HABITAT USE BY MOUNTAIN QUAIL IN NORTHERN CALIFORNIA¹

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Abstract. We studied habitat use by Mountain Quail (*Oreortyx pictus*) at four sites in northern California. Vegetative cover types (macrohabitats) were used in proportion to availability. Significant microhabitat variables which distinguished used from available microhabitat structure included proximity to water and tall, dense shrubs. Mountain Quail population densities ranged from 9 to 30 birds per 100 ha; populations with greater densities used a larger range of the available microhabitat structure.

Key words: Habitat use; habitat availability; habitat selection; population density; logistic regression; northern California; Mountain Quail.

INTRODUCTION

The Mountain Quail (*Oreortyx pictus*) inhabits upland forest and woodland habitats in the western United States and Baja California Norte, Mexico (AOU 1983). Although this quail is mentioned in at least 270 published accounts (Gutiérrez 1975), most of these reports consist of anecdotal information and only a few (e.g., Grinnel et al. 1918, McLean 1930, Rahm 1938, Miller and Stebbins 1964) contain significant information about the natural history of this species.

Gutiérrez (1980) has provided the only quantitative assessment of habitat use by Mountain Quail. He reported that a dense tree canopy and steep slopes were important components of Mountain Quail habitat in the Coast Range Mountains of central California. Because his study was conducted at only one area, a general pattern of habitat use was not established.

The purpose of this study was to examine habitat use by Mountain Quail at four sites located over a broad geographic area. Characterization of the habitat features, with which birds are associated, is the foundation of life history, behavioral, and evolutionary studies (Thorpe 1945, Southwood 1977, Rotenberry 1981). Our emphasis was on how different populations of this quail were related to an array of vegetative and topographic features. The objectives of this paper are to (1) provide a quantitative analysis of the structural and floristic aspects of habitat use by Mountain Quail during spring and summer, and (2) examine the relationship between habitat use and variation in local population density.

STUDY AREAS

The four study areas (Fig. 1) were chosen because they represented the major physiognomic regions inhabited by Mountain Quail in northern California. The topographic and vegetative structure differed significantly among areas (Fig. 2) and a breeding population of Mountain Quail was present at each area (Brennan 1984). In contrast to the resident population studied by Gutiérrez (1980), populations of Mountain Quail at our study areas were migratory, forced by deep snow to lower elevations each winter. Areas ranged from 500 to 1,200 ha in size, and from 1,100 to 2,100 m in elevation.

COAST RANGE (SECS. 14,23; T4N R4E)

This area was within the mixed evergreen forest with chinquapin (*Castanopsis chrysophylla*) (Küchler 1977) of Humboldt County. Three cover types were present: mixed evergreen forest, mixed brush, and oak (*Quercus* spp.) woodland. The mixed evergreen forest was dominated by Douglas-fir (*Pseudotsuga menziesii*), and tanoak (*Lithocarpus densiflorus*). The areas of mixed brush were composed of deerbrush (*Ceanothus integerrimus*), blue elderberry (*Sambucus cerulea*), and willow (*Salix* spp.). The oak woodland was dominated by Oregon white oak (*Quercus garryana*).

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KLAMATH MOUNTAINS (SECS. 34,35; T46N R8W)

This area was within the Klamath yellow pine forest (Küchler 1977) of Siskiyou County. Two cover types were present: mixed forest and mixed brush. The mixed forest was composed of Jeffrey pine (*Pinus jeffreyi*) and Douglas-fir. The areas of mixed brush were dominated by whiteleaf manzanita (*Arctostaphylos viscida*) and deer brush.

