

# RICHNESS OF BREEDING BIRD SPECIES IN MIXED-CONIFER FORESTS OF THE SIERRA NEVADA, CALIFORNIA

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**ABSTRACT.**—We report relationships between bird species richness (BSR) and physical and biotic attributes of 51 sites in mixed-conifer forests of the Sierra Nevada of California. Three sites were in uncut forest and one was in a permanent shrubfield. The remaining 47 had been logged one to several times in the previous 10 years. Mean BSR in "unforested" sites ( $n = 20$ ) was 7.6 for 1978 and 1979, combined; that in "forested" sites ( $n = 31$ ) was 20.1. On 6-ha subplots in the forested sites, BSR averaged 16.7 breeding species in 1978 and 16.5 in 1979. Total crown volume was the best single predictor of BSR in each year separately and in the pooled data set for both years. Total crown volume accounted for 76% of the variance in BSR in the pooled data. Total crown volume and site size made up the best 2-variable subset for predicting BSR in each year separately and in both years combined. Addition of 3 and 4 variables to the predictor subsets accounted for little additional variance in all cases. The simple correlation between foliage height diversity (FHD) and BSR was significant, but when the covariance of FHD with other independent variables, especially total crown volume, was controlled through partial correlation, FHD was among the least useful variables for predicting BSR. BSR was less well predicted on forested and unforested sites separately, with 2-, 3-, and 4-variable subsets accounting for only 38–61% of the variation, compared with 76–84% for all sites combined. Received 18 March 1988, accepted 16 January 1989.

In a comparative study of avian assemblages in various habitats in North America, James and Rathbun (1981) reported that pure stands of coniferous forest had the lowest bird species richness (BSR) when data were standardized to the number of species expected in a 6-ha area. But their study was not conclusive for conifer forests, because it included data from only three such forest types. Further investigation of this trend is appropriate. In addition, relatively few studies have explored potential predictors of BSR in western coniferous forests (e.g. see Balda 1969; Szaro and Balda 1979; Beedy 1981, 1982).

MacArthur and MacArthur (1961) pioneered efforts to identify habitat variables that might explain differences among assemblages of bird species in different habitats. They first showed that BSD was closely correlated with foliage height diversity (FHD). Many subsequent studies found a similar relationship, but others did not (reviewed by Larson 1981). Other attributes of vegetation structure have been found to pre-

dict BSR or BSD in certain circumstances. These include foliage volume (Karr and Roth 1971), percent vegetation cover (Karr 1968, Karr and Roth 1971, Willson 1974), percent canopy cover (Crawford et al. 1981, Wiens and Rotenberry 1981, Beedy 1982, James and Wamer 1982), patchiness of shrub distribution (Roth 1976), and tree-diameter (DBH) diversity (Young 1977). Sizes of vegetation patches (habitat islands) can also be used to predict BSD and BSR (e.g. Beals 1960, Galli et al. 1976, Gavareski 1976, Whitcomb et al. 1977, Stauffer and Best 1980, Whitcomb et al. 1981, Temple 1986). Finally, many bird species exhibit strong associations with special habitat components that can influence BSD and BSR. These include plant taxa (e.g. Balda 1969, Holmes et al. 1979, Holmes and Robinson 1981, Wiens and Rotenberry 1981, Rice et al. 1984, Robinson and Holmes 1984, Rotenberry 1985, Sherry and Holmes 1985, Terborgh 1985), tree species richness or diversity (Winternitz 1976, Young 1977, James and Wamer 1982), snags (Raphael 1981, Davis et al. 1983 and many papers therein), or a specific food source (e.g. nectar; Wolf 1975, Feinsinger 1976, Ford and Paton 1985, Terborgh 1985).

Beyond the apparent general consensus that

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habitat attributes can be used to predict the richness and diversity of bird assemblages, many inconsistencies remain unexplained. Some apparently result from different methods used to measure vegetation structure, from sampling a narrow range of habitats (see Lovejoy 1974, Willson 1974, Karr 1980), or from failing to test for nonlinear relationships (see Meents et al. 1983, Rotenberry 1986). Others are related to measuring only some components of vegetation structure (Rice et al. 1984, Rotenberry 1985) or to sampling too few sites to permit a valid, comprehensive analysis of the components measured (Karr 1980). Still others can be explained as responses to real differences in major structural attributes among habitat types such as grasslands, shrublands, and forests (Beecher 1942, Karr and Roth 1971, Willson 1974, Erdelen 1984). Finally, habitat features not traditionally measured, such as microclimates, are likely to influence bird assemblages (Karr 1980, Karr and Freemark 1983). We thus should expect some puzzling relationships when our attention is focused only on attributes of vegetation.

Many ecologists have questioned the use of species diversity as a measure of animal assemblages (e.g. Tramer 1969, Hurlbert 1971, James and Rathbun 1981, Verner 1984, Rotenberry 1985). Species richness, a component of species diversity, is more easily and more accurately measured than species diversity. It is highly correlated with species diversity (Tramer 1969), and it can be interpreted clearly. Although we computed BSD indices in this study with the Shannon-Wiener index ( $H' = -\sum p_i \ln p_i$ , where  $p_i$  was the proportion of observations of the  $i$ th species), BSD significantly correlated with BSR in each year and for both years combined ( $r = 0.93, 0.94, \text{ and } 0.94$ ). Consequently, we have confined our analysis to BSR.

Our primary objectives were to compare BSR in mixed-conifer forests of the west-central Sierra Nevada with predictions from the more extensive study of James and Rathbun (1981), and to determine the best predictor(s) of BSR in those forests.

#### STUDY AREAS

Fifty-one sites were sampled during the breeding seasons of 1978 and 1979 in the mixed-conifer forest zone of the Sierra National Forest, on the west slope of the Sierra Nevada, Fresno and Madera counties,



Fig. 1. The Sierra National Forest in California in relation to adjacent Yosemite and Kings Canyon national parks; general locations of study areas indicated by crosshatching. The number of study sites in each area, from top to bottom, was 18, 9, 8, and 16, respectively. The location of the weather station near Wishon Reservoir is marked by an asterisk.

California (Fig. 1). Three sites were in uncut forest fragments. Another was a "natural" shrubfield on which trees have not grown for at least 100 yr. Forty-seven sites had been subjected to various logging treatments, from clearcutting (all or nearly all trees removed) to sanitation cutting (<20% of the overstory removed). In addition, logged sites had been subjected to a variety of follow-up treatments such as shrub removal, slash burning, removal of pole-sized trees, thinning, and planting of seedlings. Jeffrey pine (*Pinus jeffreyi*) was used most often for restocking, generally in grids with about 2.5-m spacing. The "natural" shrubfield and all logged sites were bounded by forest habitat. The shrubfield site and 19 clearcut sites together made up a subset referred to as the "unforested" sites (regenerating trees <3 m tall; few or no trees remaining from previous forest stand). The remaining 31 sites made up the "forested" subset. Forested sites had >74 m<sup>3</sup>/100 m<sup>2</sup> of tree crown volume; all unforested sites except one had <44 m<sup>3</sup>/100 m<sup>2</sup> of tree crown volume. One unforested site, a dense plantation of Jeffrey pines 2-3 m tall, had 105 m<sup>3</sup>/100 m<sup>2</sup> of tree crown volume (1 forested site had less).

Land configuration in the area ranged from deep granitic canyons and prominent granite outcroppings and domes to dense coniferous forests with wet meadows. Prominent tree species were sugar pine (*Pinus lambertiana*), Jeffrey pine, ponderosa pine (*P. ponderosa*), lodgepole pine (*P. contorta*), white fir (*Abies concolor*), red fir (*A. magnifica*), and incense-cedar (*Calo-*

*cedrus decurrens*), with some California black oak (*Quercus kelloggii*) at lower elevations. Willows (*Salix* spp.) and white alders (*Alnus rhombifolia*) occurred along streams and some wet meadows. Canopy height occasionally exceeded 50 m in sites with mature trees. Shrubs included mountain whitethorn (*Ceanothus cordulatus*), gooseberries (*Ribes* spp.), manzanita (*Arctostaphylos* spp.), and scattered bush chinquapin (*Castanopsis sempervirens*), and kit-kit-dizze or "mountain misery" (*Chamaebatia foliolosa*). Vegetation occurred in various degrees of patchiness on the different sites.

