

# HABITAT USE AND POPULATION CHARACTERISTICS OF THE WHITE-TAILED PTARMIGAN IN THE SIERRA NEVADA, CALIFORNIA<sup>1</sup>

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*Abstract.* We studied an introduced population of White-tailed Ptarmigan (*Lagopus leucurus*) during 1987 and 1988. Ptarmigan colonized alpine habitat 79 km north and 114 km south of their release site within 18 years of their liberation in the Sierra Nevada, California. Population densities were the lowest reported for the species. However, sex and age ratios were similar to native populations. Breeding season habitats were in areas of tall (>30 cm) willow (*Salix*) shrubs and contained more subshrub, moss, and boulder cover than in unused habitats. In the postbreeding season, ptarmigan used topographic depressions within breeding territories; brooding hens used moist meadows, while flocks occupied sites with abundant boulders. Ptarmigan primarily used the *Salix anglorum antiplasta* vegetation alliance on rocky, north-facing slopes. Willow abundance and proximity to water were the most discriminatory variables in logistic regression analyses between habitats used and unused by ptarmigan during the breeding and postbreeding seasons.

*Key words:* White-tailed Ptarmigan; *Lagopus leucurus*; demography; habitat use; limiting factors; colonization; logistic regression; Sierra Nevada.

## INTRODUCTION

White-tailed Ptarmigan (*Lagopus leucurus*) have been released in several alpine areas in western North America, including the Willowa Mountains, Oregon; the Sierra Nevada, California; Pike's Peak, Colorado; and the Uinta Mountains, Utah. All transplants were apparently successful (Spencer 1976; DeSante and Gaines 1977; Braun et al. 1978; Hoffman and Giesen 1983; Gaines 1988; V. L. Coggins, Oregon Department of Fish and Wildlife, LeGrande, pers. comm.; R. D. Thomas, California Department of Fish and Game, Sacramento, pers. comm.). The Sierra Nevada release was particularly noteworthy because the mountain range is outside the species' historic distribution (Aldrich 1963). Successful transplants of ptarmigan in California and Oregon were fortuitous because no objective means for assessing ptarmigan habitat characteristics existed at the time of release (Braun et al. 1978). With one exception (Scott 1982), all analyses of White-tailed Ptarmigan habitat have been qualitative. Therefore, an objective method for evaluating habitat suitability for this ptarmigan was needed.

Summer habitats of White-tailed Ptarmigan in the Rocky Mountains consistently include moist,

low-growing alpine vegetation (Weeden 1959; Choate 1963; Jensen and Ryder 1965; Braun and Pattie 1969; Braun 1970, 1971; Herzog 1977; Scott 1982). Extreme summer drought in the Sierra Nevada restricts mesophytic alpine vegetation to protected slope exposures and topographic depressions (Klikoff 1965, Pemble 1970, Chabot and Billings 1972). In contrast, alpine areas occupied by ptarmigan in the southern Rocky Mountains experience a slight summer drought (Major and Bamberg 1967) and contain large expanses of suitable habitat (Braun and Rogers 1971). Where suitable habitat is generally limited and population levels are low, habitat selection is likely to be most restricted (Hildén 1965). The recent colonization of the Sierra Nevada by ptarmigan affords the uncommon opportunity to examine habitat factors that may limit ptarmigan abundance and influence range expansion.

In this paper, we provide a quantitative analysis of ptarmigan habitat structure based on comparisons of habitats used and not used by ptarmigan in the Sierra Nevada. We also provide some demographic characteristics of this introduced population. In addition, rates of range expansion of White-tailed Ptarmigan transplanted outside their historic range have not been studied. Therefore, we also assess ptarmigan colonizing abilities based on documented sightings in the Sierra Nevada.

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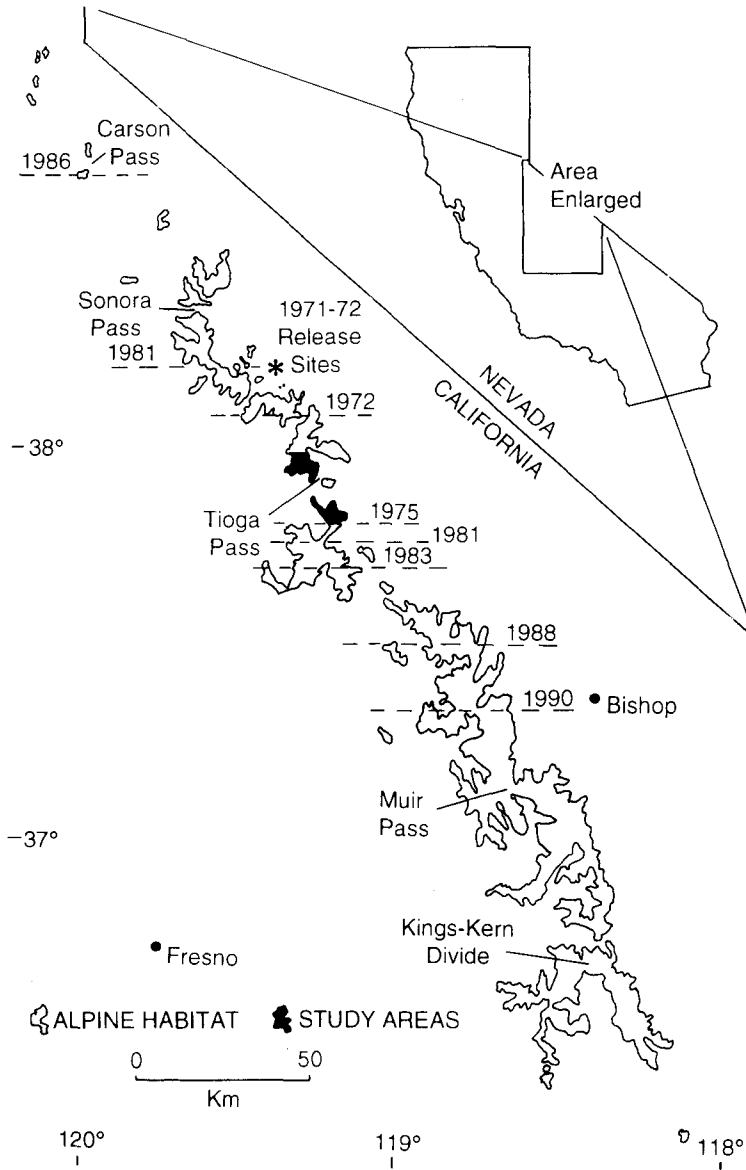


FIGURE 1. White-tailed Ptarmigan range expansion through alpine regions (redrawn from Kuchler 1977) of the Sierra Nevada showing location of 1971–1972 White-tailed Ptarmigan transplant and subsequent documented sightings during 1971–1990. Dotted lines are furthest sighting from the release site reported in a particular year. Source of sighting records is described in text.