MODOC PLATEAU (SECS. 29,30; T41N R6E)

This area was within the yellow pine/shrub forest (Küchler 1977) of Modoc County. Three cover types were present; pine-juniper forest, shrubsteppe, and basalt lava reefs. The pine-juniper forest had an overstory of Jeffrey pine and western juniper (Juniperus occidentalis), with occasional Douglas-fir and incense cedar (Calocedrus decurrens). Shrub-steppe areas were dominated by big sagebrush (Artemesia tridentata), greenleaf manzanita (Arctostaphylos patula), and antelope bitterbrush (Purshia tridentata). Pure stands of curlleaf mountain mahogony (Cercocarpus ledifolius) covered many areas. Although the lava reefs were only sparsely vegetated, this cover type was included in the analysis because Mountain Quail (1) used prominent lava rocks as crowing sites during the breeding season, (2) commonly crossed large expanses of lava to obtain drinking water, and (3) used crevices and other openings in the lava as escape cover.

NORTHERN SIERRA NEVADA (SECS. 25,26; T29N R11E)

This area was within the Sierra montane forest (Küchler 1977) of Lassen and Plumas counties. Two cover types were present: mixed forest and mixed brush. The mixed forest had an overstory of sugar pine (*Pinus lambertiana*), Jeffrey pine, Douglas-fir, white fir (*Abies concolor*), and incense cedar. Areas of mixed brush were dominated by Sierra chinquapin (*Castanopsis sempervirens*), snowbrush (*Ceanothus velutinus*), and greenleaf manzanita.

METHODS

EXPERIMENTAL DESIGN

This study was designed as a distributional rather than a behavioral investigation. Therefore, throughout this paper, we employ the term *habitat use* rather than *habitat selection* because the term *habitat use* indicates "the actual distribu-



FIGURE 1. Geographic locations of the Mountain Quail study areas in northern California.

tion of individuals," whereas *habitat selection* implies that organisms "consciously choose among alternative habitats" (Hutto 1985:457). This distinction does not, however, eliminate the possibility that processes of habitat selection might be responsible for the patterns of habitat use we observed (see Discussion).

Observed patterns of habitat use by birds often vary as a function of the scale at which the populations were sampled (Wiens 1981, 1985). With this in mind, we compared the habitats used by and available to Mountain Quail at two spatial scales: (1) macrohabitat (among cover types) and (2) microhabitat (within cover types). We defined available habitat as the array of macro and microhabitats that could be used by Mountain Quail at our study areas. We estimated the density of Mountain Quail at each study area so that we could evaluate our habitat analyses in relation to local population abundance (cf. Wiens and Rotenberry 1981, James et al. 1984).

Evaluation of macrohabitat use. We examined macrohabitat use by Mountain Quail (i.e., the use of cover types in proportion to availability) at each area by using a chi-square contingency analysis (Zar 1974:59). Expected frequency of use values were based on the proportions of available cover types which we estimated from 1:24,000 scale orthophotographic quadrangles of



INCREASING ELEVATION AND TREE CANOPY

FIGURE 2. Regional variation in the microhabitat structure used by Mountain Quail in northern California. Discriminant function analysis was based on 13 habitat variables (Table 2) measured on 25 circular, 0.02-ha plots at each area (100 plots total). Ninetynine percent of all samples were associated with the correct study site. The two discriminant functions shown account for 91% of the variation across the four regions. Some points represent more than one sample. Ellipses illustrate the range of discriminant scores for each site.

each study area. Observed frequency of use values were based on the number of sightings of quail in each cover type.

Evaluation of microhabitat use. We examined structural and topographic aspects of microhabitat use with a series of variables (based on Gutiérrez 1980, see Appendix 1, this paper) that were measured on 0.02-ha (15 m diameter) circular plots. We examined floristic aspects of microhabitat use with percent relative cover values of species of woody plants that were known to provide food resources for Mountain Quail (based on food habits data from 559 Mountain Quail collected from throughout California listed in Appendix 2 of Gutiérrez 1977).