Collectively the sites exhibited values of habitat attributes distributed along gradients of size (1–80 ha), elevation (1,650–2,300 m), snag density, tree species composition, and vegetation structure. Sizes of logged sites were determined from the outer boundaries of timber sales prescribed for each site, as shown on sale maps prepared by the Forest Service, U.S. Department of Agriculture. Sizes of unlogged sites were measured from aerial photographs, using ecotones of the stand with surrounding habitats, such as meadows, clearcuts, and shrubfields.

Precipitation at nearby Wishon Reservoir (Fig. 1) is seasonal, with most falling as snow in winter. During the winter of 1977–1978, 7.3 m of snow fell (near the maximum record), with a maximum snowpack of 3.3 m. Study areas with north-facing slopes had scattered patches of snow until early July. During the winter of 1978–1979, 6.7 m of snow fell at Wishon Reservoir, with a maximum snowpack of 2.1 m, and by mid-June all snow had melted from all study sites.

## METHODS

### BIRDS

All birds were counted by Larson at 1 station/site, located randomly in each site but at least 50 m from any site boundary, where possible. A 10-min count began 1 min after the observer reached the counting point, to permit settling of birds disturbed by the arrival. Counts were made on 7 days at each site in each of 2 breeding seasons, 1978 and 1979 (mid-May–mid-July). We sampled 7–10 sites daily from ca. ½ to ca. 4½ h after sunrise. Sampling time at each site was rotated over the 7 count days to standardize potential bias from counting at different times of day.

As nearly as we could determine, every bird included in the analysis was a breeding adult that nested within site boundaries. We did not record birds detected at the edges of sites or beyond.

Records of all birds detected within stand (site) boundaries, regardless of their distance from the observer, were used to identify the best predictors of BSR in these forests. However, to compare BSR at our sites with those reported by James and Rathbun (1981), we used only those breeding species detected within a radius of 138 m (6 ha) of the counting point in the

forested sites, summing species over the 7 visits to each site each year.

### HABITATS

We used circular-plot (James and Shugart 1970), point-centered quarter (Cottam and Curtis 1956), and point-intercept methods to sample vegetation. A 0.05-ha circular plot (12.62-m radius) was centered at each bird-counting point, and 4 other plots were placed 50 m from each counting point along each cardinal compass direction. Those 5 plots were sufficient to sample sites with few or no trees (R. C. Anderson pers. comm.). Five plots were selected similarly and sampled in forested sites, but up to 5 additional plots were sampled, as needed, to reduce to <10% the ratio of the standard error to the mean of the number of trees/quarter-circle (our criterion for a sufficient sample size). The additional plots were located 100 m from the counting point along the 4 cardinal directions, if they fell within the site. Otherwise, they were placed randomly within 100 m of the counting point. Some sites were too small or irregularly shaped to permit this sampling pattern. In these, 3–4 nonoverlapping, 0.05-ha plots were located on the long axis of the site.

In each circular plot, for each tree and shrub, we recorded species, geometric shape of crown (ellipsoid, paraboloid, cylinder, or cone), percentage of geometric shape filled by the crown, diameter of crown dripline in 2 directions at right angles to each other, height of lowest foliage, maximum height, and whether trees were alive or dead (i.e. snags). Crown characteristics were recorded only for those portions of crowns within the plot, as determined by visual extrapolation of the plot boundaries vertically. Diameter at breast height (DBH) of each tree was recorded for all trees with 50% or more of the trunk diameter within the plot. Basal area of trees was determined from these measurements, not with a basal-area prism. Ground cover (rock, soil, litter, forb, or grass) was recorded at 100 points regularly spaced 1 m apart in a square grid centered on the plot.

At each site, a grid with an interpoint distance of 20 m and including 50–100 points (depending on the size and shape of the site) was centered on the counting point. At these points, distances to the nearest tree and shrub in each quarter-circle were recorded (point-centered quarter method), unless none occurred out to the limit of the site. We estimated percent shrub and tree cover for each site by recording whether a vertical line extrapolated above each of these points intersected vegetation in the shrub or canopy layers.

Values of independent (habitat) variables are given in the Appendix, for unforested and forested sites separately. We measured aspect, slope, and distance to nearest water, but excluded them from further

TABLE 1. Variables, their codes, and units used in this analysis (see text for details).

Variables	Codes <sup>1</sup>	Units
1. Bird species richness	BSR	<i>n</i>
2. Foliage height diversity	FHD	$H' = -\sum p_i \ln p_i$
3. Tree species diversity	TSD	$H' = -\sum p_i \ln p_i$
4. Tree diameter diversity	DBHD	$H' = -\sum p_i \ln p_i$
5. Tree distance diversity	TDD	$H' = -\sum p_i \ln p_i$
6. Total crown volume	CROVOL	m <sup>3</sup> /100 m <sup>2</sup>
7. Tree crown volume	TREVOL	m <sup>3</sup> /100 m <sup>2</sup>
8. Shrub crown volume	SHBVOL	m <sup>3</sup> /100 m <sup>2</sup>
9. Basal area	BASAR	m <sup>2</sup> /ha
10. Tree density	TREDEN	stems/ha
11. Snag density	SNGDEN	stems/ha
12. Tree patchiness	TREPCD	$D = 100SD/\bar{x}$
13. Shrub patchiness	SHBPCH	$D = 100SD/\bar{x}$
14. Percent shrub cover	SHBCOV	%
15. Percent canopy cover	TRECOV	%
16. Percent litter	LITTER	%
17. Size of study site	SIZE	ha
18. Elevation	ELEV	m

<sup>1</sup> These codes identify variables shown in Tables 3-7.

analysis, however, because they showed no consistent correlations with BSR. The same was true of all measures of ground cover except litter.

#### DATA ANALYSIS

BSR was the number of breeding species detected in each site each year, summed over the 7 visits. All indices of vegetation diversity used the Shannon-Wiener information index ( $H' = -\sum p_i \ln p_i$ ). Tree species diversity was computed with  $p_i$  representing the relative density of each species. Tree DBH diversity was computed by letting  $p_i$  represent the proportion of trees with DBHs in the  $i$ th diameter class, based on 10-cm size classes. Tree distance diversity was computed using 5-m intervals for distance classes;  $p_i$  was the proportion of point-to-tree distances in the  $i$ th distance class. FHD was computed using 5 height intervals (0-2 m, 2-5 m, 5-15 m, 15-30 m, and 30-70 m) and 14 height intervals (0-1 m, 1-2 m, 2-5 m, then 5-m increments up to 50 m, and 10-m increments above 50 m). Within each layer, we computed the volumes of shrub and tree crowns, so  $p_i$  was approximately the proportion of the total crown volume of a site in the  $i$ th layer. Results did not differ significantly between the two measures. We report those using 14 height intervals because they gave slightly higher correlations between BSR and FHD.

We used crown volume as an index to foliage volume, as others have done (e.g. Balda 1969). Crown volume was computed from data on the geometric shapes of all trees and shrubs, their diameters in two directions at right angles to each other, their heights to first foliage, and their maximum heights. Substantial gaps in tree or shrub crowns were subtracted as

a percentage of the geometric shape missing. We did not correct for differences in foliage density among the crowns of different species of shrubs and trees. Tree crown volume included all foliage >2 m high, and shrub crown volume included all foliage <2 m. This convention was adopted to reflect our perceptions of the foraging responses of birds to layers of vegetation, even though it grouped some tree foliage within shrub volume. Formulas for the volumes of crowns, based on geometric shapes, were adapted from Mawson et al. (1976).

