

## EVALUATING AVIAN-HABITAT RELATIONSHIPS IN RED FIR FORESTS OF THE SIERRA NEVADA

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**Abstract:** Using data from the southern and central Sierra Nevada, we evaluated predictions from the California Department of Fish and Game's (CDFG) Wildlife Habitat Relationships (WHR) System for breeding bird species in red fir (*Abies magnifica*) forests. We counted birds on 34 study sites during the summers of 1983, 1984, and 1985 and detected 50 breeding species. Study sites included stands in each of four structural classes (all four canopy-closure classes within the medium/large-tree size class). Only two bird species that were predicted to occur by the WHR System were not recorded in any of the the four sampled structural classes of red fir habitat. However, 26 species were present in at least one class of red fir habitat in which they were not predicted. Based on mean observation frequency and abundance, we subjectively rated the potential ability of each structural class to support low, medium, and high breeding populations of each bird species. Forty-six percent of our predictions were for higher habitat suitability ratings than those in the WHR System. We suggest a historic rating for species that formerly occurred in high numbers, are uncommon or absent today, but may use the habitat again in the future.

Wildlife-habitat relationships models in California have been developed over the past decade or so (Salwasser et al. 1980). The models relate habitat suitability for vertebrate species to structural and successional stages of various vegetation types by way of selected habitat parameters such as canopy closure and tree size. The models used in California are discontinuous, with habitat parameters divided into discrete structural classes. Verner and Boss (1980) created models that predicted the occurrence of vertebrate species in major habitats of the western Sierra Nevada and rated the suitability of all structural classes within habitats for those species. They solicited opinions of wildlife experts with experience in the Sierra Nevada who made predictions based on literature reviews, their professional field experience, and the opinions and notes of other Sierran naturalists. Similar wildlife-habitat relationships matrices were created for habitats in other regions of the state (Marcot 1979, Mewaldt and Torres 1982). Using information from all of these sources and opinions of wildlife experts, the California Department of Fish and Game (CDFG) created new matrices predicting wildlife-habitat relationships (WHR) for all regularly occurring vertebrate species in California. The purpose of these matrices is to help wildlife managers make land management decisions by providing predictive models of habitat value (Salwasser and Laudenslayer 1982). The models are stored in a matrix format on CDFG's computer in Rancho Cordova, California (D. Zeiner, pers. comm.).

Few of the numerous predictions in these various WHR documents have been tested with field data, and all

published tests have addressed the matrices of either Verner and Boss (1980) or Marcot (1979). Verner (1980) compared predictions of Verner and Boss (1980) for birds in mixed-conifer forests of the Sierra Nevada with data from six studies. He found that from one to six species that were not predicted by the matrix were detected in each of seven habitat stages in mixed-conifer forest. More of the predicted species were detected in later seral stages than in earlier ones. He concluded that managers could rely on information in the Verner and Boss matrix when assessing the response of bird communities to changes in vegetation structure in mixed-conifer forests in the Sierra Nevada. However, Dedon et al. (1986) found that the proportion of detected species did not increase with increasing habitat suitability ratings in the WHR matrix in a mixed-conifer site, but did increase significantly at a black oak (*Quercus kelloggii*) site. Raphael and Marcot (1986) assessed the reliability of the North Coast/Cascades WHR models (Marcot 1979) in four seral stages of mixed-evergreen forest in northwestern California. They investigated species' occurrences and compared species' abundances between habitat stages and between substages. The numbers of breeding bird species observed differed significantly from those predicted in the four seral stages, with greatest differences in the shrub-sapling stage. Between-stage comparisons of observed abundances often differed from predicted changes of abundance. Within-stage differences were found, leading Raphael and Marcot (1986) to suggest that additional seral stages could be defined to improve the realism of the model.

We studied the distribution of bird species in red fir (*Abies magnifica*) forests in the Sierra Nevada, California, during the summers of 1983, 1984, and 1985. Our current objective is to evaluate the predictions from the

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CDFG's WHR system for bird species that breed in red fir forests.

