Development and Evaluation of Habitat Models for Herpetofauna and Small Mammals

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ABSTRACT. We evaluated the ability of discriminant analysis (DA), logistic regression (LR), and multiple regression (MR) to describe habitat use by amphibians, reptiles, and small mammals found in California oak woodlands. We also compared models derived from pitfall and live trapping data for several species. Habitat relations modeled by DA and LR produced similar results, averaging about 70% classification success of the trapping stations to the correct group (capture or noncapture habitat). Although more variables were included in DA (4-5) than in LR (2-3), those included in LR were typically a subset of those in DA. On average, MR habitat models accounted for 56% of the variation in the index of relative species' abundance. The variables included in the MR models were seldom the same as those for DA and LR. Most differences between MR and the other two methods were related to differences in spatial scale: MR modeled habitat among grids, whereas DA and LR modeled habitat within grids. Habitat models for the same species differed between the trapping methods used. Live traps are most useful for describing general habitat relations of some small mammal species across large geographic areas, whereas pitfall traps are useful for intensive sampling of a larger portion of the vertebrate community within smaller geographic areas. Thus, the choice of trapping methods must be based on the study goals, biology of the species, and the spatial scale of study. FOR. SCI. 44(3):430–437.

Additional Key Words: Multivariate statistics, reptiles, amphibians, small mammals, California oak woodlands.

RESOURCE MANAGERS REQUIRE cost-effective means of assessing the population status of wildlife. Measuring population parameters of species is costly, and the amount of time (i.e., number of years) and area to be sampled to achieve reliable estimates can be quite high (Verner 1983, Block et al. 1994). Consequently, managers often use measures of habitat conditions as indices of population status (Verner et al. 1986, Morrison et al. 1992, Block and Brennan 1993). The validity of this approach rests largely on the ability to document strong relationships between habitat characteristics and the appropriate population parameter(s).

Habitat selection has been described as the innate and learned behavioral responses of a species that predisposes it to use a specific array of environmental conditions (Block and Brennan 1993). The degree to which habitat use and selection contribute to individual fitness and population persistence is defined as habitat quality or suitability. Selection can occur at different spatial scales (Johnson 1980). Johnson (1980) organized the scales into four levels ranging from substrates used for specific purposes (e.g., a downed log used for nesting) to the geographic range of the species. Intermediate to these scales is selection of a forest or woodland stand in a certain condition (e.g., seral stage), and more

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detailed selection of a patch within that stand. Information at the latter two scales is consistent with the scale at which vegetation management is typically applied. Thus, habitat models developed for these scales could be incorporated into management prescriptions designed at creating and maintaining wildlife habitat.

Three common approaches to modeling habitat use and suitability are logistic regression (LR), discriminant analysis (DA), and multiple linear regression (MR). The merits and limitations of each approach are not well understood (Williams 1980, Williams et al. 1990, Morrison et al. 1992), although each is widely used in wildlife ecology (Brennan et al. 1986, Capen et al. 1986, Morrison et al. 1992). Brennan et al. (1986) compared LR and DA for developing habitat suitability models for mountain quail (Oreortyxpictus), but we know of no comparable study that evaluates DA, LR, and MR. Because MR is applied at the between-stand scale and DA and LR are applied at the within-stand scale, direct comparisons are not possible. However, evaluations of the predictive capabilities of each modeling approach and the variables included in the models may provide insight on key habitat relations at different spatial scales.

Most quantitative habitat modeling efforts have focused on charismatic fauna such as game species, fur-bearers, and birds. In fact, most papers in "Wildlife 2000: modeling habitats of terrestrial vertebrates" (Verner et al. 1986; see also Morrison et al. 1992) focused on birds. Equally important, however, are habitat models for other types of wildlife such as herpetofauna and small mammals, whose populations may be more sensitive to habitat change than the species emphasized traditionally.