**STUDY AREAS**

Two study areas adjoining Tioga Pass, Mono County, California, were selected in order to obtain an adequate number of independent habitat samples (Fig. 1). The 1987 study site (13 km<sup>2</sup>, hereafter called Yosemite) extended from Mono Pass south to Parker Peak Pass and west to Kuna

Crest. The 1988 study area (10 km<sup>2</sup>, hereafter called HNA) was in the Harvey Monroe Hall Natural Area of the Inyo National Forest. Study areas were approximately 10 km apart and located 41–22 km south of the transplant locations, ranged in elevation from 3,200 to 3,840 m, and were similar in vegetation and topography. The study populations were apparently separate since

no birds banded in Yosemite were observed in HNA.

Moisture availability during the typically dry growing season is the principal factor controlling vegetation patterns in the Sierra Nevada alpine (Klikoff 1965, Pemble 1970, Taylor 1984). Most cyclonic storms are diverted from the mountain range in summer; consequently, average total summer rainfall is only 5.25 cm (U.S. Department of Commerce 1930–1964). Although occasional thunderstorms may temporarily replenish soil moisture (Klikoff 1965), melting snow is the major source of moisture during the growing season. Annual snowfall in the Sierra Nevada is substantial (e.g., averaging 665 cm at Ellery Lake, 3.2 km from the study area at 2,926 m elevation; U.S. Department of Commerce 1930–1964). Snow cover persists through mid-June in most areas, with few snowbanks remaining past mid-July except on protected north- or east-facing slopes (Chabot and Billings 1972). Because the distribution and melting rate of snowbanks is uneven due to interaction of wind and topography, a distinct local vegetation pattern results (Mooney et al. 1965).

## METHODS

### POPULATION CHARACTERISTICS

Range expansion from the release sites was estimated from sightings of White-tailed Ptarmigan reported to the California Department of Fish and Game, Yosemite National Park Research Library records for 1971–1988, and from personal observation. Two additional records were obtained in 1990–1991 from knowledgeable wildlife biologists. Only records with a reliable description of bird(s) plumage, behavior, and associated habitat were included in the documentation of range expansion.

Population characteristics were estimated by marking all previously unbanded birds encountered during surveys of 1 km<sup>2</sup> sections of the study areas. Surveys began in early April to assess breeding density. C. E. Braun (pers. comm.) noted that accurate estimates of ptarmigan breeding density can only be assessed during the early spring breeding period (April–early June). Using repeated, systematic searches and tape-recorded ptarmigan calls, we believe few individuals escaped detection; non-territorial males and broodless females were the most likely birds to have been missed during surveys (Braun et al. 1973).

Birds were captured using a noose pole (Zwickel and Bendell 1967) and banded with numbered aluminum California Department of Fish and Game leg bands (size 10 and 12) and numbered, colored plastic bandettes (size 5 and 6; National Band and Tag Co., Newport, KY). Sex and age-class of each bird were estimated following Braun and Rogers (1967). All ptarmigan observations were plotted on 7.5 minute US Geological Service topographic maps and aerial photographs (scale 1:10,000). We calculated total density (i.e., number of individuals on the entire study area) and ecologic density (i.e., number of individuals within occupied habitat). Extent of occupied habitat was estimated with a planimeter by measuring the area enclosed by the boundaries of outermost ptarmigan territories. This calculation assumed birds were located in the approximate center of average-sized territories (i.e., 20 ha; Jensen and Ryder 1965, Schmidt 1969).

### HABITAT ANALYSIS

We analyzed habitat selection with a used/unused contrast rather than the more common used/available approach because (1) the latter comparison can potentially contain unknown amounts of suitable habitat (Brennan et al. 1986), and (2) we were able to verify occupancy by the conspicuous, persistent nature of ptarmigan droppings and feathers and the reliable response of ptarmigan to tape-recorded vocalizations (Braun et al. 1973). Unused habitats contained neither ptarmigan nor their feathers/feces. We further reduced the probability of misidentifying unused habitats by locating unused study plots outside areas of ptarmigan concentrations. Although an unknown number of samples in the unused habitat group may have received undetected use, such infrequently used habitats probably were relatively unimportant to ptarmigan.

We recognized two seasons in our study: (1) breeding (early April to mid-July), defined by the onset of molt of the winter plumage and by the presence of both males and females on or immediately adjacent to defended territories; and (2) postbreeding (mid-July to late August), recognized by the appearance of ptarmigan broods and flocks consisting of at least two mutually non-aggressive males.

We measured habitat variables (see Appendix) in 0.02-ha (15-m diameter) study plots in used and unused habitats at approximately the same altitudes. For the used habitat sample, we cen-

tered study plots on the first sighting of a bird (single or member of pair or flock) not sampled previously during the same season. Thus, all habitat observations were independent samples. Sites occupied by ptarmigan located with taped calls were not sampled because birds may move in response to calls. Unused habitats were sampled following a completed survey of a 1 km<sup>2</sup> section. Two to three study plots were randomly located in unoccupied areas of each section. From a randomly selected starting point within an unused section, we followed a randomly selected compass bearing approximately 30 m to the plot center. A plot was rejected if it contained previously undetected evidence of ptarmigan use. Unused habitat plots established in the breeding season were resampled the following season if they still did not contain ptarmigan, or their feathers or feces.