## STUDY AREAS

Thirty-four sites in red fir forests (Rundel et al. 1977) in Sequoia National Park (8 sites), Sierra National Forest (16 sites), and Yosemite National Park (10 sites) were randomly selected from 161 potential sites found in true fir (red and white fir, *A. concolor*) forests. All sites met the following criteria: (1) 50 percent or more of total crown volume consisted of red fir (field measurements described in Hejl et al. 1988), (2) situated in a stand of trees that was homogeneous in terms of size class and canopy-closure class (visual inspection), and (3) located in stands at least 10 ha with dimensions accommodating a rectangle of at least 200 x 400 m (visual inspection). The stands represented variable canopy closures and size classes (assumed to reflect stand ages). We originally attempted to find equal numbers of large stands in each canopy closure class. Stands were selected in clusters of two or three that were sufficiently close together to permit completion of bird counts in all between 0530 and 1130 PDT. One study site was located in each stand. All sites were at least 400 m apart and most were 800 m apart, in an attempt to assure independent measurements.

## METHODS

### Bird Observations

During all 3 years of the study, the same observer recorded all birds seen or heard at each study site twice during the breeding seasons (between 23 May and 30 July) of 1983, 1984, and 1985. A second observer (a different person each year) counted birds at all sites once each summer. Observers counted birds on each site during three different times of the day each summer: early morning (0600-0800), mid-morning (0800-0930), and late morning (0930-1100) PDT. Birds were not counted during rain, high wind, or snow.

At each site, a randomly placed transect 200 m long and at least 100 m from any edge or discontinuity in the stand was marked in the summer of 1983 and reused in 1984 and 1985. Counting points were located at the beginning, middle, and end of each transect. Birds were also counted between the three counting points along the entire length of the transect. Observers recorded each bird using the stand, regardless of its distance from the observer. Birds greater than 100 m away were so noted in 1984 and 1985. However, few such detections occurred. We recorded the sex and age of each bird, any breeding evidence, bird use of the stand, the first detection cue, and whether it was a new or repeat detection during that visit.

An 8 min count was made at the first point, followed by a slowly walked transect to the mid-point,

where another 8 min count was done. Another slow walk was made along the transect to the end point, where a third 8 min count was made. We tallied all adult birds detected, attempting to avoid double-counting individuals as we proceeded from point count to transect to point count. After the last point count, the transect was then slowly walked in the reverse direction. During the return walk, the observer recorded only those species that had not been detected earlier during that visit to the site.

### Updating the WHR Model

Sites were categorized using CDFG's WHR criteria of structural classes, with one exception. CDFG's structural classes are defined according to tree size and canopy closure. All of our sites were in the medium/large-tree size class 5. Canopy-closure classes are defined by CDFG as follows: (1) sparse canopy [S] = 10-24 percent, (2) open canopy [P] = 25-39 percent, (3) moderate canopy [M] = 40-59 percent, and (4) dense canopy [D] = 60-100 percent. We based our canopy closure estimate for each site on the presence or absence of canopy above 10 randomly located points in each of 6 randomly located 15x15 m quadrats on each site (Hejl 1987). With the inclusion in the sparse category of a stand with 8 percent canopy closure (our one exception), we had 6 sparse sites, 8 open sites, 16 moderate sites, and 4 dense sites.

We evaluated all detections of adult birds that were determined to be using the stand. Raptors, aerial feeders, ducks, vultures, and ravens were excluded from the analysis, as our methods precluded adequate counts of them. We chose to examine only the reproduction column of the matrix. Because we were comparing our results to the WHR suitability ratings for reproduction, we determined breeding status for all species using a site. Breeding status was determined by direct evidence found on or near the study sites (nests, fledglings, or the presence of frequently singing males) or by indirect evidence from information of others who have studied these species in the same habitats (Grinnell and Storer 1924, Grinnell and Miller 1944, Verner and Boss 1980, Beedy and Granholm 1985, Gaines 1988).

We subjectively predicted the suitability of each structural class for each species based on the observed frequency and abundance for that species in that class. Frequency calculations were based on all data collected, including the return walk. Frequency equaled the mean percent of sites occupied each summer. Abundance calculations were based on data from the point counts and transects, not the return walk. Abundance was defined as the mean number of detections per visit to a stand.

