 (3.7)	15.7 (2.5)	29.7 (3.4)	37.8 (3.7) *
Exposed soil (%)	24.5 (2.5)	20.0 (2.6)<	15.5 (2.6)<	25.4 (2.5)	24.1 (4.2)	35.7 (5.0)>
Rock cover (%)	6.0 (1.5)>	2.3 (0.7)	11.8 (2.0)>*	2.4 (0.1)	10.5 (2.3)>	4.9 (1.1)
Small (0–1 cm) woody cover (%)	10.3 (1.7)	3.6 (0.9)<	0 *	5.3 (1.1)	0	10.5 (2.2)
Medium (1–10 cm) woody cover (%)	5.2 (1.0)	2.8 (0.6)	0 *	4.0 (0.8)	1.8 (1.0)	3.8 (0.1)
Large (>10 cm) woody cover (%)	3.8 (1.3)	2.0 (0.9)	0 *	2.8 (0.8)	0	1.6 (1.1)
Shrub height (m)	1.5 (0.2)	1.9 (0.3)	2.3 (0.2)	1.7 (0.2)	1.9 (0.2)	3.1 (0.3)
Tree height (m)	12.4 (0.9)>	9.3 (0.9)	8.9 (0.5)	8.9 (0.4)	8.0 (0.4)	0.3 (0.5)
Shrub species richness	2.6 (0.4)	0.7 (0.2)<	1.1 (0.3)	1.4 (0.3)	0.7 (0.2)	1.8 (0.3)
Tree species richness	1.9 (0.2)	1.5 (0.2)	0.5 (0.1) *	2.0 (0.2)	0.4 (0.1)	2.0 (0.3) *
Herbaceous height (cm)	19.9 (1.6)>	21.3 (1.3)>	8.9 (0.5)>	19.0 (1.1)>	8.1 (0.5)	25.4 (2.0)
Litter cover (%)	65.0 (3.3)	71.4 (3.0)	69.4 (3.5)	66.2 (2.7)	63.8 (4.4)	55.9 (4.9)<
Litter depth (mm)	20.6 (2.2)>	12.8 (1.3)	15.5 (2.0)	15.0 (1.4)	15.6 (2.7)	11.3 (1.3)
Vegetation cover (%)						
0–1 m (above ground)	8.2 (1.8)	1.6 (1.1)	1.8 (0.9)	2.2 (1.1)	0.6 (0.4)	1.1 (0.1)
1–2 m	17.2 (2.9)	7.1 (1.4)	5.5 (0.2)	7.8 (1.5)<	2.1 (1.2)<	6.2 (0.2)
2–5 m	35.3 (4.1)	25.5 (3.5)	6.1 (0.3) *	33.4 (3.3)	4.7 (2.1)<	32.2 (5.3) *
>5 m	59.7 (5.4)>	21.9 (3.7)<	14.2 (0.4)	37.8 (4.2)	12.1 (4.3)	42.2 (5.9) *
Blue oak cover (%)						
2–5 m	0<	15.2 (3.0)>	1.5 (1.2)	13.7 (2.5)>	2.6 (0.2)	18.9 (4.0)
>5 m	0<	11.9 (3.0)>	2.7 (1.5)	13.9 (3.1)>	5.6 (3.1)	28.4 (4.6)
Interior live oak cover (%)						
2–5 m			4.5 (0.3)		1.5 (1.0)<	11.9 (4.0)
>5 m			5.8 (0.4)		2.1 (1.6)	10.3 (4.0)
Canyon live oak cover (%)						
2–5 m	26.2 (3.9)	0.3 (0.3)<		5.4 (1.9)<		
>5 m	51.8 (5.6)>	0.7 (0.5)<		7.5 (2.6)<		

TABLE 3. Logistic regression models for common amphibians and reptiles found in three California oak woodlands—Sierra Foothill Range Field Station (SF), San Joaquin Experimental Range (SJ), and Tejon Ranch (TR)—1986–1988. The order that variables appear in the model reflects the order that they were entered into the model during the stepwise procedure. The logistic model takes the general form $P\{1|x\} = e^z/(1 + e^z)$, where $z = B_0 + \Sigma B_iX_i$. Goodness-of-fit value measures the probability of the data fitting the logistic model; $P > 0.05$ indicates that the data fit the model.