We identified plant communities at the center of each study plot using Pemble's (1970) classification; the hierarchical classification ranks nine vegetation associations in five alliances. We calculated mean slope orientation ( $\theta$ ) and its dispersion ( $r$ ) for both used and unused sites (Batschelet 1981:7); and we employed Rayleigh's test (Zar 1984:442) to test if the sample was uniformly distributed. We used the Watson-Williams test (Batschelet 1981:95) to examine differences in mean slope orientation between used and unused habitats, and chi-square contingency analysis to test for seasonal changes in slope orientation (Batschelet 1981:109).

We reduced the number of structural habitat variables prior to multivariate analyses. Logarithmic and square-root transformations were used to normalize structural habitat data. We first performed a one-way analysis of variance (ANOVA; Brown and Forsythe 1974) to determine which variables had significant ( $P < 0.05$ ) between-group differences. Second, we used Spearman's rank-correlation (Zar 1984:318) to eliminate one of a pair of statistically significant variables if  $r > 0.4$ . The variable with either the highest between-group significance or more meaningful biological interpretation was retained. We then used stepwise logistic regression (SLR; Dixon et al. 1985:330) to examine differences between used and unused habitat structure. We used step-wise discriminant analysis (SDA; Klecka 1980) to examine differences between used habitats (1) during the breeding and postbreeding season and (2) by flocks and hens with broods.

Group covariance matrices were evaluated for homogeneity of variance using Box's  $M$  statistic (Nie et al. 1975:460). We calculated chance corrected classification rates (Titus et al. 1984) for all discriminant and logistic regression analyses. Classification matrices for SDA were based on a jackknife procedure (Dixon et al. 1985:519).

We examined stability of model variables by comparing performance of SLR and SDA models (Brennan et al. 1986). Model stability was further evaluated through a cross-validation procedure recommended by Capen et al. (1986). We derived a subset model from a random sample of 75% of the observations, and used the model to classify the remaining 25% of observations. We replicated this process 20 times for each comparison and evaluated variable loading patterns and stability of model coefficients.

## RESULTS

### PTARMIGAN COLONIZATION PATTERNS IN THE SIERRA NEVADA

Seventy-two adult White-tailed Ptarmigan from Colorado were released in the central Sierra Nevada at Eagle Peak and Twin Lakes, Mono County, during 1971–1972 in upper montane-subalpine forest below 3,000 m elevation (R. D. Thomas, pers. comm.). Abandoning the release sites, the colonists dispersed 10 km to the Sierra Nevada crest. Within 18 years ptarmigan colonized alpine habitats 114 km to the south and 79 km to the north (Fig. 1). Movement must have been rapid because observations 5 months, 1 year, and 4 years after release were 11, 27, and 41 km from the release sites, respectively. The furthest southern observation was at Pine Creek Pass, Mono County. The largest gap of unsuitable, low-elevation (2,260 m) habitat (i.e., Middle Fork San Joaquin River) in their southward dispersal was 13.7 km. In their northward dispersal to Carson Pass, Alpine County, ptarmigan crossed similar areas of low-elevation forest 10–20 km wide (Fig. 1).

### POPULATION CHARACTERISTICS

We estimated the age-class of 140 of 141 ptarmigan banded on the two study areas. The combined population was 59.29% male and 40.71% female; yearlings (i.e., first year birds) comprised 30% of the breeding season population. Changes in sex and age ratios between seasons were minor and indicated little movement in or out of the study areas during summer (Table 1).

TABLE 1. Sex and age ratios of White-tailed Ptarmigan observed in the Sierra Nevada, in 1987–1988. Only known age-class birds were included.

Study site	Yearling male : adult male		Yearling female : adult female		Yearling : adult		Male : female	
	Breeding season	Entire year	Breeding season	Entire year	Breeding season	Entire year	Breeding season	Entire year
Yosemite	0.4:1 (31) <sup>a</sup>	0.5:1 (37)	0.1:1 (17)	0.4:1 (25)	0.3:1 (48)	0.5:1 (62)	1.8:1 (48)	1.5:1 (62)
HNA	0.3:1 (25)	0.4:1 (46)	0.9:1 (27)	0.7:1 (32)	0.6:1 (52)	0.5:1 (78)	0.9:1 (52)	1.4:1 (78)

<sup>a</sup> Sample size.

Population density (ptarmigan per 100 ha) for the entire area surveyed ranged from 4.4 to 5.7 in the breeding season, and from 4.7 to 7.1 in the postbreeding season. Densities within occupied habitat (i.e., ecological density) were greater than total densities and this relationship increased two-fold (e.g., breeding = 10.5–14.2; postbreeding = 21.8–27.7) between seasons. The number of breeding pairs per 100 ha was 1.8 and 2.8 in the Yosemite and HNA study sites, respectively.

We located 23 different broods in July and August. Average annual brood size ranged from 2.6 to 2.8 chicks per brood (Table 2).

#### SEASONAL DISTRIBUTION

Ptarmigan distribution was closely associated with availability of mesic vegetation in spring and summer. Edges of snow-free patches on upland slopes were used extensively for foraging and roosting during spring ( $n = 48$  of 66 observations). As vegetation on these slopes became dry, ptarmigan moved to late developing plant communities in snow-free depressions. This pattern was reflected by a significant difference in use of vegetation alliances during the breeding season ( $\chi^2 = 12.233$ ,  $df = 3$ ,  $P < 0.05$ ; Fig. 2). Moist plant communities, particularly with willow (*Salix* spp.) and ericaceous shrubs as important components, were used more often. The *Salix anglorum antiplasta* alliance was the most frequently occurring community in used breeding and postbreeding season habitats sampled. Conversely, drier plant alliances (e.g., *Carex breweri*–*Calyptridium umbellatum* and *Arenaria kingii*–*Senecio werneriaefolius*) occurred predominantly in unused habitats (68.8%).