Shrub patchiness (heterogeneity of shrub distances) was computed as the coefficient of variation of distances from each of the 50-100 points (on the grid centered on the counting point) to the centers of shrub clumps in each quarter circle. Tree patchiness (heterogeneity of tree distances) was similarly computed using point-to-tree distances.

Relationships among BSR and the 17 independent variables (Table 1) were examined with simple and partial correlations and simple and all-possible-subsets multiple regression (BMDP-9R, Dixon and Brown 1977) for each year separately and for both years combined. The thrust of this study was exploratory. We included significance values, and used several types of analyses, to give some feeling for the internal consistency of the analyses, not to claim confirming evidence.

Several relationships between BSR and various independent variables were nonlinear. To make the relationships more linear, natural log transformations were performed on the values of total crown volume, tree and shrub crown volume, basal area, site size, snag density, and tree density. Arcsine square-root transformations were performed on percent tree and

shrub cover and percent litter. We examined the residuals from linear models that used transformations, and they appeared to have normal distributions. Regressions were rerun with transformed variables and the results of the latter analysis are reported.

Because all subsets among the top 10 in each group (2-, 3-, and 4-variable subsets) accounted for nearly the same amount of variance in the dependent variables, we did not necessarily accept the "best" in each group as selected by the model. Instead, we used the subset that consisted of the most frequent variables in the top 10 subsets in each group. In case of a tie, we chose the variable that accounted for more variance when taken together with the other variables chosen in the subset. Finally, we used partial correlations to examine the remaining correlation structure after the effects of given independent variables were removed. Thus, conclusions about the "best" predictors of BSR in our study sites depended on the consistent appearance of independent variables as good predictors in these various analyses. Unless otherwise indicated, we have used an alpha level of 0.05.

## RESULTS

### BIRD SPECIES RICHNESS

Fifty-two species of birds (lumping Dusky and Hammond's flycatchers) were detected as actual or probable breeders on the 51 study sites (Table 2). Most species (see Table 2 for scientific names) were uncommon: 22 were detected on 5 or fewer sites, and Sharp-shinned, Cooper's, and Red-tailed hawks, American Kestrels, Blue Grouse, Spotted Owls, Common Nighthawks, Winter Wrens, Swainson's Thrushes, and Evening Grosbeaks were each detected at only one site. Dark-eyed Juncos were most common (49 sites), followed by Mountain Chickadees (44 sites), the 2 *Empidonax* flycatchers (Hammond's and Dusky) together (40 sites), and White-headed Woodpeckers (40 sites). The high frequency of White-headed Woodpeckers was unexpected, because many sites had few or no trees or snags. However, White-headed and Hairy woodpeckers occasionally excavated nest cavities in stumps left in clearcuts. Those nest cavities also were used secondarily by Mountain Chickadees and Mountain Bluebirds.

The total count of all individuals of all species in 1978 (2,941) was significantly less than that (3,816) in 1979 (Wilcoxon signed-ranks test,  $P < 0.0001$ ), although Wilcoxon signed-ranks tests showed no significant difference in BSR between years. As reported earlier (Verner 1980),

species richness was lowest in clearcut sites and increased with development of shrub and tree layers to a peak in stands of mature forests with crown cover ca. 45–55%. It then declined slightly on sites where little or no timber had been removed and canopy cover exceeded 65%.

Considering all breeding species, mean BSR on the unforested sites for 1978 and 1979 combined was 7.6 (SD = 3.15; range = 0–13). The site with no breeding species ranked last among the 20 unforested sites in shrub crown volume ( $0.01 \text{ m}^3/100 \text{ m}^2$ ), fifteenth in tree crown volume ( $3.0 \text{ m}^3/100 \text{ m}^2$ ), and last in size (0.5 ha). It had been logged recently and was primarily barren ground. The site with 13 species ranked first among unforested sites in tree crown volume ( $104.9 \text{ m}^3/100 \text{ m}^2$ ), third in shrub crown volume ( $39.5 \text{ m}^3/100 \text{ m}^2$ ), and tied for fourteenth in size (4.0 ha). It was a well-developed pine plantation with most trees nearly 3 m tall.

Only the Mountain Bluebird nested exclusively on unforested sites, and no species nested primarily on them (Table 2). BSR on the unforested sites increased with increasing shrub and tree crown volumes. The relationship to shrub cover is best seen (Fig. 2) for obligate shrub-nesting species: Yellow and MacGillivray's warblers, Green-tailed and Rufous-sided towhees, and Fox Sparrows. BSR of this assemblage was correlated with percent shrub cover ( $r = 0.77$ ,  $P < 0.001$ ,  $n = 51$ ), and consistently 3 or more of these species nested on a site only after shrub cover reached about 20% (Fig. 2). Only 2 sites with <20% shrub cover had 3 obligate shrub-nesting species, and both adjoined large shrub-fields.

Considering all breeding species, mean BSR on the forested sites (data from 1978 and 1979 pooled) was 20.1 (SD = 4.40; range = 9–28), significantly greater than that on the unforested sites ( $t = 10.8$ ;  $P < 0.001$ ). The site with only 9 breeding species ranked 17th among the 31 forested sites in tree crown volume ( $450.6 \text{ m}^3/100 \text{ m}^2$ ), 29th in shrub crown volume ( $0.45 \text{ m}^3/100 \text{ m}^2$ ), and last in size (1.0 ha). The site with 28 breeding species ranked 5th in tree crown volume ( $933.8 \text{ m}^3/100 \text{ m}^2$ ), 14th in shrub crown volume ( $3.1 \text{ m}^3/100 \text{ m}^2$ ), and 5th in size (30.0 ha).

Twenty-five species nested exclusively and another 9 nested primarily on forested sites (Table 2). Ten of 20 species (other than cavity nesters) that nested exclusively in trees—Olive-

TABLE 2. Total count of species believed to have nested on one or more of the 51 sites in 1978, 1979, or both (number of sites where detected is given in parentheses).