The center of each habitat plot corresponded either to locations used by Mountain Quail or randomly located points. We used organism-centered habitat samples to estimate the microhabitat structure used by Mountain Quail. The location of the first quail (whether in a covey, in a pair, or a single bird) detected was used as the center of a habitat plot. We sampled available habitat structure with a systematic random design where the number of plots at each area was stratified by the proportions of cover types present. Within each cover type, we located a random starting point. From each starting point, the location of the first habitat plot was obtained by selecting a random compass bearing, and then randomly choosing a distance between 0 and 100 m along this bearing. Subsequent plots were spaced at 50- or 100-m intervals (depending on the patch size of the cover type) along the random bearing. A total of 100 randomly located plots (25 at each area) were contrasted with an equal number of organism-centered plots for our within-site analyses. In our pooled analyses we contrasted 114 organism-centered plots with 100 randomly-located ones.

We contrasted microhabitat use and availability in both univariate and multivariate space. Univariate tests for differences between and among individual variables were based on a Brown-Forsythe one-way analysis of variance (ANOVA) without the assumption of equal within-group variation (Brown and Forsythe 1974). We felt justified in pooling data from across four distinct areas because we wanted to obtain a general estimate of habitat use by Mountain Quail. Floristic aspects of use and availability were examined using Spearman's rank-correlation analysis (Zar 1974:243). Our multivariate contrast of use and availability was based on a logistic regression analysis (Cox 1970, Engelman 1981) of the structural and topographic variables that had statistical differences between the used and available groups (see Results). In general, logistic regression is used to derive a classification function from a series of "predictor" (in this case habitat) variables and then assess how well this function can predict which group the samples came from, much like discriminant analysis. A fundamental difference between logistic regression and discriminant analysis is that in logistic regression the analysis must be constrained to a two-group contrast. During the exploratory phase of our analysis, we observed that logistic regression was superior to discriminant analysis for evaluating our use and availability data in multivariate space (Brennan et al. 1986).

Density estimation. We estimated Mountain Quail density with variable-width line transect methods using the Fourier series estimator (Burnham et al. 1980). The observers walked transects (total lengths ranged from 12 to 14 km at each area) and recorded distance and sighting angle deviation from the transect line to each detected quail (methods detailed in Brennan and Block 1986). We used the program TRANSECT (Laake et al. 1979) to calculate our density estimates.

		Number sigh	of quail tings		
Study area Cover type ^a	Propor- tion	Ob- served	Ex- pected ^b	Р	
Coast Range					
Mixed forest	0.32	16	13		
Mixed brush	0.60	30	35		
Oak woodland	0.08	4	2	>0.10	
Klamath Mtns.					
Mixed forest	0.36	11	14		
Mixed brush	0.64	29	26	>0.10	
Modoc Plateau					
Pine-juniper	0.32	14	16		
Shrub-steppe	0.36	31	18		
Lava reefs	0.32	5	16	< 0.001	
N. Sierra Nevada					
Mixed forest	0.64	29	32		
Mixed brush	0.36	21	18	>0.25	

 TABLE 1. Chi-square contingency analysis of macrohabitat use by Mountain Quail at four sites in northern California.

* See study area descriptions for species composition of cover types.
b Expected values based on proportions of available cover types.

Sampling effort. We spent 250 person-days in the field locating and/or censusing Mountain Quail (16 June to 10 October 1982, 14 April to 7 October 1983). We collected density data during May and June 1983.

RESULTS

MACROHABITAT USE

The Modoc Plateau was the only one of the four areas where macrohabitat use by Mountain Quail was not in proportion to the relative areas of available cover types (Table 1). Mountain Quail used all of the vegetative cover types in proportion to their availability. The Modoc area was unique insofar as the lava reefs were used infrequently by Mountain Quail.