Another factor to consider when developing and evaluating empirical models is the method and scale used to obtain field data. Although many studies haveexamined the effectiveness of different methods for trapping herpetofauna and small mammals (e.g., Williams and Braun 1983, Boonstra and Krebs 1984, MengakandGuynn 1987, Heyer etal. 1994), few haveevaluated the influence of different trapping methods on resulting habitat descriptions (Taylor et al. 1988). We know of no study that has examined both different trapping methods and statistical modeling techniques together.

We used pitfall and live trap methods to estimate population characteristics and habitat relations of amphibians, reptiles, and small mammals in California oak woodlands. We applied discriminant analysis, logistic regression, and multiple linear regression to develop descriptive habitat models based on correlates of habitat with population size or species presence. To evaluate descriptive capabilities of models developed using data collected by different sampling methods, we tested whether models developed for small mammals based on live trap captures could be applied to pitfall-generated data, and vice versa.

Methods

Study Area

'The study area was the Tejon Ranch, Kern County (35°53'N, 118°46W), in the Tehachapi Mountains of southern California. Major land uses include cattle grazing, fuelwood harvest, and recreation. Elevation ranges from 1100 to 1700 m. Tejon Ranch is mountainous, consisting of steep slopes facing all cardinal directions. This topography contributes to a diverse flora. Blue (Quercus douglasii), interior live (Q. *wislizenii*), canyon live (Q. *chrysolepis*), California black (Q. kelloggii), valley (Q. lobata), and Brewer's (Q. *garryana* var. breweri) oaks constitute the overstory. Blue oakdominates the more xeric south- and east-facing slopes; canyon live and Brewer's oaks are typically found on mesic north-facing slopes; interior live and California black oaks are mostly on west-facing slopes; and valley oak is found on benches and valleys that support deeper soils. The woody understory consists of buckbrush (Ceanothus cuneatus), redberry (Rhamnuscrocea), chamise (Adenostorna fasciculaturn), big-berry manzanita (Arctostaphylos *glauca*), and mountain mahogany (Cercocarpus betuloides). Annual and perennial grasses and forbs comprise the herbaceous understory.

Pitfall Trapping

Pitfall traps consisted of 3.8 1 buckets buried to ground level and covered with a square piece of plywood elevated 5 to 10 cm above the lip of the bucket. Traps were in 6×6 grids with 20 m spacing between buckets. We placed 13 grids at Tejon Ranch for a total of 452 traps (16 traps destroyed by cattle were omitted from analysis); traps were monitored for a total of 65,850 trap days. Grids were at least 800 m apart to strive for sampling independence. Although this distance does not guarantee spatial independence of sampling units (i.e., grids), we contend that the probability of individuals visiting >1 grid was minimal. Traps were monitored from January 4 to May 20 1987, December 10, 1987, to June 20, 1988, and November 10, 1988, to April 30, 1989. Because our objective was to develop models to describe habitat use throughout the year, samples were pooled across time for analysis. Traps were checked periodically, and captures were identified and removed from the trapping grid.

Live Trapping

We used Sherman live traps to sample small mammal populations on ten grids from July through December 1986; March, April, November, and December 1987; November and December 1988; and January through March 1989. All capture data were pooled across time for analysis. Traps were in 8×8 grids with 15 m spacings between traps ($n = 640$ traps stations). The total live trapping effort included 8,996 trap nights. Animal captures were identified, aged, measured, marked by toe clipping, and released. We used only the first capture of an individual in model development. All pitfall and live trap grids were separated by >800 m.