Ptarmigan also used a wider range of plant associations, including drier types, during the breeding season than in the postbreeding season

(Fig. 3). The relatively moist *Cassiope mertensiana*–*Phyllodoce breweri* association received consistently high use both seasons. Females with broods primarily used wet meadows; however, the frequency of occurrence of plant associations used by flocks and hens with broods was similar.

Mean slope orientation of habitats used by ptarmigan during the breeding and postbreeding seasons was  $44 \pm 14$  degrees ( $r = 0.64$ ,  $n = 72$ ) and  $19 \pm 18$  degrees ( $r = 0.59$ ,  $n = 52$ ), respectively. Used habitats showed significant slope orientation during both seasons (Rayleigh's  $Z$ -test; breeding:  $Z = 29.49$ ,  $P < 0.001$ ; postbreeding:  $Z = 18.10$ ,  $P < 0.001$ ). Distribution of slope orientations used by ptarmigan did not differ between seasons ( $\chi^2 = 12.42$ ,  $df = 4$ ,  $P > 0.01$ ). However, mean slope orientation differed between used and unused habitats in both seasons (Watson-Williams test; breeding:  $F = 9.24$ ,  $df = 1,151$ ,  $P < 0.01$ ; postbreeding:  $F = 3.94$ ,  $df = 1,100$ ,  $P < 0.01$ ). Whereas 46% of used habitats had northeast to northwest slope orientations, 28% of unused sites were on slopes with northern orientations ( $\chi^2 = 22.1$ ,  $df = 8$ ,  $P < 0.001$ ).

TABLE 2. Number of broods and average brood size of White-tailed Ptarmigan populations in the Sierra Nevada, California, 1987–1988. Number of broods does not include reobservation of individual broods during a sampling period.

Date	Average number of chicks per brood	
	Yosemite	HNA
July 1–15	2.0 (3) <sup>a</sup>	6.0 (1)
July 16–31	4.0 (2)	3.1 (7)
August 1–15	2.3 (3)	2.0 (4)
August 16–31	ND (0)	2.0 (3)
Average	2.6 (8)	2.8 (15)

<sup>a</sup> ( $n$ ) = number of broods observed during the period.

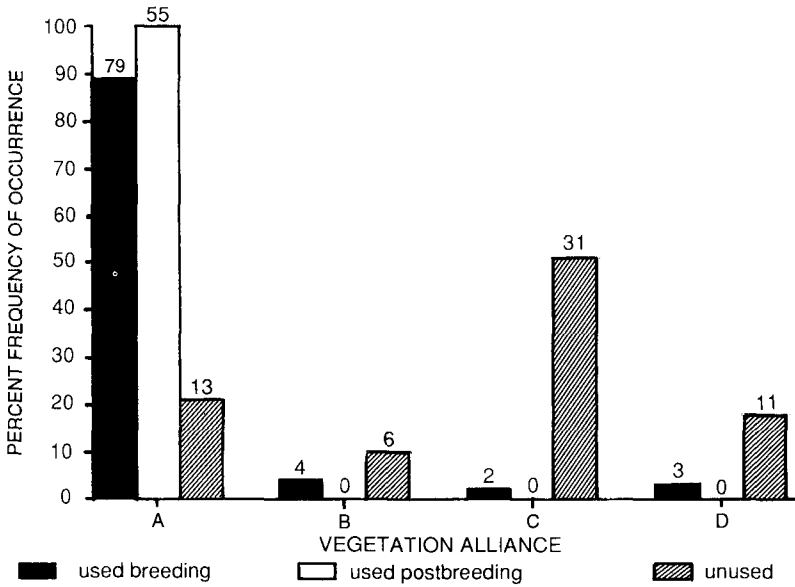


FIGURE 2. Distribution of vegetation alliances between used and unused White-tailed Ptarmigan habitat in the Sierra Nevada, California. Alliance codes: A = *Salix anglorum* var *antiplasta*, B = *Saxifraga aprica*-*Gentiana newberryi*, C = *Carex breweri*-*Calyptridium umbellatum*, D = *Arenaria kingii*-*Senecio werneriaefolius* (Pemble 1970). Numbers atop bars are sample size.

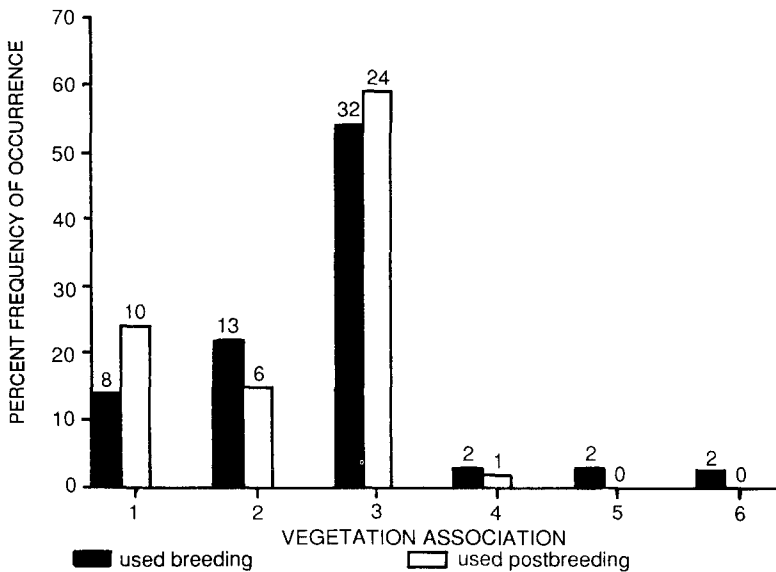


FIGURE 3. Distribution of vegetation associations between White-tailed Ptarmigan habitat used during the breeding and postbreeding season in the Sierra Nevada, California. Association codes: 1 = *Carex subnigricans*-*Pedicularis attollens*, 2 = *Trifolium monanthum*-*Phleum alpinum*, 3 = *Cassiope mertensiana*-*Phyllodoce breweri*, 4 = *Salix nivalis*, 5 = *Carex helleri*-*Poa suksdorfii*, 6 = *Arabis platysperma*-*Penstemon heterodoxus* (Pemble 1970). Numbers atop bars are sample size. Note associations 1-4 are within vegetation alliance 'A' and associations 5-6 are within alliance 'C.'