We rated habitat suitability in a similar manner to the creators of CDFG's WHR matrix, except we used field data as part of our decision-making process. We evaluated the relative probability of occurrence of each

species in a habitat relative to all other habitats in the state and throughout its range. For comparisons with other habitats, we used our knowledge from field experience in other habitats, consulted the literature, and solicited the opinions of other naturalists. CDFG habitat ratings are defined as: (1) high = habitat can meet the life history needs in support of a relatively high population density (as implied by probability of occurrence), (2) medium = habitat can meet the life history needs in support of a relatively moderate population density (as implied by probability of occurrence), and (3) low = habitat can meet the life history needs in support of a relatively low population density (as implied by probability of occurrence). We then compared our habitat suitability ratings to those of CDFG for the Yosemite Valley latilong in the Sierra Nevada. Most of our study sites were located in the Yosemite Valley latilong. We used only this latilong because we understand that similar predictions were made by CDFG for each habitat in each latilong in the Sierra Nevada. The WHR predictions were obtained from D. Zeiner in January 1988.

## RESULTS

### Presence/Absence

Fifty bird species bred in our red fir sites during the summers of 1983, 1984, and 1985 (Table 1). Species' occurrences ranged from the Swainson's thrush (see Table 1 for scientific names), which was found on one 5P site in 1 year, to yellow-rumped warblers and dark-eyed juncos, which were found on all sites in all 3 summers. Only two species that were predicted to occur in these red fir habitats by the WHR models were not detected on any site (yellow-bellied sapsucker and solitary vireo). Three other species (white-breasted nuthatch, ruby-crowned kinglet, and Swainson's thrush) were not detected in one structural class (5D) for which they were predicted. However, 26 species were present in at least one of the classes of red fir habitat in which they were not predicted. Most of those species were detected in other structural classes for which they were predicted. Of the species that were present but not predicted, 16 were found in sparse, 14 in open, 13 in medium, and 13 in dense canopy-closure classes.

### Hejl and Verner Predictions

Based on the mean percent of sites occupied (frequency) and the mean abundance of each bird species, we rated each species for each structural class and compared our predictions to those from CDFG's WHR System (Table 1). Forty-six percent of our predictions were for higher habitat suitability ratings than CDFG's, 42 percent matched CDFG's, and only 12 percent were rated lower than CDFG's (Table 2). Sixty percent of our increased ratings were for species we detected that were not

predicted in certain classes of red fir habitat by CDFG's WHR System, and 22 percent of our increased ratings involved marked changes (absent to medium or high, low to high). Conversely, only five of our decreased ratings involved marked changes (Table 2), those for the ruby-crowned kinglet and Swainson's thrush (Table 1). From 37-48 percent of our predictions matched CDFG's in any one structural class and most of the differences between CDFG's and our predictions were low (Table 3).

## DISCUSSION

We temper our predictions of habitat suitability for each of these species in red fir classes with several considerations. Clearly, our predictions are based on data collected during a short time period (3 years) and in only a portion of the habitat (34 study sites in central and southern Sierra Nevada). We have shown elsewhere that bird numbers in true fir forests in the Sierra Nevada fluctuate greatly and often (Hejl et al. 1988). Bird numbers in red fir and higher elevations were probably low for all but a few species in 1983 (DeSante 1985, Hejl et al. 1988). The abundances of common species increased in red fir in 1984, but the abundances of most uncommon species did not increase until 1985 (Hejl et al. 1988). Therefore, our predictions here are based on data from at least 1 year with low bird numbers (1983) and 2 years of increasing bird numbers (1984 and 1985). Consequently, our frequency and abundance estimates are most likely low; it is surprising to us that only two predicted species, the solitary vireo and the yellow-bellied sapsucker, were not encountered. Solitary vireo populations could have been low, or the species could have been missed through sampling error (only four sites were surveyed in 5D, the predicted structural class). However, no other recent study of birds in the Sierra Nevada lists solitary vireos as breeding in red fir (Beedy 1981, Beedy 1982, Granholm 1982).