Habitat Sampling

Habitat variables were measured within a 5 m radius circular plot centered on each trap station. To determine vegetation composition and structure, we estimated cover of woody vegetation by species using the point-intercept method (Heady et al. 1959). We placed a 10 m long transect centered on the trap station along a random bearing with I m spacings between points. Cover of woody vegetation by species was recorded at four height strata (<1 m, 1 to 2 m, 2 to 5 m, and

>5 m). Cover by grasses, forbs, rock, lichens, dead woody debris of three diameter classes (<1 cm, 1 to 10 cm, and >10 cm), leaf litter, and moss was estimated as the percentage of the ten points intercepted. Shrub height was measured by use of a meter stick; tree height was measured with a clinometer. Average shrub height and average tree height were calculated by averaging the heights of up to five shrubs and trees randomly sampled within the plot. If fewer than five trees or shrubs were present within the plot, we measured the heights of all trees or shrubs in the plot and calculated the average height. Average litter depth and herbaceous plant height were calculated by averaging five measurements taken systematically along the transect (every 2 m). The number of residual stumps from tree harvest was counted within the plot. For indices of stand decadence, we measured the length and diameter of logs, and estimated the length of dead limbs >10 cm diameter on trees. Slope was measured in degrees with a clinometer, aspect in degrees with a compass. Capture habitat for a species was defined as the environmental attributes at the trapping stations where the species was trapped at least once. All other trapping stations were defined as noncapture habitat. Although a species may have been present but not captured, we assumed that the probability of use by that species during our sampling period was small. For contrasts of capture and noncapture habitat, we randomly selected a sample of noncapture stations. The sample size of noncapture stations was roughly equal to that of the sample of capture stations.

Data Analyses

We reduced the number of habitat variables prior to using discriminant and logistic analyses to strive for an adequate sample size-to-variable ratio (Williams et al. 1990). Williams et al. (1990) proposed a minimum of two samples per variable for DA when overlap between groups is low. Our analyses were done with sample size-to-variable ratios ≥ 5:1. We only used variables with significant differences between capture and noncapture habitats (F-test, $P < 0.05$). If a pair of variables exhibited a Pearson product-moment correlation >0.5, we retained the one with the highest between-group significance (Brennan et al. 1986, Morrison et al. 1987, 1992). We used this screening process to derive the set of variables to be used in DA, LR, and MR for each species. Most variables were nonnormally distributed, and standard transformations did not normalize all variables; however, most variances were similar between groups. The multivariate methods we used are robust to violations of assumptions given adequate and equal sample sizes (see Morrison et al. 1992 for review); these criteria were met in this study.

Models were developed for herpetofauna based on the pitfall data; for small mammals, separate models were developed using pitfall and live trap data. Stepwise DA provided a linear combination of habitat variables that classified stations as capture or noncapture habitat (Green 1978). We used all stations where the species was captured and a random sample of roughly an equal number of noncapture stations to construct the discriminant function. The criterion for inclusion of a variable in the model was one that significantly reduced the value of the Wilks' lambda statistic (Dillon and Goldstein 1984).

We also used stepwise LR (Hosmer and Lemeshew 1989) to compare capture and noncapture stations. LR is a nonlinear analysis that is suitable for both continuous and discrete variables (e.g., Efron 1975, Press and Wilson 1978). To permit comparisons with DA results however, we only used continuous variables in our analysis. Variables were entered according to the significance of the Wald statistic (Hosmer and Lemeshew 1989). For both DA and LR, classification success and the type and order of entry for variables were used to evaluate model results.

Multiple linear regression (Draper and Smith 1981) was used to correlate the number of unique captures per grid ($n =$ 13 pitfall and 10 live-trap grids) with a linear combination of habitat variables. Habitat characteristics were estimated for the entire grid by pooling measures taken at each trapping station. Adjusted R^2s and the type and order of entry for variables were used to evaluate model results.

We also evaluated how well models developed using pitfall data classified data from live-trap captures, and vice versa. These evaluations were done for both DA and LR models. This is a robust method of determining the ability of a model to classify unknowns; that is, samples not included in initial model development (Morrison et al. 1992). This also tested whether data collected using one trapping method were consistent with data collected using the other.