TABLE 3. Characteristics of habitats used and unused by White-tailed Ptarmigan during the breeding season in the Sierra Nevada, California.

Variable <sup>a</sup>	Used ( <i>n</i> = 72)		Unused ( <i>n</i> = 82)		<i>P</i> <sup>b</sup>
	$\bar{x}$	SE	$\bar{x}$	SE	
Altitude (m)	3,303.9	11.99	3,319.1	13.53	0.401
Slope (°)	15.7	0.69	15.3	0.76	0.759
Shrub height (cm)					
Maximum	61.9	9.43	137.8	22.76	0.075
Minimum	9.8	1.53	12.9	2.13	0.879
Distance (m) to					
Snow	16.1	5.87	28.9	3.72	0.596
Water	8.1	1.77	53.5	6.84	<0.001
Shrub	7.3	1.63	32.4	7.02	0.014
Willow shrub	42.6	8.08	113.6	11.76	<0.001
Percent cover					
Soil	2.9	0.36	3.2	0.84	0.016
Gravel	8.7	1.15	15.4	2.32	0.286
Rock	9.8	0.92	7.7	1.12	0.005
Boulder	24.6	2.14	20.8	2.88	0.008
Snow	15.6	2.41	29.5	4.3	0.827
Shrub	3.7	1.17	7.5	1.51	0.046
Subshrub	2.3	0.51	0.3	0.14	0.001
Dwarf willow	6.6	0.87	0.1	0.76	<0.001
Turf	17.3	1.41	9.2	1.56	<0.001
Forb	4.6	0.54	4.5	0.92	0.881
Herb	22.3	1.67	14.2	2.21	<0.001
Moss	2.1	0.28	0.9	0.23	<0.001

<sup>a</sup> See Appendix for explanation of habitat variables.

<sup>b</sup> One-way ANOVA; *df* = 1, 152.

#### BREEDING SEASON HABITAT STRUCTURE

We measured habitat characteristics at 72 ptarmigan locations during the breeding seasons. Each location was an independent sample (i.e., a color-marked bird). Thirteen structural habitat variables differed ( $P < 0.05$ ) between used and unused breeding habitat (Table 3). Our data fit the logistic model ( $\chi^2 = 83.6$ , *df* = 147,  $P = 1.0$ ), and stepwise inclusion of each variable, except percent boulder cover, improved the predictive power of the model ( $P \leq 0.05$ ). The probability of a habitat being used increased with increasing cover by dwarf willow, subshrubs, moss, and boulders, and with decreasing distance from water and willow shrubs. Based on a logistic cut-point of 0.435, the full model correctly classified 75.4% of habitats ( $Z = 9.34$ ,  $P < 0.001$ ).

Although group covariance matrices were unequal (Box's  $M = 525.24$ ,  $F = 23.95$ ,  $P < 0.001$ ), we inferred from the cross validation analyses that this did not seriously affect model performance. The same six predictor variables entered the full model and subset models in similar order (Table 4). Percent dwarf willow cover entered all

models and consistently ranked first. All variables, except boulder cover and subshrub cover, entered  $\geq 12$  of 20 subset models. Moreover, signs of coefficients were consistent and their values similar for the subset and full models (Table 4). Mean correct classification was 62.8% (SE = 2.38,  $P < 0.001$ ). All variables, except subshrub cover and boulder cover, had structure coefficients  $> 0.52$  in the SDA model.

#### POSTBREEDING SEASON HABITAT STRUCTURE

We measured habitat characteristics at sites occupied by 52 different, color-marked ptarmigan during the postbreeding seasons. Fourteen variables differed ( $P < 0.05$ ) between habitats used and not used by ptarmigan (Table 5). Although boulder cover was not statistically different, it was retained for further analyses for biological reasons (i.e., the birds will use boulders for cover). Mean distance to snow was probably too great for snow to be an important factor in habitat selection ( $\bar{x} = 124.2$  m). However, snowmelt from adjacent slopes and higher elevations facilitated

TABLE 4. Step-wise order of variable selection, regression coefficients, and error terms in subset and full data logistic regression analyses of White-tailed Ptarmigan habitat in the Sierra Nevada.

Season variable	Subset models ( <i>n</i> = 20)				Step	Full model	
	Step		Regression coefficient			Regression coefficient	SE of coefficient
	$\bar{x}^1$	SE	$\bar{x}^2$	SE			
<b>Breeding</b>							
Dwarf willow cover	1.0	0.00	0.0538	0.002	1	0.0513	0.014
Subshrub cover	2.6	0.05	0.0209	0.002	2	0.0095	0.006
Moss cover	2.8	0.31	0.2019	0.008	3	0.1863	0.083
Dist. to water	3.4	0.28	-0.0444	0.002	4	-0.0342	0.016
Dist. to willow	3.4	0.23	-1.1310	0.084	5	-0.9433	0.422
Boulder cover	4.3	0.53	0.0601	0.004	6	0.0409	0.028
Constant			-0.9467	0.235		-0.6876	0.759
<b>Postbreeding</b>							
Dwarf willow cover	1.2	0.01	0.8548	0.046	1	0.0381	0.012
Dist. to water	1.9	0.02	-0.7577	0.042	2	-0.0345	0.103
Soil cover	2.9	0.02	3.8877	2.633	3	0.1813	0.093
Constant			-8.4021	5.363		-1.2734	0.768

<sup>1</sup>  $\bar{x}$  = mean entry of variable into model, SE = standard error.