Species	Count	Species	Count
Sharp-shinned Hawk <sup>1</sup> ( <i>Accipiter striatus</i> )	1 (1)	Golden-crowned Kinglet <sup>1</sup> ( <i>Regulus satrapa</i> )	153 (21)
Cooper's Hawk <sup>1</sup> ( <i>Accipiter cooperii</i> )	1 (1)	Western Bluebird ( <i>Sialia mexicana</i> )	10 (2)
Northern Goshawk <sup>1</sup> ( <i>Accipiter gentilis</i> )	2 (1)	Mountain Bluebird <sup>3</sup> ( <i>Sialia currucoides</i> )	58 (9)
Red-tailed Hawk <sup>1</sup> ( <i>Buteo jamaicensis</i> )	1 (1)	Townsend's Solitaire <sup>2</sup> ( <i>Myadestes townsendi</i> )	83 (24)
American Kestrel <sup>1</sup> ( <i>Falco sparverius</i> )	1 (1)	Hermit Thrush <sup>2</sup> ( <i>Catharus guttatus</i> )	102 (16)
Blue Grouse <sup>1</sup> ( <i>Dendragapus obscurus</i> )	1 (1)	American Robin ( <i>Turdus migratorius</i> )	222 (39)
Mountain Quail ( <i>Oreortyx pictus</i> )	33 (14)	Solitary Vireo <sup>1</sup> ( <i>Vireo solitarius</i> )	7 (4)
Band-tailed Pigeon <sup>1</sup> ( <i>Columba fasciata</i> )	3 (3)	Warbling Vireo <sup>1</sup> ( <i>Vireo gilvus</i> )	173 (23)
Spotted Owl <sup>1</sup> ( <i>Strix occidentalis</i> )	1 (1)	Nashville Warbler ( <i>Vermivora ruficapilla</i> )	10 (6)
Common Nighthawk <sup>1</sup> ( <i>Chordeiles minor</i> )	4 (1)	Yellow Warbler ( <i>Dendroica petechia</i> )	61 (5)
Calliope Hummingbird ( <i>Stellula calliope</i> )	29 (11)	Yellow-rumped Warbler <sup>2</sup> ( <i>Dendroica coronata</i> )	370 (30)
Red-breasted Sapsucker <sup>3</sup> ( <i>Sphyrapicus ruber</i> )	38 (16)	Hermit Warbler <sup>1</sup> ( <i>Dendroica occidentalis</i> )	323 (26)
Williamson's Sapsucker <sup>1</sup> ( <i>Sphyrapicus thyroideus</i> )	7 (2)	MacGillivray's Warbler ( <i>Oporornis tolmiei</i> )	133 (19)
Hairy Woodpecker ( <i>Picoides villosus</i> )	33 (14)	Wilson's Warbler <sup>1</sup> ( <i>Wilsonia pusilla</i> )	41 (5)
White-headed Woodpecker ( <i>Picoides albolarvatus</i> )	188 (40)	Western Tanager <sup>1</sup> ( <i>Piranga ludoviciana</i> )	390 (30)
Northern Flicker <sup>2</sup> ( <i>Colaptes auratus</i> )	28 (12)	Black-headed Grosbeak <sup>1</sup> ( <i>Pheucticus melanocephalus</i> )	13 (6)
Pileated Woodpecker <sup>1</sup> ( <i>Dryocopus pileatus</i> )	10 (8)	Green-tailed Towhee ( <i>Pipilo chlorurus</i> )	204 (16)
Olive-sided Flycatcher <sup>2</sup> ( <i>Contopus borealis</i> )	87 (20)	Rufous-sided Towhee ( <i>Pipilo erythrophthalmus</i> )	14 (3)
Western Wood-Pewee <sup>2</sup> ( <i>Contopus sordidulus</i> )	247 (30)	Chipping Sparrow ( <i>Spizella passerina</i> )	181 (21)
Hammond's & Dusky flycatchers ( <i>Empidonax hammondi</i> & <i>E. oberholseri</i> )	422 (40)	Fox Sparrow ( <i>Passerella iliaca</i> )	666 (37)
Steller's Jay <sup>2</sup> ( <i>Cyanocitta stelleri</i> )	207 (29)	Dark-eyed Junco ( <i>Junco hyemalis</i> )	963 (49)
Common Raven <sup>1</sup> ( <i>Corvus corax</i> )	3 (3)	Brown-headed Cowbird ( <i>Molothrus ater</i> )	19 (9)
Mountain Chickadee ( <i>Parus gambeli</i> )	504 (44)	Pine Grosbeak <sup>1</sup> ( <i>Pinicola enucleator</i> )	3 (2)
Red-breasted Nuthatch <sup>1</sup> ( <i>Sitta canadensis</i> )	303 (28)	Purple Finch <sup>1</sup> ( <i>Carpodacus purpureus</i> )	19 (5)
Brown Creeper <sup>1</sup> ( <i>Certhia americana</i> )	90 (19)	Cassin's Finch <sup>2</sup> ( <i>Carpodacus cassinii</i> )	167 (25)
Winter Wren <sup>1</sup> ( <i>Troglodytes troglodytes</i> )	2 (1)	Evening Grosbeak <sup>1</sup> ( <i>Coccothraustes vespertinus</i> )	2 (1)

<sup>1</sup> Probably nested exclusively on forested sites.

<sup>2</sup> Nested primarily on forested sites (75% of nesting sites were forested, weighting the number of forested sites on an equivalent basis with the number of unforested sites).

<sup>3</sup> Probably nested exclusively on unforested sites.

sided Flycatcher, Western Wood-Pewee, Steller's Jay, Brown Creeper, Golden-crowned Kinglet, Warbling Vireo, Yellow-rumped and Hermit warblers, Western Tanager, and Cassin's Finch—were found regularly on sites with relatively little tree cover. The data suggest a threshold effect of tree crown volume on BSR of these obligate tree nesters (Fig. 3). The number of such species increased from 1 to 10 over a gradient in tree crown volume from 33 to 281 m<sup>3</sup>/100 m<sup>2</sup> ( $r = 0.86, P < 0.001$ ), but the number failed to increase significantly over the gradient from 281 to 1,388 m<sup>3</sup>/100 m<sup>2</sup> ( $r = 0.34, P > 0.10$ ).

Based on records only from the 6-ha subplots centered at each counting point in the 31 forested sites, BSR averaged 16.7 (SE = 0.75, range = 8–24) in 1978 and 16.5 (SE = 0.70, range = 7–24) in 1979. These results represent an effort of 70 min/subplot.

#### PREDICTING BSR OVER ALL SITES

*Simple correlations and regressions.*—All independent variables except shrub patchiness,

shrub crown volume, and percent shrub cover were significantly correlated with BSR in each year separately and in both years combined. Most independent variables, however, were intercorrelated: 96 of 136 possible correlations were significant. Total crown volume was the best single predictor of BSR in each year separately and both years combined (Fig. 4). In fact, the top 3 single predictors of BSR were the same in each data set (Table 3).

*All-possible-subsets multiple regressions.*—As with simple correlations, all-possible-subsets multiple regressions revealed many examples of independent variables that were nearly equivalent as predictors of BSR. The “best” 2-, 3-, and 4-variable subsets chosen by the model were typically little better than the second- or third-best subsets, or even than the tenth-best (Table 4). The greatest difference in adjusted  $R^2$  values between the best and the tenth-best subsets in any data set was only 0.06, and in some cases it was less than 0.01.

Total crown volume and site size appeared in all subsets (Table 5). Addition of a second vari-

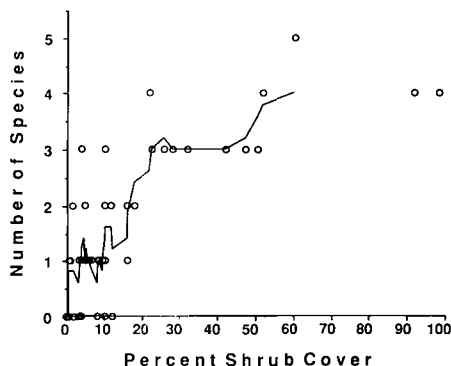


Fig. 2. Relationship between percent shrub cover and the number of obligate shrub-nesting species on all 51 sites; data pooled for 1978 and 1979. The curve connects 5-site running averages of the number of shrub-nesting species.

able increased adjusted  $R^2$  an average of 0.05, from 0.73 to 0.78 (cf. Tables 3 and 5); addition of a third increased adjusted  $R^2$  an average of 0.01 above that of 2-variable subsets; and addition of a fourth increased adjusted  $R^2$  an average of 0.03 above that of 3-variable subsets. The variance explained by these subsets was near the maximum possible. For example, the maximum  $R^2$  possible for BSR in both years combined, using any linear combination of the 17 independent variables, was 0.88. Actual adjusted  $R^2$  would necessarily be less than that: 0.76, 0.79, 0.80, and 0.84 for our best 1-, 2-, 3-, and 4-variable subsets, respectively.

Because our method of sampling birds did not include the full extent of the larger sites (up to 80 ha), we performed the same analyses with site size attenuated at 40 ha and 20 ha. Results in both cases were virtually the same as with the unattenuated sample.

Total crown volume was among the most time-consuming independent variables to measure. However, basal area was the best predictor of total crown volume (adjusted  $R^2 = 0.85$ ), and that combined with percent shrub cover was the best 2-variable subset (adjusted  $R^2 = 0.95$ ). Consequently, basal area and percent shrub cover predicted BSR about as well as total crown volume, and they were much less time-consuming to measure. Replacing total crown volume with basal area in the 2-variable subsets resulted in an average loss of only 0.02 in adjusted  $R^2$  (e.g. see Fig. 5). Similarly, we lost an average of 0.03 in adjusted  $R^2$  when we used basal area,

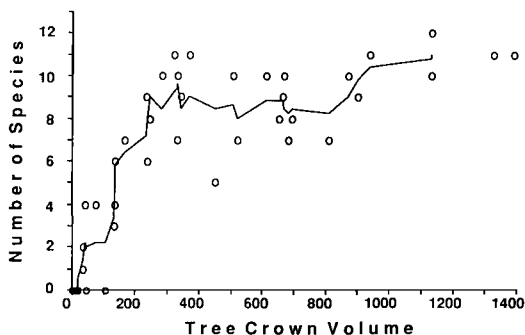


Fig. 3. Relationship between tree crown volume ( $\text{m}^3/100 \text{ m}^2$ ; untransformed values) and the number of obligate tree-nesting species on all 51 sites; data pooled for 1978 and 1979. The curve connects 5-site running averages of the number of tree-nesting species.

percent shrub cover, and site size in place of our "best" 3-variable subsets for predicting BSR in the 3 data sets.