Results

Comparison of Analytical Methods

Eighteen species—four amphibian, five reptile, and nine small mammal—were captured in pitfall traps, and ten small mammal species were captured in live traps (Table 1). Seven species were captured in adequate numbers of pitfall traps to permit model construction: yellow-blotched ensatina (Ensatina eschscholtzii croceater), western fence lizard (Sceloporus occidentalis), Gilbert's skink (Eumeces gilberti), ornate shrew (Sorex *ornatus*), brush mouse (Peromyscus boylii), deer mouse (Perornyscus *maniculatus*), and pinyon mouse (Peromyscus truei). The brush mouse, deer mouse, and pinyon mouse were captured at enough live trap stations to permit model construction.

Yellow-Blotched Ensatina

The DA of capture versus noncapture habitat classified 68% of capture and 72% of noncapture stations correctly, with an overall classification success of 74% (Table 2). Capture habitat was positively related to cover by canyon live oak, slope, and litter depth. That is, the probability of a station being classified as ensatina habitat increased as values for these variables increased. The probability of a station not being ensatina habitat increased as blue oak and grass cover increased.

Overall classification success from the LR was 68%, with 57% classification success for traps where ensatina was captured, and 78% in traps where it was not (Table 2). As with DA, increasing cover of canyon live oak was positively related to capture sites, whereas increasing cover by blue oak was related to noncapture sites. Average tree height, entered into the MR model, which accounted for 47% (R^2) of the

Table 1. Numbers of amphibians, reptiles, and small mammals captured in pitfall (n = 452 traps) and live traps (n= 640 trap stations) from 1986–1988 at Tejon Ranch, Kern County, California.

	Pitfalls	Live traps
Trap days or nights	65,850	8,996
Amphibians		
Ensatina eschscholtzii croceater	105	
Batrachoseps nigriventris	40	
Bufo boreas	1	
Hyla regilla	2	
Reptiles		
Diadophis punctatus	1	
Sceloporus occidentalis	174	
Eumeces gilberti	117	
Elgaria multicarinatus	5	
Anniella pulchra	1	
Small mammals		
Sorex ornatus	30	1
Scapanus latimanus	1	0
Perognathus californicus	11	11
Dipodomys heermanni	0	3
Thomomys bottae	23	0
Reithrodontomys megalotis	0	7
Peromyscus boylii	234	118
Peromyscus truei	59	119
Peromyscus maniculatus	107	58
Peromyscus californicus	1	2
Neotoma fuscipes	0	4
Microtus californicus	12	1

variation in ensatina abundance among grids. Average tree height was positively related to the relative abundance of ensatina.

Gilbert's Skink

Overall classification success from the DA was 70%, with 78% classification success for traps where skinks were captured and 62% where they were not captured (Table 2). The probability of classifying stations as skink habitat increased with increasing herbaceous vegetation height and cover by blue oak, whereas noncapture stations were positively related to canyon live oak cover, shrub species richness, and the number of large (>30 cm diameter) logs.

Overall classification success from the LR was 71%, with 79% classification success for traps where skinks were captured and 62% in traps where they were not (Table 2). The height of herbaceous vegetation was positively related to capture sites, whereas the cover by canyon live oak and shrub species richness were positively related to noncapture sites. The MR model included grass cover and height of herbaceous vegetation, and accounted for 70% (R^2) of the variation in the data set. Both of these variables were positively related to skink abundance.

Western Fence Lizard

DA correctly classified 74% of all cases, **83%** of stations where fence lizards were captured, and 65% of the stations where they were not (Table 2). The probability of classifying stations as fence lizard habitat increased as blue oak cover and herbaceous height increased, whereas noncapture stations were positively associated with slope, canyon live oak cover, and cover 1 to 2 m above the ground.

LR correctly classified 73% of all cases, 77% of stations where fence lizards were captured, and 69% of the stations where they were not (Table 2). Capture stations were positively associated with blue oak cover and herbaceous vegetation and negatively related to slope. MR provided a function including slope and herbaceous vegetation height that accounted for 72% (R^2) of the variation in the data set. Slope was negatively correlated and herbaceous vegetation height was positively correlated to fence lizard abundance.