<sup>2</sup>  $\bar{x}$  = mean regression coefficient, SE = standard error of the mean regression coefficient.

development of greater vegetation cover in used ( $\bar{x} = 45.0\%$ , SE = 2.5) than in unused ( $\bar{x} = 29.2\%$ , SE = 3.8) habitats ( $F = 19.73$ ; df = 1,100;  $P < 0.001$ ). A logistic model was appropriate for our data ( $\chi^2 = 43.3$ , df = 98,  $P = 1.0$ ), and its predictive power was improved by inclusion of each variable ( $P \leq 0.05$ ). The probability of a habitat being used by ptarmigan increased with increasing cover of dwarf willow and soil, and with decreasing distance to water. Based on a logistic cutpoint 0.046, the full model correctly classified 86.2% of habitats ( $Z = 8.70$ ,  $P < 0.001$ ); mean correct classification rate was 78.6% (SE = 2.64,  $P \leq 0.004$ ).

Although covariance matrices were unequal (Box's  $M = 347.3$ ,  $F = 15.47$ ,  $P < 0.001$ ), high correct classification rates and cross-validation results indicated the models were stable. Percent dwarf willow cover and distance to water were most consistent in their contribution to subset models, entering 19 and 17 times, respectively. Additionally, percent soil cover entered the subset models 14 times; however, its low structure coefficient (-0.33) from SDA indicated it was not a highly discriminatory variable; structure coefficients of remaining variables were  $> 0.70$ . While signs of coefficients were consistent between the subset and full models, their values were relatively unstable (Table 4).

Boulder cover distinguished ptarmigan flock and brood habitat in the SDA model ( $Z = 4.61$ ,  $P < 0.001$ ). Flocking habitats contained more

boulders ( $P < 0.001$ ) while having less turf ( $P = 0.018$ ) than brood habitats. Covariance matrices were equal for these analyses (Box's  $M = 1.49$ ,  $F = 1.45$ ,  $P = 0.229$ ).

#### COMPARISON OF BREEDING AND POSTBREEDING SEASON HABITAT STRUCTURE

Ptarmigan moved into less steep topographic depressions with more dwarf willow ( $P < 0.001$ ) and gravel cover ( $P = 0.003$ ) after the breeding season had ended. The SDA model did not reliably distinguish used ptarmigan habitats between seasons; correct classification rates of most (70%) subset models were not significantly ( $P > 0.01$ ) better than a classification based solely on prior probabilities of group membership. Covariance matrices were unequal (Box's  $M = 11.83$ ,  $F = 3.87$ ,  $P < 0.01$ ).

#### DISCUSSION

##### POPULATION CHARACTERISTICS

Documented sightings of White-tailed Ptarmigan in the Sierra Nevada indicated a rapid rate of range expansion (Fig. 1). Within 18 years of their release, ptarmigan had colonized over 190 km of alpine habitat. In comparison, range expansion following transplants and experimental removals of ptarmigan in the Rocky Mountains was considerably slower. For example, ptarmigan transplanted to Pike's Peak, Colorado, required four years to colonize all suitable habitats



TABLE 5. Characteristics of habitats used and unused by White-tailed Ptarmigan during the postbreeding season in the Sierra Nevada, California.

Variable <sup>a</sup>	Used (n = 52)		Unused (n = 50)		P <sup>b</sup>
	$\bar{x}$	SE	$\bar{x}$	SE	
Altitude (m)	3,311.0	10.83	3,359.2	15.34	0.011
Slope (°)	11.4	0.76	14.9	1.02	0.006
Shrub height (cm)					
Maximum	24.2	3.95	92.1	21.08	0.031
Minimum	7.1	1.24	11.5	2.78	0.693
Distance (m) to					
Snow	124.2	12.42	177.4	15.33	0.018
Water	13.5	3.3	88.2	10.01	<0.001
Shrub	9.5	1.54	35.3	8.84	0.485
Willow shrub	29.1	4.61	119.8	15.37	<0.001
Percent cover					
Soil	3.8	0.57	2.3	0.58	0.006
Gravel	13.0	1.36	24.0	2.79	0.007
Rock	11.4	1.2	11.8	1.49	0.764
Boulder	25.7	2.28	31.8	3.74	0.583
Snow	0.0	—	0.0	—	—
Shrub	0.6	0.34	6.3	1.73	0.002
Subshrub	1.1	0.4	0.4	0.25	0.127
Dwarf willow	13.7	1.63	0.3	0.2	<0.001
Turf	22.3	1.57	13.3	2.1	<0.001
Forb	3.6	0.81	7.3	1.68	0.054
Herb	26.2	1.83	21.1	3.13	0.009
Moss	2.8	0.37	1.0	0.29	<0.001

<sup>a</sup> See Appendix for explanation of habitat variables.

<sup>b</sup> One-way ANOVA; df = 1, 100.

within 5 km of the release site (Hoffman and Giesen 1983). Breeding territories in the Uinta Mountains, Utah, established the year following a release were located within 5 km of the release site (Braun et al. 1978). Ptarmigan repopulated an isolated 5 km<sup>2</sup> area in northern Colorado within two years of an experimental removal of all birds; the nearest colonization source was 3.2 km away (Braun 1975).

Our estimated population densities were within the range of values (3.71–6.57 birds per 100 ha) reported by Clarke and Johnson (1992) for the south-half of our HNA study area during the previous six years. These are the lowest densities reported for White-tailed Ptarmigan. Overall breeding season density (birds per 100 ha) at Logan Pass, Montana, was 6.8, while density within suitable habitats was 19.3 (Choate 1963). Breeding density of three un hunted populations in Colorado ranged from 9.6 to 11.9 and averaged 10.8 over a five year period (Braun and May 1971, Braun and Rogers 1971). Postbreeding ptarmigan density for these populations was 10.6 in Montana and averaged 19.3 (range 15.7–23.4)

in Colorado (Choate 1963, Braun and May 1971, respectively).