Species Area	$B_0 + \Sigma B_iX_i$	Goodness of fit	% correct
Ensatina eschscholtzii			
TR	−1.4 + 0.02*(slope) + 0.1*(canyon live oak cover) −3.3*(blue oak cover)	0.68	72.3
Eumeces gilberti			
TR	−1.5 − 0.5*(# shrubs spp.)**1/2 +0.6*(grass height)**1/2 −1.3* (canyon live oak cover)**1/2	0.66	70.9
SJ	1.2 − 1.0*(% exposed soil)**1/2	0.40	66.7
Sceloporus occidentalis			
TR	−0.1 − 0.4*(slope) + 0.4*(grass height)**1/2 +0.3*(blue oak cover)	0.04	73.3
SJ	−0.1 + 1.2*(rock cover)**1/2 − 1.1*(interior live oak cover)**1/2	0.42	64.7
SF	−0.6 + 1.1*(moss cover)**1/2 + 0.8*(log cover)**1/2	0.48	68.9

ined. In general, trap locations where *Eumeces* was captured had greater grass and blue oak cover, taller herbaceous vegetation, less small (<1 cm) woody cover, less exposed soil, and less canyon live oak cover than trap sites where *Eumeces* was not captured (Table 2). Classification success from the logistic regression was 70.9% of all stations (Table 3). Cover by canyon live oak was the first variable that entered the model and was negatively associated with the presence of *Eumeces,* followed by height of herbaceous vegetation (positive association) and shrub species richness (negative association).

We captured *Eumeces gilberti* in 23% of the 144 pitfall traps at San Joaquin. Height of herbaceous vegetation and rock cover were greater but with less exposed soil at traps where *Eumeces* was captured compared to those where it was not captured (Table 2). Overall classification success from logistic regression was 66.7% (Table 3). Only exposed soil entered in the model, and it was negatively associated with stations where *Eumeces* was captured.

Eumeces at Tejon Ranch was found on steeper slopes with greater tree species richness and dead and downed woody debris than stations where *Eumeces* was captured at San Joaquin. Capture sites at San Joaquin were rockier and with greater grass and forb cover than at Tejon Ranch. Foliage profiles were similar between the two areas, although greater mid-story cover, 2–5 m above ground, existed at Tejon Ranch than at San Joaquin (Fig. 2).

Sceloporus occidentalis was captured in 19% of the traps at Tejon Ranch. In general, there was greater cover by blue oak, less cover by canyon live oak, less cover between 1–2 m above the ground, greater grass cover, taller herbaceous vegetation, and less slope at trap stations where it was captured than where it was not captured (Table 2). Logistic regression correctly classified 73.3% of all plots (Table 3). Three variables were included in the logistic function: slope (negative association), blue oak cover (positive association), and herbaceous vegetation height (positive association).

At San Joaquin, *Sceloporus* was captured in 24% of the traps. Rock cover was greater and woody vegetation cover at two height intervals—1–2 m and 2–5 m—including interior live oak cover 2–5 m above the ground was less at traps where it was captured than traps where it was not (Table 2). Logistic regression correctly classified 64.7% of all stations (Table 3). Two variables—rock cover (positive association) and cover by interior live oak (negative association)—were included in the model.

At Sierra Foothill, *Scelopmus* was captured at 26% of all traps stations. These stations had greater exposed soil and less litter cover than traps where *Sceloporus* was not captured (Table 2). Logistic regression correctly classified 68.9%

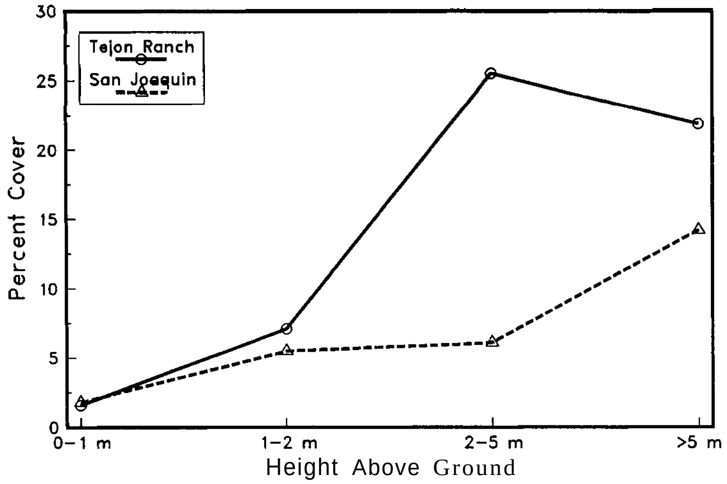

FIG. 2. Comparison of vegetation structure for *Eumeces gilberti* between Tejon Ranch, Kern County, California and San Joaquin Experimental Range, Madera County, California, 1986–1988.

of all plots (Table 3). Two variables were included in the logistic model: log cover (positive association) and moss cover (positive association).