*Partial correlations.*—Results from all-possible-subsets multiple regressions were generally supported by partial correlation analyses. When we controlled for variation in BSR attributable to total crown volume, the significant correlations between BSR and most other independent variables disappeared. Only partial correlations of BSR with site size and tree species diversity were significant (Table 6). When the variation in BSR attributable to FHD was removed, the correlation between BSR and total crown volume dropped only from 0.85 to 0.62, and the

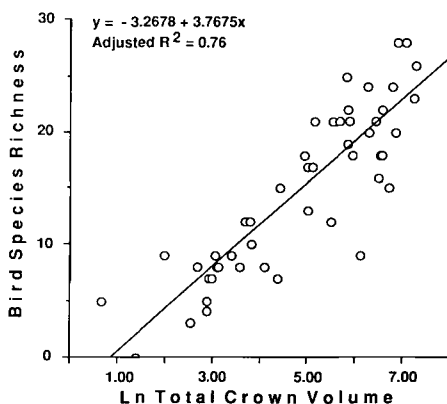


Fig. 4. The relationship between BSR and the natural log of total crown volume ( $\text{m}^3/100 \text{ m}^2$ ) over all sites for both years combined.

TABLE 3. Top 3 single predictors of BSR over all sites. Adjusted  $R^2$  shown in parentheses; codes of predictor variables are from Table 1.

1978		1979		1978 + 1979	
CROVOL	(0.72)	CROVOL	(0.73)	CROVOL	(0.76)
TREVOL	(0.68)	TREVOL	(0.67)	TREVOL	(0.71)
BASAR	(0.68)	BASAR	(0.66)	BASAR	(0.71)

latter coefficient was still significant ( $P < 0.001$ ). Thus partial correlation analysis suggested that basal area, FHD, percent tree cover, DBH diversity, tree patchiness, and shrub patchiness may all be correlated with BSR primarily through their covariance with total crown volume.

Partial correlation analysis in which variation due to site size was removed had little effect on the relationship between BSR and the independent variables with which it had significant simple correlations (Table 6). Similarly, using partial correlations in which the effects of all variables but one were removed, site size had the highest partial correlation with BSR in each data set. These results indicate that site size was

least affected by covariance with other independent variables, but that total crown volume covaried with several others. Interestingly, the partial correlation of FHD with BSR was among the smallest when effects of all other variables were removed.

#### PREDICTING BSR ON UNFORESTED SITES

The same procedures used to analyze all sites together were used to analyze the 20 unforested and 31 forested sites separately, but only for the pooled data sets for 1978 and 1979. Variations in BSR were not so effectively explained when the forested and unforested sites were analyzed separately as when all sites were treated to-

TABLE 4. Comparison among yearly samples of the best 2-, 3-, and 4-variable subsets for predicting BSR over all sites (predictor codes as in Table 1). The best subset chosen by all-possible-subsets multiple regression (BMDP-9R) is shown for each year separately and both years combined; when the best differed between years, the rank and adjusted  $R^2$  of the corresponding subset is given for the other year(s).

1978			1979			1978 + 1979		
Subset	$R^2$	Rank	Subset	$R^2$	Rank	Subset	$R^2$	Rank
<b>Two-variable subsets</b>								
BASAR SIZE	(0.76)	First	BASAR SIZE	(0.75)	Second	BASAR SIZE	(0.78)	Second
CROVOL SIZE	(0.76)	Second	CROVOL SIZE	(0.75)	First	CROVOL SIZE	(0.79)	First
<b>Three-variable subsets</b>								
BASAR SIZE TRECOV	(0.81)	First	BASAR SIZE TRECOV	(0.77)	Second	BASAR SIZE TRECOV	(0.81)	First
CROVOL SIZE LITTER	(0.77)	Tenth	CROVOL SIZE LITTER	(0.79)	First	CROVOL SIZE LITTER	(0.80)	Seventh
<b>Four-variable subsets</b>								
BASAR SIZE TRECOV ELEV	(0.82)	First	BASAR SIZE TRECOV ELEV	(0.80)	Second	BASAR SIZE TRECOV ELEV	(0.84)	First
CROVOL SIZE BASAR TRECOV	(0.81)	Third	CROVOL SIZE BASAR TRECOV	(0.81)	First	CROVOL SIZE BASAR TRECOV	(0.84)	Second



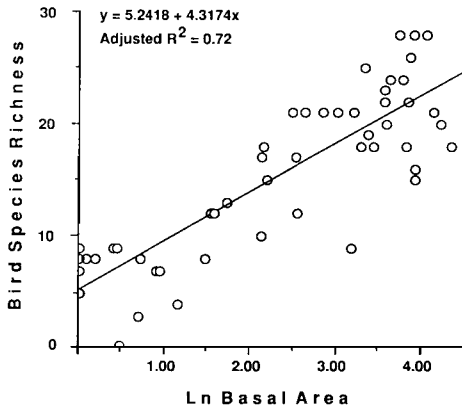


Fig. 5. The relationship between BSR and the natural log of basal area ( $\text{m}^2/\text{ha}$ ) over all sites for both years combined.

gether. Fourteen independent variables were significantly correlated with BSR in the all-sites analysis, but only 4 were on the forested sites: total crown volume ( $r = 0.64$ ;  $0.01 > P > 0.001$ ), shrub crown volume ( $r = 0.48$ ;  $0.01 > P > 0.001$ ), shrub patchiness ( $r = 0.48$ ;  $0.01 > P > 0.001$ ), and site size ( $r = 0.46$ ;  $0.05 > P > 0.01$ ). When effects of total crown volume and shrub crown volume were controlled by partial correlation, these relationships were unchanged. Multiple regression analysis showed that measures of crown volume accounted for the highest percentage of the variance in each of the 1-, 2-, 3-, and 4-variable models (Table 7). Shrub patchiness entered the 2-variable model and remained in the 3- and 4-variable models. Surprisingly, site size did not appear in any of the multiple-variable models for unforested sites, despite the fact that the site sizes could be unambiguously determined from their well-defined boundaries (most or all trees harvested).

#### PREDICTING BSR ON FORESTED SITES

As with unforested sites, variations in BSR were not so effectively explained on the forested sites as for all sites together. BSR was significantly correlated with tree species diversity ( $r = 0.36$ ;  $0.05 > P > 0.02$ ), shrub patchiness ( $r = 0.50$ ;  $0.01 > P > 0.001$ ), total crown volume ( $r = 0.49$ ;  $0.01 > P > 0.001$ ), tree crown volume ( $r = 0.47$ ;  $0.01 > P > 0.001$ ), and site size ( $r = 0.57$ ,  $P < 0.001$ ). When variation in BSR attributable to crown volume was controlled by par-

tial correlation, only site size and tree species diversity were still significantly correlated with BSR. The best single predictor of BSR in the forested sites was site size ( $R^2 = 0.33$ ), which contrasts with total crown volume as the best predictor over all sites ( $R^2 = 0.72$ ). Similarly, all-possible-subsets multiple regressions showed lower  $R$ -squares and less consistency in the variables entering the best 2-, 3-, and 4-variable subsets for predicting BSR on forested sites than was the case for all sites together (Table 7).