Brush Mouse

Live Trapping

DA correctly classified 69% of all trapping stations, 64% of the stations where brush mice were captured, and 74% of the stations where they were not (Table 2). The probability of

Table 2. Classification success (%) by discriminant analysis (DA) and logistic regression (LR), and R^2 for multiple regression (MR) for habitat models of amphibians, reptiles, and small mammals in California oak woodlands, 1986–1988.

	Sample size[a]		Classification success		
	Capture	Noncapture	DA	LR	MR
Pitfall traps					
Ensatina eschscholtzii	59	60	74	68	47
Eumeces gilberti	69	69	70	71	70
Sceloporus occidentalis	87	87	74	73	72
Peromyscus boylii	126	122	65	63	ns[b]
Peromyscus maniculatus	72	72	77	76	45
Peromyscus truei	37	35	ns[c]	ns[c]	ns[b]
Sorex ornatus	25	25	74	74	ns[b]
Live traps					
Peromyscus boylii	120	115	69	70	41
Peromyscus maniculatus	66	66	73	71	77
Peromyscus truei	109	108	71	69	40

[a] Number of traps: n for MR is number of grids.
[b] Regression equation not significant ($P < 0.05$).
[c] No variables significant ($P < 0.05$) in separating capture and noncapture habitats.

classifying stations as brush mouse habitat increased as slope, litter depth, dead woody debris (1 to 10 cm diameter), height of herbaceous vegetation, and low canopy cover (I to 2 m height interval) increased, whereas the probability of classifying noncapture stations correctly increased as blue oak cover (2 to 5 m height interval) and grass cover increased.

LR correctly classified 70% of all trapping stations, 68% of trapping stations where brush mice were captured, and 71% of the stations where they were not (Table 2). Capture stations were positively associated with increasing slope, dead woody debris (1 to 10 cm diameter), and average litter depth, whereas noncapture stations were positively related to increasing blue oak cover (2 to 5 m height interval). MR provided a model that included only slope which was positively correlated with brush mouse abundance and accounted for 41% of the variation in the data set.

Pitfall Traps

DA correctly classified 65% of all trapping stations, 64% of the stations where brush mice were captured, and 65% of the stations where they were not captured (Table 2). The probability of classifying stations as capture habitat increased as herbaceous vegetation height, number of burrows, and California black oak cover (2 to 5 m height interval) increased, whereas classification of stations as noncapture habitat increased with increasing forb cover and blue oak cover (2 to 5 m height interval).

LR correctly classified 63% of the trapping stations, 64% of the stations where brush mice were captured, and 62% of the stations where they were not (Table 2). As with DA, increasing herbaceous vegetation height and number of burrows were positively related to capture habitat, whereas increasing forb cover was positively related to noncapture habitat. The MR produced no significant correlations.

Deer Mouse

Live Trapping

DA correctly classified 73% of all trapping stations, 74% of stations where deer mice were captured and 71% where they were not (Table 2). The probability of classifying stations as capture habitat increased as number of animal burrows increased, whereas classification of stations as noncapture habitat increased with increasing leaf litter cover, number of trees, and cover by dead and down wood of <1 cm diameter.

LR correctly classified 71% of all trapping stations, 72% of capture stations and 71% of random stations (Table 2). The probability of classifying stations as capture habitat increased with increasing numbers of animal burrows; classification of stations as noncapture habitat was positively related to leaf litter cover and number of trees. The MR had an R^2 of 77% indicating that deer mouse abundance was positively correlated with the number of burrows.

Pitfall Trapping

DA correctly classified 77% of all pitfall trap stations, including 83% of capture stations and 71% of random stations (Table 2). Capture stations were positively related with increasing grass cover, whereas noncapture stations were positively associated with slope, logs, number of shrubs and trees, dead woody debris (<1 cm and 1 to 10 cm diameter) and litter depth.