Habitats of Sceloporus captured in Tejon Ranch pitfalls differed from San Joaquin and Sierra Foothill by occurring on steeper slopes and having less grass and forb cover. Habitat at Tejon Ranch and Sierra Foothill differed from San Joaquin by having greater canopy cover above 2 m (Fig. 3) and greater tree species richness.

Time-constrained Sampling.—A total of 333 animals representing 15 species was found during the time-constrained searches. These included three salamander, one frog, six lizard, and five snake species (Table 1). Two salamanders, *Batrachoseps nigriventris* and *Ensatina eschscholtzii croceater,* were captured at Tejon Ranch, and one at both San Joaquin (B. nigriventris) and Sierra Foothill (B. attenuatus). The most commonly captured lizard at all study areas was Sceloporus *occidentalis,* followed by Eumeces gilberti at Tejon Ranch and San Joaquin, and Elgaria *multicarinatus* at Sierra Foothill.

At Tejon Ranch, Batrachoseps nigriventris comprised about 14% of all animals captured during time-constrained searches (Table 1). Nearly 85% of all Batrachoseps were found under logs or downed branches. The remaining animals were located under leaf litter. Ensatina eschscholtzii comprised about 39% of the animals captured

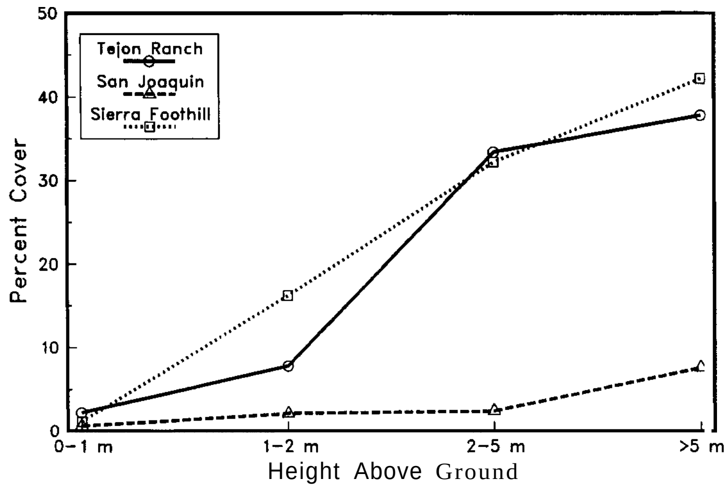

FIG. 3. Comparison of vegetation structure for *Sceloporus occidentalis* between Tejon Ranch, Kern County, California, San Joaquin Experimental Range, Madera County, California, and Sierra Foothill Range Field Station, Yuba County, California, 1986–1988.

at Tejon Ranch. Greater than 95% of them were found under downed logs or branches from canyon live, California black, and valley oaks. *Eumeces* gilberti comprised 14% of all captures and were located under logs or branches. About 26% of the animals captured at Tejon Ranch were Sceloporus occidentalis; all were found on or under logs or downed branches. Elgaria *multicarinatus* comprised about *6%* of the captures. All Elgaria but one were captured on or under logs or downed branches; the exception was an animal captured under a rock.

At Sierra Foothill, *Batrachoseps* attenuatus comprised about 12% of all animals captured during time-constrained searches (Table 1). *Batrachoseps* were captured under logs and downed branches (58%) and rocks (42%), and typically in association with interior live oak. Roughly 48% of the time-constrained captures at Sierra Foothill were Sceloporus occidentalis. Most *Sceloporus* were found under logs and downed branches (53%), on standing live or dead trees (21%), or rocks (17%). Elgaria *multicarinatus* comprised about 23% of all time-constrained search captures. About 45% of these animals were found on or under logs or downed branches, 45% on the ground or in leaf litter, and 10% on or under rocks.