#### DISCUSSION

##### BIRD SPECIES RICHNESS

BSR values in the 6-ha subplots on the forested sites were more than double those expected from an analysis of Breeding Bird Censuses by James and Rathbun (1981). A similar effort gave 70–80% of the species known to breed on two 20-ha spot-mapping grids in oak-pine woodlands in the foothills of the western Sierra Nevada (Verner and Ritter 1985: fig. 4). If sampling efficiency in the coniferous forest sites was about equivalent, the BSR values should be increased to about 22 breeding species per 6-ha subplot, ranking our forested sites among the richest habitats analyzed by James and Rathbun (1981).

Reasons for this discrepancy are unclear. In relation to our study, forests sampled were relatively rich in habitat diversity and tree species diversity. In addition, our method of estimating the number of breeding species to be found on a 6-ha plot may not have produced estimates of BSR comparable to those reported by James and Rathbun. In relation to James and Rathbun's study, the conifer sites reported in the annual Breeding Bird Censuses that met their selection criteria may not be representative of conifer sites in general. For example, all were at relatively high elevations. Also, in our opinion, the sampling effort (52, 48, and 110 min/ha [censuses 31, 32, and 34, respectively, from their table 1]) on at least 2 sites was well below that needed to obtain reasonable estimates of the number of territorial pairs on a mapping grid. Our experience with mapping grids suggests a required effort of about 150 min/ha in both montane coniferous forests and structurally simpler oak-pine woodlands. In any case, results indicate a need for a more thorough and

TABLE 5. Comparisons of the "best" 2-, 3-, and 4-variable subsets over all sites (predictor codes as in Table 1), using the most common predictors from among the top 10 subsets in each category from all-possible-subsets multiple regressions.

Year	Variables in subset		
	2	3	4
1978	CROVOL (0.76) <sup>a</sup> SIZE	CROVOL (0.78) SIZE BASAR	CROVOL (0.82) SIZE TRECOV LITTER
1979	CROVOL (0.78) SIZE	CROVOL (0.78) SIZE BASAR	CROVOL (0.79) SIZE TRECOV LITTER
1978 + 1979	CROVOL (0.79) SIZE	CROVOL (0.80) SIZE BASAR	CROVOL (0.84) SIZE TRECOV BASAR

<sup>a</sup> Adjusted  $R^2$ .

systematic approach to estimating BSR in conifer forests, particularly addressing the effects of latitude, elevation, stand homogeneity, and tree species richness.

#### PREDICTING BIRD SPECIES RICHNESS

*Total crown volume.*—Total crown volume, our index of foliage volume, was the best independent variable for predicting BSR in our data set. Because this was the sum of tree and shrub crown

volumes, its power as a predictor makes sense. Total crown volume increased with shrub volume on sites undergoing secondary succession, and shrub-dependent bird species were able to establish breeding territories. This was clearly the case with the obligate shrub nesters: Yellow and MacGillivray's warblers, Rufous-sided and Green-tailed towhees, and Fox Sparrows. With the addition of trees, total crown volume continued to increase, and species that nested and foraged primarily in tree canopies were added.

TABLE 6. Comparisons of correlations and partial correlations of BSR in 1978 and 1979 with some independent variables (codes as in Table 1). Significant partial correlations are indicated by asterisks.<sup>a</sup> (Only significant simple correlations are shown.)

Variable controlled	Independent variable	BSR 1978		BSR 1979	
		Simple correl.	Partial correl.	Simple correl.	Partial correl.
CROVOL	BASAR	0.83***	0.22	0.82***	0.13
	FHD	0.76***	0.26	0.74***	0.20
	TRECOV	0.75***	-0.01	0.75***	-0.04
	DBHD	0.74***	0.26	0.70***	0.12
	TREPCH	0.64***	0.16	0.66***	0.20
	SIZE	0.58***	0.43**	0.59***	0.45**
	TSD	0.43**	0.29*	0.39**	0.22
	SHBPCH		0.05	0.28*	0.08
SIZE	CROVOL	0.85***	0.81***	0.86***	0.82***
	BASAR	0.83***	0.81***	0.82***	0.79***
	FHD	0.76***	0.75***	0.74***	0.73***
	TRECOV	0.75***	0.67***	0.75***	0.67***
	DBHD	0.74***	0.78***	0.70***	0.73***
	TREPCH	0.64***	0.63***	0.66***	0.65***
	TSD	0.43**	0.27	0.39**	0.22
	SHBPCH		0.17	0.28*	0.19

<sup>a</sup> \*\* (0.05 >  $P$  > 0.01); \*\*\* (0.01 >  $P$  > 0.001); \*\*\*\* ( $P$  < 0.001).

TABLE 7. The "best" 2-, 3-, and 4-variable subsets for forested and unforested sites, using the most common predictors (codes as in Table 1) from among the top 10 subsets in each category from all-possible-subsets multiple regressions (data pooled over 1978 and 1979).

Variables in subset		
2	3	4
<b>Unforested sites</b>		
CROVOL (0.38)* SHBPCH	SHBVOL (0.55) SHBPCH FHD	CROVOL (0.61) SHBPCH SHBVOL FHD
<b>Forested sites</b>		
SIZE (0.44) SHBPCH	SIZE (0.53) CROVOL TRECOV	SIZE (0.56) CROVOL TRECOV BASAR

\* Adjusted  $R^2$ .

Similarly, Karr and Roth (1971) concluded that foliage volume (indexed by percent cover) was a better predictor of BSD than FHD in a forest plot in the Bahamas. And although Szaro and Balda (1979) did not find a significant relationship between BSD and foliage volume in a southwestern ponderosa pine forest, we reanalyzed their data using the natural log of foliage volume and found a significant correlation with BSD ( $r = 0.90$ ,  $P < 0.05$ ).

The strength of total crown volume as a predictor of BSR in our study was shown by the facts that in spite of differences in bird abundances between years, it was the best single predictor over all sites for each year separately and for both years combined, and it appeared in all multiple-variable models. Of course, we cannot be certain that replication of this study would produce the same results. For example, Hejl (1987) found little consistency among years in the best single predictors and sets of predictors of BSR on study sites in true fir forests of the Sierra Nevada, and total crown volume rarely entered the predictive models. However, the first year of Hejl's study followed the winter with the greatest snowfall ever recorded in the Sierra Nevada, and BSR on the study sites exhibited a significant linear increase over the 3 yr of the study, 1983-1985 (Hejl et al. 1988).

To a point, total crown volume should be correlated with percent vegetation cover. Karr and Roth (1971) found increasing BSD with percent canopy cover, to an asymptote at about 230% cover, in a comparison of habitats in Illinois, Texas, Panama, and the Bahamas. (Cover

values of multiple layers of vegetation were summed, resulting in some total cover values >100%.) They hypothesized that "We might expect decreases after that point because of the restriction of mobility of the avifauna in the very dense foliage. This might explain the decrease in diversity exhibited in dense, single species stands such as conifer plantations" (Karr and Roth 1971: 430). Our results suggest an alternate, but not exclusive, hypothesis. As a forest canopy closes, natural pruning of lower branches occurs and shrub cover shrinks because less light reaches the ground. Consequently, foliage volume should decline in both the shrub and tree layers as a forest matures and reaches old-growth conditions. (In total crown volume, the 3 unlogged sites among our 51 sites ranked 42, 44, and 46.) If foliage volume is, in fact, a major determinant of BSR, then BSR should increase on a site through early successional stages, reach a maximum as the forest matures and the canopy closes, and decline slightly thereafter, just as observed in this and other studies.

Although total crown volume was also the best predictor of BSR in the unforested sites separately (where total crown volume was made up mainly of shrub crown volume), that was not the case on the forested sites. It did, however, enter the best 3- and 4-variable models for forested sites. The fact that predictor models for the forested and unforested sites accounted for considerably less variance than for all sites together probably resulted from a combination of factors. First, the range in values of many tree

and shrub measures was considerably less on the forested and unforested sites separately than over all sites. Similarly, Hejl (1987) studied only forested sites in the same area as our study and found relatively low levels of predictability of BSR, compared with those found in our forested sites. Tree crown volumes on Hejl's sites differed by only ca.  $740 \text{ m}^3/100 \text{ m}^2$  (38–800), compared with a range of ca.  $1,300 \text{ m}^3/100 \text{ m}^2$  (74–1,388) between extremes on our forested site.