LR correctly classified 76% of pitfall trap stations, 83% of capture stations, and 69% of random stations (Table 2). The probability of classifying stations as noncapture habitat increased as slope, and numbers of shrubs and logs increased. The MR had an R^2 of 45%, with deer mouse abundance being negatively correlated to tree density.

Pinyon Mouse

Live Trapping

DA correctly classified 71% of all stations, 73% of capture stations, and 68% of the noncapture stations (Table 2). The probability of classifying stations as capture habitat was positively related to increasing slope, number of logs (10 to 30 cm diameter size class), and litter depth, whereas classification of noncapture sites was related to increasing cover by blue oak (2 to 5 m height interval).

LR correctly classified 69% of all stations, 74% of capture stations, and 64% of random stations (Table 2). Increasing slope and more large logs were related to capture sites, whereas higher levels of cover by blue oak (2–5 m height interval) were related to noncapture sites. The MR had an R^2 of 40% and was positively correlated with canyon live oak cover 2–5 m above the ground.

Pitfall Trapping

No habitat variables differentiated between used and random sites by any of the analyses.

Ornate Shrew

Pitfall Trapping

DA correctly classified 74% of all trap stations, 72% of capture stations, and 76% of noncapture stations (Table 2). The probability of classifying a station as capture habitat increased with increasing litter depth, large logs (>30 cm diameter class), and slope. Noncapture sites were positively correlated with increasing grass cover.

LR correctly classified 74% of all stations, 84% of capture stations, and 64% of random stations (Table 2). Grass cover was positively correlated with noncapture sites. The MR produced no significant correlation.

Comparison of Trapping Methods

Models developed using pitfall data and tested with live trap data were more successful in classifying used habitat than were models of the converse (61% vs. 41%; Table 3). However, neither data set showed much overall predictive power; that is, only about 50%, so not much different than random classification in the 2-group, used versus random situation. By animal species, none of the models was very successful in classifying used and random habitats (Table 3).

Discussion

Comparison of Analytical Methods

Each of the three statistical methods differed in how habitat relations were modeled. The two methods based on capture–noncapture habitat contrasts (DA and LR) were

Table 3. Classification success (%) using models developed for *Peromyscus* species with pitfall data to predict habitat used by live trapped animals, and vice versa.

	Pitfall models predicting live traps			Live trap models predicting pitfalls		
	Capture	Noncapture	Overall	Capture	Noncapture	Overall
P. maniculatus	67	54	61	36	78	57
P. truei	45	36	41	41	49	44
P. *boylii*	71	36	53	45	54	49
Overall	61	42	52	41	60	50

consistent in terms of classification success (both averaging about 70%), despite using both linear (DA) and nonlinear (LR) algorithms to develop models. Although they often differed in the number of variables selected (DA models included four to five variables and LR included two to three), the variables included in LR were typically a subset of those included in DA. The variables that appeared in both DA and LR models apparently were the best at discriminating used from random habitat at the within-stand scale. LR is considered the preferred method when data sets include both continuous and discrete variables (e.g., Efron 1975, Press and Wilson 1978, Brennan et al. 1986); our analyses included only the former.

For DA and LR, a unique set of variables emerged in the models constructed for each species, and classification success also differed among species. These phenomena may be related to differences in habitat selection and habitat quality for each species, and also the level of resolution possible from our study design. For example, habitat for a species could be ubiquitous (i.e., abundant throughout the study area) possibly because the species is a habitat generalist; thus, used areas may not be easily distinguished from random areas at the level of resolution we studied (i.e., the area proximal to the trap location). In contrast, habitat for a specialist could be patchily distributed and easily distinguished based on one or more multiple characteristics. The point is that habitat distribution and quantity likely differ for each species, with different variables being necessary to characterize habitat. These variables reflect a combination of habitat correlates for each species, and the distribution of these correlates within woodland stands.