At San Joaquin, Eumeces gilberti comprised 36% of the species captured during time-constrained searches (Table 1). About 77% of all captures were on or under rocks; the other 23% were under blue oak logs and downed branches. Sceloporus occidentalis comprised 51% of all animals captured during time-constrained searches. Most (67%) were found on or under rocks; the remaining animals were associated with a variety of cover or substrate items including downed wood (20%), live and dead trees (7%), and exposed soil (7%).

Discussion

Sampling Methods.—Researchers in the Pacific Northwest (Raphael, 1988; Aubry and Hall, 1991; Corn and Bury, 1991) have used both pitfall traps and active search methods to sample amphibians and reptiles. Presumably, using different methods allows one to sample more species within the herpetofaunal community (Greenberget al., 1994; Heyer et al., 1994). Thus, we expected to see differences in the species observed with the two methods, as well as differences in capture frequencies. For example, we captured one snake in pitfall traps (a ringneck snake), whereas five snake species were captured during time-constrained searches (Table 1). Also, rankings of species by relative abundance differed between the methods. At Tejon Ranch, for example, *Sceloporus* was the most frequently captured animal by pitfall traps, whereas Ensatina was most frequently captured by time-constrained sampling. Adding other methods (e.g., nocturnal spotlighting, cover boards) would have likely expanded our species list and provided additional information, but were not logistically feasible.

Macrohabitat Associations.—Across all study areas, several positive relationships were found between animal abundance and habitat types dominated by specific tree species. Generally, salamanders were found in canyon live oak woodlands on north-facing slopes at Tejon Ranch, or on north-facing woodlands dominated by foothill pine and interior live oak at Sierra Foothill and San Joaquin. In contrast, lizards used more xeric and open habitats dominated by blue oak, California black oak, and valley oak. Note that many of the species we analyzed, however, showed no significant relationship with tree species relationships, indicating that they occurred across a variety of types or that samples were too small to detect differences.

Regardless, such broad distributional relationships provide an overview of habitat relationships of animals at the scale of the vegetation type. However, these broad relationships have limited predictive value as to whether or not a particular species will be present. Actual habitat use may be influenced by the degree of habitat specificity by the organism (i.e., specialist versus generalist; Pianka, 1978), the spatial scale at which the organism selects its habitat (Wiens, 1989), its morphology and physiology, and numerous other biotic and abiotic factors (Toft, 1985). Thus, more specific distribution and habitat correlates for many species may then be determined by finer-scale analysis done at the capture location, as presented below.

Microhabitat Associations.—Microhabitat use varied little among study areas for species occurring at more than one. Most microhabitat differences could be attributed to physiognomic differences between the study areas. Similarity of microhabitat use between areas suggests a certain consistency in habitat selection, provided those conditions existed within the study area.

There were significant relationships between the occurrence of an amphibian or reptile species and percent cover by a species of oak. This was especially evident at the Tejon Ranch where Ensatina was positively associated with canyon live oak, but negatively associated with blue oak. *Eumeces* gilberti showed the opposite relationship (positive with blue oak, negative with canyon live oak). Thus, at the Tejon Ranch, habitat relationships were often correlated with the presence of canyon live oak and blue oak.

Corn and Bury (1991), Aubry and Hall (1991), and Welsh and Lind (1991) investigated habitat associations of amphibians and reptiles in

Douglas-fir forests of the northwest. Although the structure and composition of these forests differed substantially from Tejon Ranch, microhabitat associations of Ensatina were surprisingly similar. For example, Corn and Bury (1991) noted positive associations of Ensatina with litter depth and grass cover, Aubry and Hall (1991) found positive relationships with deciduous trees, and Welsh and Lind (1991) noted positive relationships of Ensatina with hardwood trees and log abundance. Thus, given appropriate macrohabitat conditions, this salamander tends to select certain microhabitat features.

At Tejon Ranch, we typically found Ensatina in the same woodlands as *Batrachoseps nigriventris*, and occasionally under the same cover item. Co-occurrence between Ensatina and *B. attenuatus* has been reported for coniferous forests of the northwest (Bury and Martin, 1973; Welsh and Lind, 1991). Curiously, we detected no *Ensatina* in sympatry with either *Batrachoseps* at Sierra Foothill or San Joaquin. Whether this relationship holds for all vegetation types and environments along the foothills of the Sierra Nevada is unknown, but may provide an opportunity to more clearly define the habitat limits of both species.