Second, our data suggested a threshold effect of tree crown volume on BSR of obligate tree nesters. The richness of this assemblage was not significantly affected by an increase in tree crown volume after the threshold level (about  $280 \text{ m}^3/100 \text{ m}^2$ , or a basal area of about  $20 \text{ m}^2/\text{ha}$ ) was reached. Similarly, Willson (1974) found that the addition of trees disproportionately increased BSR.

Third, a similar but less pronounced threshold effect of shrub cover (at ca. 20%) was implied for obligate shrub nesters in our study. We thus agree with Holmes et al. (1979) that observed relationships between BSR and FHD result from the addition of shrubs and trees to a habitat. Shrubs add complexity to the foraging specializations possible in a habitat and, perhaps more importantly, they provide nesting cover markedly different from that provided by the ground, by grasses, or by forbs. Trees add still other dimensions, both for foraging and nesting in foliage and boles. The only site in our study that exceeded both the tree-volume threshold and the shrub-cover threshold tied for the highest overall BSR (28 breeding species, pooling 1978 and 1979 data). Beyond these rather broad levels of habitat selection, other elements of habitats undoubtedly influence birds' settling patterns (e.g. see Rotenberry 1985).

*Site size.*—In spite of the fact that site size has repeatedly been shown to influence BSR in a wide variety of habitats (e.g. Galli et al. 1976, Gavareski 1976, MacClintock et al. 1977, Stauffer and Best 1980, Whitcomb et al. 1981), we are uneasy with results that showed site size to be an important predictor of BSR (excluding edge-dependent species) on our sites, and especially as the best predictor in forested sites. Although site size was significantly correlated with BSR in the unforested sites, where site boundaries were unambiguous, it did not enter the best 2-, 3-, and 4-variable models. The Forest Service sale maps we used to delineate boundaries of

forested sites showed only the boundaries within which timber was harvested. Within those boundaries, timber was never harvested uniformly, resulting in interspersed patches of open ground, shrubs, timber intermediate in density, and uncut timber with a density like that of the forest beyond sale boundaries. As a result, sites that were not totally or nearly clearcut lacked distinct boundaries separating them from the surrounding forest matrix. Furthermore, because many of our forested sites were large enough that we could not sample their full extent, it is unreasonable to expect that we sampled the whole bird assemblage within sale boundaries.

We believe that our sample methods may, in part, account for the observed relationships between site size and BSR. Because we truncated counts at site boundaries, we had access to smaller bird assemblages on small sites. On many of the larger sites, however, boundaries exceeded the limits of our ability to detect birds, so all birds detected were included in the counts. In addition, we believe that logging-induced patchiness on a scale larger than that detected by our methods, interrelatedness of forest patches, general lack of habitat isolation, and abundance of corridors combine to offer the best explanation for the relationship we observed between BSR and site size. Pine species, fir species, and incense-cedar have different foliage configurations and are used as foraging substrates by many bird species. These tree species often occurred in nearly monotypic stands, portions of which were left intact during timber harvest to serve as seed sources for regenerating timber, which added to the patchiness of the vegetation. Such patchiness could bring together, in an area small enough to be sampled by our point-counting method, several bird species more or less dependent on conditions found in each of the various patch types. And, of course, larger sites had more patches to bring a greater variety of species into the stand. Although we detected few birds beyond 150 m from the counting point, birds whose territories overlapped and extended well beyond that perimeter would sometimes come within range of detection. This gave access to the bird assemblage that used a relatively large proportion of even our larger stands.

Habitat isolation was not likely a significant factor restricting the distribution of any forest-

interior species. The eastern habitats in which isolation has been shown to be a significant factor were in forest remnants surrounded by agricultural lands—essentially 3-dimensional islands in a 2-dimensional sea. Many of our habitat islands were clearcuts surrounded by a forest matrix—2-dimensional islands in a 3-dimensional sea. This is a fundamental difference to be considered when results of studies in forest fragments in the East are applied to habitat mosaics in the West (Verner 1980). The corridor phenomenon is not yet a factor in these western forests, as a forest-interior bird would rarely, if ever, need to cross a clearcut to access other forested habitat.

*Basal area and percent shrub cover.*—It was probably no coincidence that these variables made up the best 2-variable subset for predicting total crown volume, because basal area was highly correlated with tree crown volume ( $r = 0.97$ ) and percent shrub cover was highly correlated with shrub crown volume ( $r = 0.91$ ). Tree and shrub crown volume together made up total crown volume. The power of basal area and percent shrub cover together to predict total crown volume makes them a tempting surrogate, because they can be measured quickly, more objectively, and probably more accurately. In fact basal area is a standard measure regularly recorded by foresters during timber inventories.

*Percent tree cover and DBH diversity.*—As with basal area, the ability of these measures to predict BSR resulted from their high correlation with total crown volume. Nonetheless, they can be easily and objectively measured, and DBH is routinely measured during timber inventories. In the absence of other measures, these could be useful and reasonably accurate predictors of BSR in the mixed-conifer forest zone of the western Sierra Nevada.

*Snag density.*—In spite of the fact that snag density was significantly correlated with BSR, it did not appear in any subset of the multiple-regression models. Therefore, it was a poor predictor of BSR in the range of sites we sampled. This should not be interpreted to mean that snags were unimportant to many bird species on our sites. Their importance has been amply documented (e.g. Balda 1975, Mannan et al. 1980, Raphael 1981). The fact that both primary cavity nesters (White-headed and Hairy woodpeckers) and secondary cavity nesters (Mountain Chick-

adees and Mountain Bluebirds) used stumps that were only 0.5–1.5 m high confounded attempts to measure snag dependence. The woodpeckers and chickadees foraged mainly in the surrounding forest or in isolated tree patches within some cuts. These special situations would not commonly exist in natural habitats, but they show what can happen in small, logged patches within larger areas of forest. The results point to the need to study the potential role of stumps, particularly high-cut stumps, as partial compensation for snag removal in forest management.

*Foliage height diversity.*—Since the pioneering work of MacArthur and MacArthur (1961), FHD has been the most common habitat variable shown to be correlated with BSD or BSR. We found consistently that simple correlations between FHD and BSR dropped significantly when effects of total crown volume were controlled, but the reverse was not true. This was especially apparent when all sites from clearcuts to uncut forest were analyzed. Our results indicate that crown volume was a composite measure of a variety of habitat attributes that bird species used to select breeding sites. Whether correlations of BSD and BSR with FHD in other studies also resulted because FHD was a good predictor of foliage volume is unknown.

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APPENDIX. Untransformed values of all habitat variables, by site. Unforested sites (U) and forested sites (F) are ranked in increasing order of total crown volume. Sites F22, F24, and F26, to the best of our knowledge, had never been logged. Variable codes and units of measurement are as in Table 1.