Multiple regression, unlike DA and LR, models habitat at a larger spatial scale and can potentially account for gradients in abundance across multiple stands (i.e., the landscape). Only one or two variables were included in any MR model, and these variables were seldom the same as those entered in the DA or LR models, even when the percent classifications were similar across methods (e.g., for the skink and fence lizard). An exception was the brush mouse, for which slope was selected as the first variable in all three models. Here again, however, the MR model only entered this single variable. These differences are largely explained by the fact that MR used relative abundance rather than presence-absence as the dependent variable and the experimental units used in MR were grids rather than individual trap stations. Thus, the different results provided by MR are likely related to differences in the spatial scale of observation, and should not be taken as a negative conclusion regarding MR relative to DA or LR. In fact, MR applied in conjunction with DA or LR may provide the superior approach for describing habitat. MR could be used to describe habitat among stands, and then DA or LR could be used to describe habitat within the stands identified by MR as having a high probability of being a species' habitat.

A step often employed in model development is testing and validation. Model testing can be done a number of ways including cross-validation, jackknifing, bootstrapping, and applying independent data sets (Morrison et al. 1992). Models are evaluated in terms of classification success and the variables included, as well as their coefficient loadings. We applied two ad hoc validation methods to the DA and LR models. One was to simply compare variables included in DA and LR models for a given species. As noted above, variables overlapped extensively in both models, lending validity to the habitatrelations suggested independently by eachmethod. The other approach was to use pitfall data to test live trap models, and vice versa. However, biases inherent to each trapping method (see below) probably contributed unexplained variation to the results. A more parsimonious validation approach would be to test pitfall models with independent pitfall data and likewise for live trap models.

At odds with our application of DA and LR is the question of independence among trapping stations. As discussed earlier, DA and LR model habitat relations at the within-stand scale to describe patch-level correlates of habitat use by the species. To facilitate these analyses, we grouped trapping stations into "capture" and "noncapture" stations and compared habitat features between the two groups. Although no individuals of the species were captured at noncapture stations, a chance existed that they might use that area. However, our trapping efforts were fairly substantial, as each pitfall trap was open for a minimum of 92 days. Brush mouse, the most frequently captured species, was captured in about 28% (126 of 452) of the pitfall traps (Table 2). Each live trap station was sampled for 12 to 15 days, but the rate of occupancy of new stations by brush mice, for example, declined after about 7 days of trapping (Figure 1). Further, they were trapped at about 19% (120 of 640) of the live trap stations (Table 2). Thus, we concluded that the probability of the species using noncapture stations was relatively small, and violations of the assumption of sampling independence were negligible.

Logistical Considerations

Logistically, MR will require a greater sampling effort than DA and LR to meet sample size considerations. Although our sampling included 13 pitfall and 10 live trapping grids, the grid-to-variable ratio was only 2 to 3:1. Tabachnick and Fidell (1983, p. 92) suggested a minimum ratio of 4 to 5:1

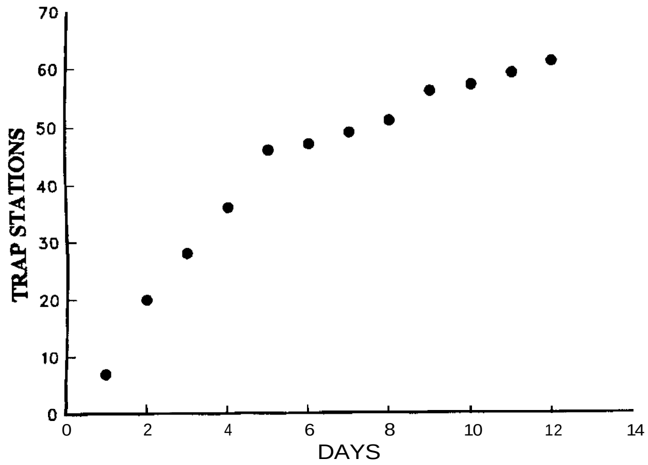

Figure 1. Number of live-trap stations used by Peromyscus *boylii* with increasing sampling effort from 1986 to 1988 at Tejon Ranch, Kern County, CA.

for MR. Even though our sampling efforts were substantial, improving the grid-to-variable ratio to meet Tabachnick and Fidell's minimum would require at least doubling our sampling effort. In contrast, the case-to-variable ratios for our DA analyses exceeded the minimum ratio (2:1) suggested by Williams et al. (1990).