MICROHABITAT USE

The average microhabitat structure used by Mountain Quail varied greatly among the four study areas; 8 of the 13 variables showed statistically significant differences (P < 0.01) across the four areas (Table 2). When we contrasted microhabitat use with availability, we detected significant differences (P < 0.01) in 4 of 13 variables (Table 3). A mathematical combination of these four variables (distance to water, distance to cover, maximum shrub height, and percent



FIGURE 3. Predicted probabilities of membership in the used habitat group based on a logistic regression analysis of four variables measured on 214 (114 organism-centered; 100 randomly-located) habitat plots pooled across the four areas. Each point represents one habitat plot. Pictorial interpretation shows variation in vegetative structure.

shrub canopy cover) using logistic regression showed a substantial improvement over classification of the organism-centered and randomlylocated plots based solely on prior probabilities of group membership (Table 4). Histograms of the predicted probabilities of group membership illustrate the classification results of all habitat samples pooled across the four areas (Fig. 3). The distribution of the organism-centered samples was skewed toward the high end of the probability scale. Conversely, probability scores for the habitat samples from the randomly-located group were distributed more-or-less evenly across the entire probability scale (Fig. 3). The samples in the randomly-located group contained a wider variety of habitat components (including the proportion of microhabitat structure used by Mountain Quail) than the organism-centered plots.

The relative cover values of species of woody plants that were known to provide foods eaten by Mountain Quail were greater in the organismcentered group than in the randomly-located group (Table 5). Nine of the 12 species used in this analysis were shrubs. The observed r_s (0.6) did not exceed the critical r_s (0.9; df = 8; P >0.05), therefore the two groups of relative cover values appeared to be statistically independent.

	Coast F	Range	Klamath	Mtns.	Modoc F	lateau	N. Sierra	Nevada	
Variable ^a	Ŕ	SE	\$	SE	<i>x</i>	SE	x	SE	F-ratio ^b
Basal area (m ² /ha)	0.1	0.06	0.2	0.16	0.2	0.14	0.2	0.06	ns
Elevation (m)	1,231.0	16.0	1,152.0	14.0	1,445.0	4.0	1,896.0	22.0	469.0
Distance to cover (m)	1.1	0.34	0.4	0.18	0.1	0.06	1.2	0.42	3.1
Distance to edge (m)	2.0	0.44	3.2	1.2	3.5	1.2	2.2	0.44	ns
Distance to water (m)	94.0	21.4	166.0	32.0	199.0	30.0	94.0	17.4	4.1
Litter depth (cm)	1.4	0.26	2.1	0.18	2.0	0.3	2.4	0.2	2.8
Maximum shrub height									
(m)	3.3	0.3	2.3	0.16	2.7	0.22	1.8	0.14	8.3
Minimum shrub height									
(m)	0.1	0.02	0.4	0.04	0.2	0.04	0.1	0.02	11.6
Percent dead material	19.7	4.1	15.0	4.4	17.2	3.7	23.5	5.1	ns
Percent herb cover	25.5	4.3	7.1	3.8	26.8	4.7	14.3	5.3	4.0
Percent shrub canopy	37.1	4.4	48.8	5.2	41.8	4.7	50.6	5.6	ns
Percent tree canopy	21.3	6.1	25.1	4.2	10.3	3.6	20.9	5.9	ns
Slope (°)	24.6	2.3	19.9	2.3	5.1	1.5	20.3	1.9	17.5

TABLE 2. Average microhabitat structure in four regions of the breeding range of Mountain Quail. Data are from 25 organism-centered circular plots (0.02 ha) measured at each region (100 plots total).

* See Appendix for an explanation of the habitat variables. * All *F*-ratios significant at P < 0.01, unless noted as not significant (ns); one-way analysis of variance.

DENSITY IN RELATION TO MICROHABITAT USE AND AVAILABILITY

affected our ability to distinguish used from available microhabitat structure.