Breeding success (i.e., ratio of yearlings to adults during postbreeding season) in our study sites was less than reported for native populations in the Rocky Mountains (Choate 1963, Braun and Rogers 1971). However, the proportion of yearlings in the breeding season population was comparable to Rocky Mountain populations and indicated adequate over-winter survival. Clarke and Johnson (1990) reported that breeding success in the Sierra Nevada varied between years but did not differ significantly from breeding success of naturally occurring populations. Average brood size in our study areas also was below reported values. Average annual brood size for five study areas in southern Colorado during four years was 3.6 (range 3.2–4.5; Braun and Rogers 1971). Brood size at flight age in Montana ranged from 3.25 to 3.47 (Choate 1963).

Below average population density, small brood size, and variable breeding success in Sierra Nevada ptarmigan may be attributable to the limited availability and quality of ptarmigan habi-

tat. White-tailed Ptarmigan are closely associated with mesic, low-growing alpine vegetation in our study sites as well as throughout the Rocky Mountains (Weeden 1959; Choate 1963; Jensen and Ryder 1965; Braun 1969, 1970, 1971; Braun and Pattie 1969; Herzog 1977; Scott 1982). Mesic vegetation in the Sierra Nevada is limited to topographic lows and protected slope exposures where late-lying snowbanks provide moisture throughout the otherwise dry growing season (Klikoff 1965, Pemble 1970, Chabot and Billings 1972). Consequently, total plant cover, especially the coverage of mesic communities, is lower and more patchy in the Sierra Nevada alpine than in the Rocky Mountains (Chabot and Billings 1972, Billings 1978). In years with high spring snow depth, snow cover further reduces availability of ptarmigan nesting and foraging sites required for breeding (Clarke and Johnson 1990). Deep spring snowpack in the Sierra Nevada inhibits ptarmigan breeding activity (i.e., delays nesting and hatching dates) and reduces breeding success (Clarke and Johnson 1992). In addition, we suggest that breeding density may decline with greater snow depth if birds must search a larger area for snow-free territories. In contrast to Clarke and Johnson (1992), several years of low spring snow depth potentially may affect breeding success by reducing productivity of plant forage. If soil drought occurs during the period following plant emergence, plant growth is curtailed (Billings and Bliss 1959, Klikoff 1965), which may directly or indirectly (i.e., through its effect on insect populations) influence ptarmigan chick growth and development. The effects of low spring snow depth may not be evident for several years, whereas Clarke and Johnson (1992) detected an immediate correlation between high spring snow depth and ptarmigan reproduction.

#### HABITAT ECOLOGY

Ptarmigan distribution in the Sierra Nevada is influenced primarily by distinct vegetation patterns resulting from limited, uneven water distribution. Our analyses indicate that distance to water is an important predictor of suitable ptarmigan habitat in the Sierra Nevada. Plant communities most commonly used by ptarmigan are restricted to the wettest habitats above timberline. In general, these communities occur along borders of lakes and streams and in topographic depressions (Pemble 1970). In addition, ptarmigan select north-facing slopes where snow-

banks, protected from direct solar radiation, provide moisture. In contrast, south-facing slopes, ridges, and exposed summits which are dryer are rarely used by these grouse.

Ptarmigan distribution was most patchy in summer when few snowbanks remained and most alpine habitats were dry. During this season, flocks and hens with broods concentrated use in topographic depressions where mesic vegetation cover was most extensive. As the breeding season progressed into summer, amount of occupied habitat declined from 42% to 25% of the study sites. Moreover, the increase in density following the breeding season was greater than reported for populations occupying large expanses of suitable habitat in the Rocky Mountains (Choate 1963).

White-tailed Ptarmigan have high energy and nutrient requirements due to an unusually high metabolic rate (Johnson 1968, May 1975) and nearly continuous molt. Consequently, they must maximize their use of plant productivity by closely tracking plant phenology. Willow is a nutritious and important food item for White-tailed Ptarmigan (Weeden 1967, May and Braun 1972, May 1975). Previous investigators have suggested that willow availability is the principal factor controlling ptarmigan distribution (Braun and Pattie 1969; Braun 1970, 1971, 1975). Our comparisons of used and unused habitats support the importance of dwarf willow (*Salix anglorum*) for predicting suitable ptarmigan habitat. However, the best predictive models also included cover of ericaceous subshrubs and moss-like plants which may be an indication of the importance of the plant community in general. Similarly, Choate (1963) reported that all habitat samples in his Rocky Mountain study area contained dwarf willow, heath, and mosses.

While vegetation cover features and proximity of water were important discriminators of ptarmigan habitat, most occupied habitats also contained boulders. Boulders were used extensively by ptarmigan as cover; we recorded 66 observations of birds using boulders as roosting or escape cover and 42 observations of flocks using boulders for shelter. White-tailed Ptarmigan are poorly adapted to high ambient temperatures (Johnson 1968, May 1975) and apparently required boulder cover to reduce thermoregulatory energy demands, particularly on hot or windy days. Protection from direct solar radiation was possibly a critical factor in the Sierra Nevada where cloud cover and humidity in summer were

substantially less than in the Rocky Mountains (Major and Bamberg 1967, Chabot and Billings 1972). Despite a frequent association of ptarmigan and boulders, boulder cover was a poor discriminator of used habitats. This was partly due to the abundance of exposed bedrock in our heavily glaciated study areas. Ptarmigan primarily used rock fragments > 30 cm in diameter and fractured rock-shelves.

#### COLONIZATION OF THE SIERRA NEVADA

Dispersal abilities of White-tailed Ptarmigan are well documented (Braun 1969, Schmidt 1969, Braun 1975, Hoffman and Braun 1975, Hoffman and Giesen 1983). The rate of range expansion is controlled primarily by yearling dispersal from wintering areas to breeding territories (Schmidt 1969, Braun 1975, Hoffman and Braun 1975). Yearling males unsuccessful in obtaining territories on natal areas commonly disperse over 10 km in search of a suitable territory; yearling females may traverse longer distances (> 20 km) in search of unmated territorial males (Braun 1975, Hoffman and Braun 1975). Suitable breeding and flocking areas in the Sierra Nevada are limited and widely distributed (pers. observ.). Habitat availability is further reduced during years with deep spring snow depth (Clarke and Johnson 1992). Consequently, ptarmigan must disperse further to colonize new areas in the Sierra Nevada than in alpine systems with more continuous expanses of suitable habitat. Patchy distribution of suitable habitat apparently promotes greater dispersal behavior and more rapid range expansion in Sierra Nevada ptarmigan than in previously studied populations. Strong dispersal behavior by birds occupying a patchy environment is advantageous since it may lead to colonization of unoccupied but favorable habitat patches (Wiens 1976).