Including the yellow-bellied sapsucker as a breeding species in red fir forests of the western Sierra Nevada is now an error in the CDFG matrices, as the taxonomy of these sapsuckers has recently been changed (AOU 1983, 1985). The red-breasted sapsucker and the red-naped sapsucker (*Sphyrapicus nuchalis*) are currently recognized as species distinct from the yellow-bellied sapsucker. The red-breasted sapsucker is correctly listed in the WHR matrix, but the yellow-bellied sapsucker should be deleted. It is possible, but not likely, that the red-naped sapsucker breeds in red fir on the east slope of the Sierra Nevada (some nesting records for the east slope are reported in Beedy and Granholm 1985, Gaines 1988, but the habitat type is not given). These east-slope areas may be included in the Yosemite Valley latilong, the area for which we obtained predictions from CDFG.

In general, the use of large, heterogeneous areas

Table 1. Frequency (percent of stands in which found each summer) and abundance (detections per visit to a stand each summer) in each structural class, California Department of Fish and Game's Wildlife Habitat Relationships System's (WHR) predictions, and Hejl and Verner (HV) predictions for each species breeding in each structural class.

Species	Structural <sup>1</sup> class	Frequency		Abundance		Predictions <sup>2</sup>	
		mean	SD	mean	SD	WHR	HV <sup>3</sup>
Blue grouse ( <i>Dendragapus obscurus</i> )	5S	17	17	0.06	0.09	H	H
	5P	13	13	0.06	0.12	H	H
	5M	4	3	0.01	0.04	M	M
	5D	8	14	0.03	0.06	H	H
Mountain quail ( <i>Oreortyx pictus</i> )	5S	50	17	0.35	0.37	M	M
	5P	29	19	0.19	0.24	L	L
	5M	25	10	0.11	0.15	-	L
	5D	17	14	0.11	0.22	-	L
Band-tailed pigeon ( <i>Columba fasciata</i> )	5S	17	0	0.06	0.06	-	L
	5P	17	19	0.07	0.08	-	L
	5M	19	17	0.07	0.11	-	L
	5D	33	14	0.11	0.16	-	L
Calliope hummingbird ( <i>Stellula calliope</i> )	5S	0	0	0.00	0.00	-	-
	5P	4	8	0.01	0.04	-	L
	5M	2	3	0.01	0.03	-	L
	5D	0	0	0.00	0.00	-	-
Yellow-bellied sapsucker ( <i>Sphyrapicus varius</i> )	5S	0	0	0.00	0.00	L	-
	5P	0	0	0.00	0.00	L	-
	5M	0	0	0.00	0.00	L	-
	5D	0	0	0.00	0.00	L	-
Red-breasted sapsucker ( <i>Sphyrapicus ruber</i> )	5S	44	20	0.24	0.13	L	M
	5P	38	13	0.26	0.41	L	M
	5M	54	10	0.39	0.34	L	M
	5D	42	14	0.25	0.29	L	M
Williamson's sapsucker ( <i>Sphyrapicus thyroideus</i> )	5S	56	20	0.50	0.47	L	H
	5P	34	26	0.26	0.27	L	H
	5M	46	16	0.31	0.35	L	H
	5D	25	25	0.11	0.13	L	H
Hairy woodpecker ( <i>Picoides villosus</i> )	5S	39	26	0.28	0.20	H	M
	5P	33	14	0.24	0.27	H	M
	5M	19	10	0.10	0.14	H	M
	5D	25	25	0.11	0.09	H	M
White-headed woodpecker ( <i>Picoides albolarvatus</i> )	5S	61	10	0.44	0.31	M	M
	5P	34	19	0.17	0.13	M	M
	5M	34	13	0.20	0.24	M	M
	5D	33	38	0.25	0.23	L	M
Black-backed woodpecker ( <i>Picoides arcticus</i> )	5S	11	19	0.06	0.09	L	M
	5P	4	8	0.06	0.16	L	M
	5M	13	7	0.07	0.17	L	M
	5D	33	14	0.17	0.19	L	H

Table 1. Continued.