Conservation Implications.—Our results showed that species of amphibians and reptiles selected habitats at different spatial scales. Implications of this hierarchical pattern of habitat selection have direct implications for the conservation of these species. The general consistency of results across sites and the good predictability of the logistic regression models indicated that our descriptions of habitat use were valid. The specific differences among species and sites (i.e., microhabitat differences) showed the importance of special elements (e.g., types of ground cover) and suggested the importance of specific microhabitat conditions (as related to vegetation structure and composition) for certain species. This underscores the need to maintain specific microhabitats as opposed to simply maintaining "oak woodland" per se for conservation of many of these species, especially if the goal is to maintain their populations throughout an area. These results verify the work of Block et al. (1994), who showed that general descriptions of macrohabitats are inadequate to predict the presence and abundance of many species.

As would be expected for terrestrial or fossorial animals, litter depth, the development of grass and forbs, and cover by downed woody debris and rocks were also important in the habitat models. At Sierra Foothill and San Joaquin, these latter variables, in addition to slope, were of primary importance in the habitat models. Thus, modifications to the understory that might result from fuelwood removal and livestock grazing might prove deleterious to many of the species that rely on these habitat components.

We believe that primary conservation concern should be afforded the amphibians, specifically the salamanders. These woodlands may represent environmental limits (sensu, Liebig, 1841; Shelford, 1913) for these species. Consequently, the animals present may be uniquely adapted to those conditions. These salamanders used the most restricted range of habitats of the species studied as inferred by their significant positive associations with canyon live oak woodlands. These woodlands are largely restricted to north-facing slopes and exhibited high canopy closure. Presumably, attributes and conditions of this woodland type provide favorable conditions for salamanders. Current land development practices may decrease the abundance of such woodlands while increasing fragmentation of the habitats remaining. Land-use planning now and into the future must regard such woodlands as sensitive and strive to maintain their quantity and distribution.

Acknowledgments.—We thank S. Corn, C. Greenberg, A. Lind, N. Scott Jr., H. Welsh, and two anonymous reviewers for commenting on earlier drafts of this paper and providing helpful suggestions. P. Berryhill, D. DonnerWright, M. Dixon, J. Gurule, G. Jongejan, S. Kee, D. Loughman, B. Marston, T. Tennant, and J. Wright assisted with fieldwork. P. Scott helped with data analysis. L. Merkle and K. Ross provided editorial assistance. D. Geivet, M. Connor, and D. Duncan provided logistical assistance at Tejon Ranch, Sierra Foothill, and San Joaquin, respectively. Funding for this research was provided by the University of California, Integrated Hardwood Management Program; California Department of Forestry and Fire Protection, Forest and Range Resource Assessment Program; and the USDA Forest Service, Pacific Southwest Research Station.

Literature Cited

ALLEN, B. H. 1990. Classification of oak woodlands. Fremontia 18:22–25.

AUBRY, K. B., AND P. A. HALL. 1991. Terrestrial amphibian communities on the southern Washington Cascade range. In L. Ruggiero, K. Aubry, A. Carey, and M. Huff (tech. coords.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests, pp. 326–338. USDA Forest Service Gen. Tech. Rep. PNW-285, Pacific Northwest Research Station, Portland, Oregon.

BLOCK, W. M., AND L. A. BRENNAN. 1993. The habitat concept in ornithology. In D. Power (ed.), Current Ornithology, pp. 35–91. Vol. 11. Plenum Press, New York.

———, M. L. MORRISON, J. C. SLAYMAKER, AND G.

JONGEJAN. 1988. Design considerations for the study of amphibians, reptiles, and small mammals in California's oak woodlands: temporal and spatial patterns. *In* R. Szaro, *K*. Severson, and D. Patton (eds.), Management of Amphibians, Reptiles, and Small Mammals in North America, pp. 247–253. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-166, Fort Collins, Colorado.

——— ———, J. VERNER, AND P. N. MANLEY. 1994. Assessing wildlife-habitat-relationships models: a case study with California oak woodlands. Wildl. Soc. Bull. 22:549–561.

BURY, R. B., AND M. MARTIN. 1973. Comparative studies on the distribution and foods of Plethodontid salamanders in the redwood region of northern California. J. Herpetol. 7:331–335.