Additional transplants of White-tailed Ptarmigan have occurred in Pike's Peak, Colorado; Uinta Mountains, Utah; and Wallowa Mountains, Oregon. Although these alpine systems contain different conditions for ptarmigan colonization and dispersal, all transplants were successful. Pike's Peak is a 39 km<sup>2</sup> "island" of alpine habitat isolated from the nearest alpine area by 60 km of unsuitable habitat (Hoffman and Giesen 1983). The Uinta and Wallowa Mountains are similarly isolated from more extensive alpine systems and contain limited amounts of habitats suitable for colonization by ptarmigan. In com-

parison, the Sierra Nevada is among the largest mountain ranges in North America and contains over 3,000 km<sup>2</sup> of alpine vegetation. The key to these successful transplants is the ability of White-tailed Ptarmigan to exploit patchy alpine environments while sustaining populations at low densities. Furthermore, this species is long-lived ( $\geq 15$  years; Choate 1963) and capable of maintaining populations during occasional years of poor reproduction (Clarke and Johnson 1990).

Range expansion by White-tailed Ptarmigan in the Sierra Nevada indicates that the species is a better colonizer than has been suggested by previous studies of ptarmigan in the Rocky Mountains (Schmidt 1969, Braun 1975, Hoffman and Giesen 1983). Ptarmigan crossed 10- to 20-km wide gaps of unsuitable vegetation and colonized alpine habitats over 100 km from the release sites within 18 years of their liberation. Clarke and Johnson (1990) assessed the ability of White-tailed Ptarmigan to naturally colonize the Sierra Nevada during prehistoric times. Based on paleoecologic evidence and measurements of current treeline in the South Cascade Mountains, they concluded that White-tailed Ptarmigan never successfully colonized the Sierra Nevada. We do not agree that measurement of current tree line is an accurate measure of past alpine habitat distribution. Our data from the Sierra Nevada indicates that ptarmigan are strong dispersers and probably were capable of exploiting isolated patches of suitable alpine habitat as they became available. In early postglacial times, temperatures were considerably cooler and alpine regions with mesic vegetation more extensive than today (Hoffmann and Taber 1967, Chabot and Billings 1972). A southern range extension of White-tailed Ptarmigan in western North America would have been possible at this time. During successive periods of warm climate, alpine areas were greatly restricted, likely isolating or extirpating some southern ptarmigan populations. A period of extreme climatic warming, the Hypsithermal, severely limited mesic alpine vegetation (LaMarche and Mooney 1967) and probably eliminated ptarmigan from the Sierra Nevada if they occurred in the range. This warming trend terminated about 2,900 years ago with the Little Ice Age (Adam 1967), a period which favored development of a sufficient amount of alpine vegetation to support White-tailed Ptarmigan in the Sierra Nevada, as the current introduced population demonstrates. White-tailed Ptarmi-

gan were unable to colonize the Sierra Nevada in recent times because of geographic and ecological barriers to ptarmigan dispersal between the Sierra Nevada and the nearest naturally occurring populations in the North Cascade Mountains (Clarke and Johnson 1990).

Studies of introduced populations may allow inferences about that species in its natural habitat. For example, the ability of White-tailed Ptarmigan to locate suitable habitat, disperse, and colonize habitat, as well as to exploit a patchy environment, widens our perceptions of this bird that were not apparent from studies conducted in its native range. The adaptability demonstrated by White-tailed Ptarmigan in the Sierra Nevada also suggests that conservation and restoration of the species could be enhanced by protecting critical zones which are distributed throughout key parts of degraded range.

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APPENDIX. Habitat variables measured on 0.02-ha plots. Cover values were measured along two 15-m line intercepts that crossed at plot center.

Variable	Explanation
Elevation	Elevation above sea level measured with an altimeter or estimated from a topographic map.
Slope	Slope angle measured in degrees with a clinometer.
Aspect	General slope orientation measured to nearest 10 degrees with hand-held compass.
Distance to snow	Meters to nearest snow measured with a tape or estimated with range-finder.
Distance to water	Meters to nearest water measured with a tape or estimated with range-finder.
Distance to shrub	Meters to nearest shrub > 30 cm tall measured with a tape or estimated with range-finder.
Distance to willow shrub	Meters to nearest willow ( <i>Salix</i> ) shrub > 30 cm tall measured with a tape or estimated with range-finder.
Maximum shrub height	Height (cm) of tallest shrub in plot.
Minimum shrub height	Height (cm) of shortest shrub in plot.
Percent soil cover	Average percentage of line intercepts covered by mineral soil.
Percent gravel cover	Average percentage of line intercepts covered by stones < 10 cm in diameter.
Percent rock cover	Average percentage of line intercepts covered by stones 10–30 cm in diameter.
Percent boulder cover	Average percentage of line intercepts covered by bedrock and stones > 30 cm in diameter.
Percent snow cover	Average percentage of line intercepts covered by snow.
Percent shrub cover	Average percentage of line intercepts covered by shrubs > 30 cm tall.
Percent subshrub cover	Average percentage of line intercepts covered by ericaceous shrubs ≤ 30 cm tall.
Percent dwarf willow cover	Average percentage of line intercepts covered by dwarf willow ( <i>Salix anglorum</i> and <i>S. nivalis</i> ).
Percent turf cover	Average percentage of line intercepts covered by graminoids.
Percent forb cover	Average percentage of line intercepts covered by perennial forbs.
Percent herb cover	Average percentage of line intercepts covered by sum of turf and forb cover.
Percent moss cover	Average percentage of line intercepts covered by moss and moss-like plants.