Density estimates of Mountain Quail ranged from 9.0 (Modoc Plateau) to 30.0 (Klamath Mountains) birds per 100 ha. There was an inverse relationship between density values and the average percentage of correctly classified habitat plots among the four study areas (Fig. 4). A sample size of n = 4 precluded a regression analysis of this relationship; however, it was apparent that variation in local population abundance influenced patterns of habitat use which in turn

DISCUSSION

Our analyses were based on statistical correlations and thus can only indicate a mathematical association between Mountain Quail and certain habitat features (cf. Wiens 1985). Therefore, we can only infer that mechanisms which govern habitat selection might be responsible for the statistical differences between use and availability that we observed. Several potential biases may

TABLE 3. Average values of the microhabitat structure used by and available to Mountain Quail. Values given were obtained by pooling habitat samples from four regions in northern California.

	Organism centered $(n = 114)$			Randomly located $(n = 100)$			
Variable ^a	X	SE	Range	X	SE	Range	F-ratio ^b
Basal area (m ² /ha)	0.12	0.18	0-3.7	0.24	0.04	0–2.6	ns
Elevation (m)	1,470.0	28.0	1,050-2,161	1,494.0	32.0	1,033-2,066	ns
Distance to cover (m)	0.83	0.20	0-13.0	3.9	0.66	0-45.0	15.2
Distance to edge (m)	2.49	0.362	0-27.0	3.90	0.68	0-45.0	ns
Distance to water (m)	131.0	12.0	0-500	255.0	23.0	0-500	23.9
Litter depth (cm)	1.8	0.11	0-6.7	1.8	0.10	0-4.6	ns
Maximum shrub height (m)	2.4	0.12	0-6.4	1.9	0.12	0-5.0	8.2
Minimum shrub height (m)	0.28	0.07	0-1.0	0.14	0.02	0-1.0	ns
Percent dead material	16.0	1.5	0-87.0	20.9	2.31	0-96.0	ns
Percent herb cover	17.7	2.0	0-99.0	18.5	2.55	0-98.0	ns
Percent shrub canopy	45.8	2.3	0-10	32.1	2.7	0-100	15.2
Percent tree canopy	18.4	2.2	0-100	25.5	3.17	0-100	ns
Slope (°)	17.6	1.1	0-59.0	19.4	1.19	059	ns

^a See Appendix for an explanation of the habitat variables. ^b *F*-ratios significant at P < 0.01, unless noted as not significant (ns); one-way analysis of variance.

TABLE 4.	Classification	results of	Mountain	Quail
and random	ly-located hab	itat plots by	y stepwise lo	ogistic
regression, b	based on four l	habitat var	iables. ^a	

	Percentage of habitat samples classified in the correct group ^b				
Study area sample size (quail : random)	Organism centered	Randomly located	Average		
Coast Range					
(25:25)	88.5	68.0	78.4		
Klamath Mtns.					
(25:25)	83.0	60.0	71.4		
Modoc Plateau					
(25:25)	91.0	100.0	96.0		
N. Sierra Nevada					
(25:25)	78.6	84.0	81.3		
All Areas					
(114:100)	85.1	60.0	73.0		

* Distance to water, distance to cover, maximum shrub height, percent shrub canopy

^b Prior probability of correct classification based on relative sample size of each group. For individual study areas prior probabilities were 50:50, for the analysis across all areas they were 53:47.

have affected these statistical differences. First, our results may be biased in favor of the most conspicuous individuals because we used "the first quail seen" as the criterion for our samples of habitat use. Second, the effect of observer influence is difficult to assess. Most of the time it was impossible to know if the quail detected us before we detected them, which may have caused them to move (and thus bias the location of the sample). Thus, we often did not know if the first quail seen had been feeding, moving to water, roosting, involved in a social interaction with another quail, or moving in response to the approaching observer. Using the locations of quail other than the first seen would have introduced even more bias. Because of these problems, we made no distinctions between different types (e.g., feeding, roosting, etc.) of habitat use, and instead chose to treat the observations within a basic context of distribution. Time-dependent interactions were another potential source of bias. We tried to minimize this confounding effect by sampling habitat use throughout the entire day. A study of time-activity patterns with prolonged observations of undisturbed quail would be a good way to avoid these sources of potential bias. Such an approach was, however, beyond the scope of this study.