CORN, P. S. 1994. Straight-line drift fences and pitfall traps. *In* W. Heyer, M. Donnelly, R. McDiarmid, L. Hayek, and M. Foster (eds.), Measuring and Monitoring Biological Diversity: Standards and Methods for Amphibians, pp. 109–117. Smithsonian Inst. Press, Washington, D.C.

———, AND R. B. BURY. 1991. Terrestrial amphibian communities in the Oregon Coast Range. *In* L. Ruggiero, *K*. Aubry, A. Carey, and M. Huff (tech. coords.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests, pp. 304–317. USDA Forest Service Gen. Tech. Rep. PNW-285, Pacific Northwest Research Station, Portland, Oregon.

CRUMP, M. L., AND N. J. SCOTT, JR. 1994. Visual encounter surveys. *In* W. Heyer, M. Donnelly, R. McDiarmid, L. Hayek, and M. Foster (eds.), Measuring and Monitoring Biological Diversity: Standards and Methods for Amphibians, pp. 85–92 Smithsonian Inst. Press, Washington, D.C.

DAVIS, J., AND N. A. M. VERBEEK. 1972. Habitat preferences and the distribution *Uta stansburiana* and *Sceloporus occidentalis* in Coastal California. Copeia 1972:643–646.

GREENBERG, C. H., D. G. NEARY, AND L. D. HARRIS. 1994. A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. J. Herpetol. 28:319–324.

HEADY, H. F., R. P. GIBBENS, AND R. W. POWELL. 1959. A comparison of charting, line intercept, and line point methods of sampling shrub types of vegetation. J. Range Manage. 21:370–380.

HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L. C. HAYEK, AND M. S. FOSTER (eds.). 1994. Measuring and Monitoring Biological Diversity: Standards and Methods for Amphibians. Smithsonian Inst. Press, Washington, D.C.

HOSMER, D. W., AND S. LEMESHEW. 1989. Applied Logistic Regression. John Wiley and Sons, New York.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

LIEBIG, J. 1841. Chemistry and Its Application to Agriculture and Physiology. Taylor and Walton, London.

MARCELLINI, D., AND J. P. MACKEY. 1970. Habitat preferences of the lizards, *Sceloporus occidentalis* and *S. graciosus* (Lacertilia, Iguanidae). Herpetologica 26: 51–56.

MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN. 1992. Wildlife-habitat Relationships: Concepts and Applications. Univ. Wisconsin Press, Madison.

———, I. C. TIMOSSI, AND K. A. WITH. 1987. Development and testing of linear regression models predicting bird-habitat relationships. J. Wildl. Manage. 51:247–253.

PIANKA, E. R. 1978. Evolutionary Ecology. 2nd ed. Harper and Row, New York.

RAPHAEL, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. *In* R. Szaro, R. Severson, and D. Patton (eds.), Management of Amphibians, Reptiles, and Small Mammals in North America, pp. 23–31. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Gen. Tech. Rep. RM-166, Fort Collins, Colorado.

ROSE, B. R. 1970. Habitat and prey selection of *Sceloporus occidentalis* and *Sceloporus graciosus*. Ecology 57:531–541.

SCOTT, N. J., JR. 1994. Complete species inventories. In W. Heyer, M. Donnelly, R. McDiarmid, L. Hayek, and M. Foster (eds.), Measuring and Monitoring Biological Diversity: Standards and Methods for Amphibians, pp. 78–84. Smithsonian Inst. Press, Washington, D.C.

SHELFORD, V. E. 1913. Animal Communities in Temperate America. Univ. Chicago Press, Chicago.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. Freeman and Company, San Francisco.

SOUTHWOOD, T. R. E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46:337–365.

TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1–21.

WELSH, H. H., JR., AND A. J. LIND. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon. *In* L. Ruggiero, K. Aubry, A. Carey, and M. Huff (tech. coords.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests, pp. 395414. USDA Forest Service Gen. Tech. Rep. PNW-285, Pacific Northwest Research Station, Portland, Oregon.

WIENS, J. A. 1989. Spatial scaling in ecology. Funct. Ecol. 3:385–397.

WILLIAMS, B. K., K. TITUS, AND J. E. HINES. 1990. Stability and bias of classification rates in biological applications of discriminant analysis. J. Wildl. Manage. 54:331–342.

Accepted: 14 October 1997.