SITE	BSR	SIZE	ELEV	CROVOL	FHD	TRECOV	BASAR	TREPCH	TDD
U1	5	8.0	2,225	0.95	0.10	0	0	0	0
U2	0	0.5	2,118	3.00	0.76	0.5	0.60	0	0
U3	9	6.0	2,164	6.13	1.33	1.0	0.56	0	0
U4	3	2.0	2,164	11.61	1.38	2.0	1.00	0	0
U5	8	8.0	2,195	13.42	1.20	2.9	1.03	47.1	2.24
U6	4	3.0	2,195	16.40	1.16	6.0	2.16	57.6	1.93
U7	5	18.0	2,072	16.48	0.10	0	0	0	0
U8	7	8.0	2,256	17.26	1.35	5.6	1.48	56.9	2.30
U9	7	5.0	2,155	18.76	1.20	7.1	1.56	55.5	2.38
U10	9	3.0	2,256	19.85	0.16	0	0	0	0
U11	8	16.0	2,012	20.82	0.64	2.0	0.20	0	0
U12	8	17.0	2,072	21.26	0.91	2.0	0.08	0	0
U13	9	19.0	2,042	29.19	1.10	6.0	0.48	0	0
U14	8	4.0	2,164	35.01	1.12	12.2	3.36	48.3	2.24
U15	12	10.0	2,164	38.36	1.27	18.9	3.60	64.7	2.19
U16	12	7.0	2,195	42.73	1.45	10.4	3.84	59.7	1.79
U17	10	7.0	2,164	44.45	1.87	10.0	8.32	60.5	2.16
U18	8	2.0	1,737	57.57	0.28	0	0	0	0
U19	7	20.0	2,316	76.18	0.39	0	0	0	0
U20	13	4.0	1,646	144.39	1.22	13.0	4.56	68.0	1.21
F1	15	9.0	2,042	80.95	2.18	8.6	7.88	49.4	1.79
F2	18	6.0	2,042	134.97	1.80	16.0	7.48	62.3	1.87
F3	17	14.0	1,707	143.49	2.31	19.4	7.40	68.2	2.00
F4	17	2.0	1,798	160.01	2.10	5.0	11.40	54.8	1.93
F5	21	10.0	2,164	169.23	1.92	28.0	10.96	83.0	1.83
F6	12	7.0	2,134	237.92	1.51	30.0	11.78	89.6	1.48
F7	21	80.0	1,920	244.78	1.97	40.0	12.68	64.7	1.76
F8	21	10.0	2,286	246.22	1.96	18.0	15.97	67.1	1.58
F9	21	10.0	2,012	281.21	2.31	30.0	23.22	68.1	1.52
F10	25	32.0	2,164	323.50	1.94	36.0	26.60	73.1	1.60
F11	22	12.0	2,164	332.23	2.08	31.0	33.64	76.4	1.42
F12	19	11.0	2,164	335.15	2.10	36.0	27.74	67.7	1.39
F13	21	7.0	2,164	344.61	1.36	38.0	19.12	75.7	1.44
F14	18	13.0	2,190	368.42	1.97	36.0	25.97	80.8	1.51
F15	9	1.0	2,073	451.06	2.12	36.0	22.84	54.0	1.49
F16	24	10.0	2,134	507.37	1.97	42.0	36.43	79.7	1.49
F17	20	15.0	1,768	528.37	1.86	62.0	34.80	80.7	1.39
F18	21	20.0	2,134	604.80	2.17	50.0	61.02	70.5	1.40
F19	16	7.0	1,737	659.98	2.20	65.0	49.60	72.4	1.20
F20	18	8.0	2,063	662.51	2.13	38.0	30.00	51.5	1.31
F21	22	9.0	1,829	681.29	2.17	56.0	44.78	70.9	1.21
F22	18	16.0	2,042	684.61	2.11	78.0	74.67	56.2	1.08
F23	18	10.0	2,103	691.22	2.08	30.0	43.80	47.2	1.90
F24	15	16.0	2,164	811.97	2.25	74.0	48.98	61.1	1.47
F25	24	12.0	1,798	869.55	2.15	45.0	42.24	64.7	1.55
F26	20	40.0	2,286	901.45	1.99	70.0	66.00	66.5	1.05
F27	28	30.0	1,981	936.83	2.37	46.0	40.16	48.9	1.59
F28	28	10.0	1,829	1,130.44	2.24	48.0	47.27	54.6	1.50
F29	28	20.0	1,737	1,131.33	2.19	52.0	55.94	63.9	1.13
F30	23	24.0	1,828	1,326.84	2.10	46.0	34.33	66.6	1.46
F31	26	31.0	1,707	1,390.10	2.28	44.0	46.22	59.1	1.40



## APPENDIX. Continued.

TREVOL	TREDEN	TSD	DBHD	SNGDEN	SHBPCH	SHBVOL	SHBCOV	LITTER
0	0	0	0	4	78.1	0.95	3.1	24.8
2.99	7	0	0	2	0	0.01	0	57.0
3.27	28	0.96	0.80	4	78.1	2.86	5.4	23.4
7.38	16	0.56	1.04	9	0	4.23	8.0	32.8
10.65	70	0	1.00	1	85.6	2.77	9.5	36.7
16.27	68	0.80	1.12	14	60.8	0.13	0.5	68.0
0	0	0	0	0	64.4	16.48	47.2	30.4
17.02	116	0.64	0.82	10	54.7	0.24	0.8	67.4
17.30	248	0.41	0.59	2	69.7	1.46	3.4	33.8
0	0	0	0	0	80.9	19.85	50.3	54.0
4.64	104	1.04	0	0	84.3	16.18	31.9	34.8
9.78	40	1.05	0	2	86.3	11.48	25.5	22.6
11.53	268	0.08	0	2	75.6	17.66	42.0	25.4
32.67	468	0.60	0.75	1	72.0	2.34	3.7	45.2
35.15	880	0.51	0.26	4	79.0	3.21	4.8	33.4
39.88	236	0.83	1.00	4	65.6	2.85	6.0	33.0
43.75	400	0.69	1.16	16	64.0	0.70	1.6	59.0
0	0	0	0	2	99.0	57.57	91.4	66.8
0	0	0	0	0	0	76.18	98.0	95.0
104.90	876	0.71	0.47	10	57.6	39.49	60.0	26.0
74.02	104	0.69	1.24	1	62.5	6.93	11.6	48.2
134.38	88	0.19	1.82	24	76.5	0.59	2.0	31.8
134.28	400	0.89	0.74	7	99.9	9.21	21.9	42.4
131.48	92	0.73	1.97	16	99.9	28.53	51.7	16.4
166.45	496	1.23	1.07	7	80.0	2.78	5.1	38.2
235.13	473	0.33	1.29	13	78.4	2.79	8.0	56.3
233.18	340	1.34	1.28	9	99.8	11.60	22.3	60.8
242.49	200	0.23	1.44	17	95.6	3.73	18.0	53.7
280.98	206	0.29	1.83	60	58.3	0.23	4.0	43.7
320.27	1,070	0.83	1.16	20	80.7	3.23	5.9	65.1
330.07	268	0.89	1.96	22	83.4	2.16	8.0	71.4
329.69	672	0.91	1.33	30	89.9	5.46	8.3	51.2
341.32	624	0.74	1.37	25	78.6	3.29	6.5	68.6
367.40	213	0.16	1.95	14	73.9	1.02	8.0	32.8
450.61	172	0.19	2.00	8	95.6	0.45	8.0	42.6
505.84	588	0.09	1.70	35	73.8	1.53	10.0	68.3
521.78	1,248	1.33	1.25	18	84.7	6.59	15.9	74.6
600.23	290	0.57	2.14	40	77.7	4.57	6.0	65.0
653.39	2,030	0.84	0.82	20	91.2	6.59	9.4	82.4
662.08	240	0.57	1.97	20	96.0	0.43	4.0	47.9
676.75	713	1.30	1.35	13	80.8	4.54	10.1	71.0
683.41	850	0.63	1.60	40	80.0	1.20	10.0	92.3
690.72	424	0.37	1.78	35	53.4	0.50	0.9	68.0
808.48	735	0.37	1.45	34	91.5	3.49	12.0	71.3
867.77	276	0.48	2.03	20	72.4	1.78	5.0	72.6
899.34	612	0.89	1.88	40	72.3	2.11	4.5	78.6
933.77	347	0.66	1.60	7	65.1	3.06	28.0	70.9
1,129.95	351	0.79	1.91	22	58.3	0.49	4.0	55.2
1,130.04	797	0.98	1.75	44	58.8	1.29	6.0	78.3
1,325.51	262	0.61	1.77	13	75.0	1.33	16.0	64.8
1,387.50	284	1.27	2.00	16	63.5	2.60	10.0	52.6