MACROHABITAT USE

Macrohabitat use by Mountain Quail in this study was similar to what Gutiérrez (1980) reported. Ninety-seven percent of his observations of



FIGURE 4. Relationship between Mountain Quail density estimates from the four study sites (abscissa) and the average percentage of organism-centered and randomly-located habitat plots from each site that were correctly classified by logistic regression (ordinate).

Mountain Quail were in mixed evergreen forest and chaparral cover types. Ninety-five percent of our observations were also in mixed forest and brush cover types.

Macrohabitat use by Mountain Quail differed from macrohabitat availability only on the Modoc Plateau. The availability of lava reefs clearly exceeded the frequency with which Mountain Ouail used them. Lava reefs were the only type of habitat at our study areas not previously identified as a habitat used by Mountain Quail (cf.

TABLE 5. Relative cover values of species of woody plants that may provide food resources used by Mountain Quail. Data were obtained from 25 0.02-ha plots at four northern California areas (100 plots total).

······································	Relative cover (%) ^a		
Species	Organism centered	Randomly located	
Arbutus menziesii	11.5	1.0	
Arctostaphylos spp. ^b	16.0	15.8	
Castanopsis sempervirens	3.0	2.0	
Ceanothus spp. ^c	34.0	26.7	
Sambucus cerulea	1.9	0.4	
Symphoricarpos albus	3.9	1.5	
Quercus spp. ^d	1.4	0.1	

• Relative cover values do not sum to 100% in each category because 25 additional species of woody plants make up the balance of the relative cover values.

Includes A. viscida, A. patula.
 Includes C. cuneatus, C. integerrimus, C. velutinus.
 Includes Q. kelloggii, Q. garryana.

Grinnell et al. 1918). At best, lava reefs provided some escape cover and prominent places from which territorial quail call.

MICROHABITAT USE

The identification of habitat features which differ in a use vs. availability contrast is indirect evidence that birds recognize a specific configuration of habitat structure and settle in these areas to feed, loaf, roost, or breed (Hildén 1965). Our results indicated that Mountain Quail were consistently associated with a microhabitat configuration that consists of tall and dense shrubs which are in close proximity to drinking water and escape cover (Table 3, Fig. 3). These statistical results can be interpreted in terms of the biology of this quail, especially when considered in the context of a physiological need for water and food resources. Although we emphasize the importance of food and water in our interpretation, we cannot completely discount the possibility that other processes such as predation (Hildén 1965), climatic stress (Walsberg 1985) or even parasitism (Freeland 1983) may have influenced the patterns of habitat use we observed. Interspecific competition with California Quail (Callipepla californica) was largely ruled out by Gutiérrez (1980) as a process that has influenced habitat use by Mountain Quail. The respective ecologies and biogeographic histories of these two quails are vastly different (cf. Gutiérrez 1980, Gutiérrez et al. 1983).

Mountain Quail require drinking water during hot weather, and juveniles must drink soon after hatching if they are to survive (Grinnell and Swarth 1913, McLean 1930, Rahm 1938). Because of this physiological requirement, the presence of available drinking water is one habitat component with clear ecological significance for this quail. The maximum distance of adult and immature Mountain Quail from water observed by Miller and Stebbins (1964) at Joshua Tree National Monument was 1.6 and 0.8 km respectively—values which are slightly greater than those we observed (Tables 2 and 3).

Mountain Quail spent a great deal of time beneath the perennial vegetation that provides many food resources (Gutiérrez 1980). Our analysis of the relative amounts of shrub species indicated an apparent preference for those species that are known to provide food resources. Presumably, the large and well-developed shrubs provide more food than small shrubs. Tall dense shrubs might also provide more shade and relief from thermal stress than low sparse shrubs. Thus, it seems reasonable that this quail should use areas where the shrub height and canopy coverage is greater that what is generally available. Although we emphasize the role of shrubs in our analysis, other variables which showed little difference between the used and available groups (such as percent herb cover or litter depth) might also be important biologically.