Thus, we assert that our trapping efforts were likely sufficient to assess presence–absence at the trap station scale and relative abundance at the grid scale. Given that our effective sample of stations greatly exceeded that of grids, DA and LR were probably the preferred methods to model habitat relations for our study. However, analysis at the grid scale using MR was useful because it revealed potentially important habitat relations not evident in the DA or LR models.

Predictions of Habitat Quality

Our data are insufficient for assessing habitat quality directly. Habitat quality is a measure of an area to contribute to individual fitness and population persistence (Van Horne 1983, Block and Brennan 1993). We collected information on species presence and relative abundance, but have no relevant data on other important parameters such as survival or reproduction rates. These parameters or others may be better determinants of population persistence, habitat use, and habitat quality than presence or relative abundance. Research on identifying the appropriate population response variable to meet management objectives should be a focus of future habitat modeling efforts.

Comparison of Trapping Methods

Our models of habitat relations derived from pitfall trap data differed from those derived from live trap data. Taylor et al. (1988) also found little agreement among models generated from pitfall, live, and snap trap data for small mammals. Although we cannot partition spatial variation in grid locations from the total variation, pitfall and live traps are inherently different sampling methods that may influence the results in the following ways. First, pitfalls are open for a much longer period of time, increasing the likelihood that a trap will capture an animal. Thus, pitfall data would be expected to show less "nonuse" relative to live trap data given the increased sampling effort. This was true for the brush mouse and deer mouse that we captured in a greater percentage of the pitfall traps than in the live traps. Given that pitfall traps were sampled for more days than live traps, one might conclude that live traps are more likely to result in errors of omission than pitfall traps. That is, live traps may be more likely to classify sites as unused when the species is actually present. This hypothesis is partly supported by our application of pitfall data to models generated with live-trapping data, and the use of live-trap data to test models generated using pitfall data. Models based on live trapping performed poorly (36–45% classification success) in predicting sites that were used based on pitfall captures (Table 3). In contrast, models based on pitfall data incorrectly classified (4644% incorrect classifications) many noncapture live trap stations as capture habitat, possibly because some live trap stations were actually used even though no animals were captured during sampling periods (Table 3). A countering factor, however, is that live traps were baited, whereas pitfalls were not. Bait likely attracted individuals and could have artificially increased captures in live traps by some unknown number. Finally, the assumption of equal capture probabilities for the two trapping methods is probably tenuous. Heterogeneity in trapability likely existed among species and perhaps between age classes and sexes within a species. Thus, the probability of capture likely varied among and within species.

Pitfall traps are advantageous because they sample a greater portion of the small-vertebrate community than do live traps. This includes amphibians, reptiles, and fossorial mammals (shrews, gophers, moles), which are seldom captured in live traps. Similar results have been found by others (e.g., see Szaro et al. 1988 for review). To be effective, however, pitfalls must remain open for extended periods of time (several months in most situations; e.g., Bury and Corn 1987). whereas live trapping can usually provide a representative sample of trapable species in 3–8 days (Lancia et al. 1994, Morrison, unpubl. data). A disadvantage of pitfalls is that establishing and monitoring them can be far more time- and labor-intensive than live trapping. Whereas a live-trap grid can be established and sampled within the course of 1–2 weeks, pitfall trapping may require over 2 months to place traps, allow an area ample time to recover from the disturbance of digging holes, and finally running the traps. Thus, live traps are most useful when general habitat relationships are desired for selected species, when a large geographic area must be sampled, and when time and funds are limited. With greater resources, pitfalls may allow for more complete sampling of the small vertebrate community and of species-habitat relations. Obviously, various combinations of trapping methods could provide both intensive and extensive evaluations.

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