Our results illustrate the importance of sampling avian habitat use over a broad geographic area, and at different spatial scales (Wiens 1981, 1985). We detected significant differences between use and availability at the microhabitat level, and few differences at the macrohabitat level. By sampling microhabitat use and availability over a wide geographic area, we brought into question the value of slope as an important component of Mountain Quail habitat. Gutiérrez (1980) reported that steep slopes were an important factor in distinguishing between the habitats used by California and Mountain quails. Our data indicated that topography alone probably has little value as a component of Mountain Quail habitat. Rather, it is the juxtaposition of tall, dense shrubs in proximity to available water that characterizes the general pattern of habitat use by Mountain Quail in northern California.

DENSITY IN RELATION TO MICROHABITAT USE

Hildén (1965), Noon et al. (1980), and Wiens and Rotenberry (1981) recognized that variation in local population abundance can have marked effects on patterns of habitat use by birds. Our results also support this contention. As the density of Mountain Quail increased across the four areas, we observed that a greater range of available microhabitat structure was used (as shown by the corresponding decrease in successful classifications of the organism-centered and randomly-located plots). The inverse relationship shown in Figure 4 indicates that Mountain Quail density may be related to microhabitat use. Some ultimate measure of habitat quality such as survivorship or reproductive success (cf. Van Horne 1983) must, therefore, be obtained before we can conclude that population density is an indicator of habitat quality for this quail.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American Birds, 6th ed. American Ornithologists' Union, Washington, DC.
- BRENNAN, L. A. 1984. Summer habitat ecology of Mountain Ouail in northern California. M.S.thesis, Humboldt State Univ., Arcata, CA.
- BRENNAN, L. A., AND W. M. BLOCK, 1986. Line transect estimates of Mountain Quail density. J. Wildl. Manage, 50:373-377.
- BRENNAN, L. A., W. M. BLOCK, AND R. J. GUTIÉRREZ. 1986. The use of multivariate statistics for developing habitat suitability index models, p. 177-182. In J. Verner, M. L. Morrison, and C. J. Ralph leds.]. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.
- BROWN, M. B., AND A. B. FORSYTHE. 1974. The small sample behavior of some statistics which test the equality of several means. Technometrics 16:129-132.
- BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72:1-202.
- Cox, D. R. 1970. The analysis of binary data. Methuen, London.
- ENGELMAN, L. 1981. Stepwise logistic regression, p. 330-344. In W. J. Dixon, L. Engelman, J. W. Frane, M. A. Hill, R. I. Jennrich, and J. D. Toporek [eds.], Biomedical computer programs, P-series. Univ. California Press, Los Angeles.
- FREELAND, W. J. 1983. Parasites and the coexistence of animal host species. Am. Nat. 121:223-236.
- GRINNELL, J., H. C. BRYANT, AND T. I. STORER. 1918. The game birds of California. Univ. California Press, Berkeley.
- GRINNELL, J., AND H. S. SWARTH. 1913. An account of the birds and mammals of the San Jacinto area of southern California. Univ. Calif. Publ. Zool. 10:197-406.
- GUTIÉRREZ, R. J. 1975. Literature review and bibliography of the Mountain Quail (Oreortyx pictus). Special report. USDA Forest Service Regional Office, San Francisco, CA.
- GUTIÉRREZ, R. J. 1977. Comparative ecology of the Mountain and California Quails in the Carmel Valley, California. Ph.D.diss., Univ. California, Berkeley.
- GUTIÉRREZ, R. J. 1980. Comparative ecology of the

Mountain and California Quails in the Carmel Valley, California, Living Bird 18:71-93.

- GUTIÉRREZ, R. J., R. M. ZINK, AND S. Y. YANG. 1983. Genic variation, systematic and biogeographic relationships of some galliform birds. Auk 100:33-47.
- HILDÉN, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2:53-75.
- HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory land birds, p. 455-475. In M. L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.
- JAMES, F. C., R. F. JOHNSON, N. O. WAMER, G. J. NEIMI, AND W. J. BOECKLEN. 1984. The Grinnellian niche of the Wood Thrush, Am. Nat. 124: 17-30.
- KÜCHLER, A. W. 1977. Potential natural vegetation of California, Map. In M. G. Barbour and J. Major [eds.], Terrestrial vegetation of California, John Wiley and Sons, New York.
- LAAKE, J. L., K. P. BURNHAM, AND D. R. ANDERSON. 1979. User's manual for program TRANSECT. Utah State Univ. Press, Logan.
- McLEAN, D. D. 1930. The quail of California. Calif. Dep. Fish Game Bull. 2:1-47.
- MILLER, A. H., AND R. C. STEBBINS, 1964. The lives of desert animals in Joshua Tree National Monument. Univ. California Press, Berkeley.
- NOON, B. R., D. K. DAWSON, D. B. INKLEY, C. S. ROBBINS, AND S. H. ANDERSON. 1980. Consistency in habitat preference of forest bird species. Trans. N. Am. Wildl. Nat. Resour. Conf. 45:226-244
- RAHM, N. M. 1938. Ouail range extension in the San Bernardino National Forest. Calif. Fish Game 24: 133-158.
- ROTENBERRY, J. T. 1981. Why measure bird habitat?, p. 29-32. In D. E. Capen [ed.], The use of multivariate statistics in studies of wildlife habitat. U.S. For. Serv. Gen. Tech. Rep. RM-87. SOUTHWOOD, T.R.E. 1977. Habitat, the templet for
- ecological strategies? J. Anim. Ecol. 46:337-365.
- THORPE, W. H. 1945. The evolutionary significance of habitat selection. J. Anim. Ecol. 14:67-70.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893-901.
- WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection, p. 389-413. In M. L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.
- WIENS, J. A. 1981. Scale problems in avian censusing. Stud. Avian Biology 6:513-521.
- WIENS, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds, p. 227-251. In M. L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.
- WIENS, J. A., AND J. T. ROTENBERRY. 1981. Censusing and the evaluation of avian habitat occupancy. Stud. Avian Biology 6:522-532.
- ZAR, J. H. 1974. Biostatistical analysis. Prentice Hall, Engelwood, NJ.

APPENDIX 1. Explanations of the methods used to measure habitat variables on 0.02-ha, 15-m diameter plots at four areas in northern California. Plots correspond to Mountain Quail sightings and a random sample of available habitat stratified by vegetative cover type.

Variable	Explanation
Basal area	Sum of basal area at diameter of all trees within a plot at
Elevation	Altitude (m) above sea-level, based on an altimeter or to-
Distance to cover	Meters to nearest escape cover measured with a tape or range finder.
Distance to edge	Meters to nearest patch of vegetation different from that at plot center.
Distance to water	Meters to nearest water from plot center.
Litter depth	Average litter depth taken from 10 measurements along a 15-m line intercent
Maximum shrub height	Height of the tallest shrub on the plot.
Minimum shrub height	Height of the shortest shrub on the plot.
Percent dead ma- terial	Percentage of a 15-m tape in- tercepted by fallen logs, branches, and dead shrubs
Percent herb cov- er	Percentage of a 15-m tape in- tercepted by grasses and forts
Percent shrub canopy ^a	Percentage of a 15-m tape in- tercepted by shrub foliage.
Percent tree cano- py ^a	Percentage of a 15-m tape in- tercepted by tree foliage.
Slope	Measured in degrees with a cli- nometer.

^a Also used to obtain relative cover values for each species of woody plant along the 15-m intercept.