Species	Structural <sup>1</sup> class	Frequency		Abundance		Predictions <sup>2</sup>	
		mean	SD	mean	SD	WHR	HV <sup>3</sup>
Northern flicker ( <i>Colaptes auratus</i> )	5S	78	19	0.67	0.43	L	L
	5P	50	25	0.26	0.32	L	L
	5M	46	13	0.28	0.23	L	L
	5D	67	38	0.44	0.24	L	L
Pileated woodpecker ( <i>Dryocopus pileatus</i> )	5S	6	10	0.02	0.05	L	L
	5P	4	8	0.01	0.04	L	L
	5M	19	17	0.06	0.08	M	M
	5D	25	0	0.08	0.17	M	M
Olive-sided flycatcher ( <i>Contopus borealis</i> )	5S	67	0	0.52	0.57	H	H
	5P	25	0	0.17	0.29	H	M
	5M	19	10	0.09	0.17	M	M
	5D	50	25	0.25	0.21	L	M
Western wood-pewee ( <i>Contopus sordidulus</i> )	5S	78	9	1.28	1.23	H	H
	5P	71	7	0.81	0.83	H	H
	5M	71	16	1.01	0.96	H	H
	5D	75	0	0.61	0.64	M	H
Hammond's flycatcher ( <i>Empidonax hammondi</i> )	5S	45	25	0.43	0.18	-	M
	5P	75	13	0.85	0.74	-	H
	5M	65	3	0.91	0.78	M	H
	5D	67	14	1.25	1.08	H	H
Dusky flycatcher ( <i>Empidonax oberholseri</i> )	5S	83	17	2.04	1.19	-	M
	5P	75	13	0.83	0.61	-	M
	5M	23	7	0.19	0.29	-	L
	5D	33	14	0.19	0.32	-	L
Steller's jay ( <i>Cyanocitta stelleri</i> )	5S	83	0	1.02	0.74	-	H
	5P	75	22	0.96	0.86	L	H
	5M	83	4	1.31	0.85	M	H
	5D	92	14	1.72	1.11	M	H
Clark's nutcracker ( <i>Nucifraga columbiana</i> )	5S	56	10	0.37	0.31	-	L
	5P	33	29	0.15	0.18	-	L
	5M	15	3	0.10	0.16	-	L
	5D	8	14	0.14	0.28	-	L
Mountain chickadee ( <i>Parus gambeli</i> )	5S	100	0	4.00	1.17	H	H
	5P	96	7	2.32	0.70	H	H
	5M	98	3	2.21	0.77	H	H
	5D	100	0	2.56	1.36	H	H
Red-breasted nuthatch ( <i>Sitta canadensis</i> )	5S	100	0	2.61	0.59	L	H
	5P	96	7	2.49	0.78	M	H
	5M	100	0	2.53	0.57	H	H
	5D	100	0	3.44	0.61	H	H

Table 1. Continued.

Species	Structural <sup>1</sup> class	Frequency		Abundance		Predictions <sup>2</sup>	
		mean	SD	mean	SD	WHR	HV <sup>3</sup>
White-breasted nuthatch ( <i>Sitta carolinensis</i> )	5S	17	17	0.11	0.17	L	L
	5P	4	8	0.03	0.08	L	L
	5M	17	10	0.09	0.12	L	L
	5D	0	0	0.00	0.00	L	-
Brown creeper ( <i>Certhia americana</i> )	5S	61	26	0.35	0.33	-	L
	5P	67	36	0.63	0.25	-	M
	5M	90	10	0.92	0.37	M	M
	5D	100	0	1.55	0.33	H	H
Winter wren ( <i>Troglodytes troglodytes</i> )	5S	6	10	0.04	0.09	-	L
	5P	21	7	0.08	0.13	-	L
	5M	48	16	0.42	0.52	L	M
	5D	25	25	0.19	0.25	M	M
Golden-crowned kinglet ( <i>Regulus satrapa</i> )	5S	94	10	1.85	1.10	-	L
	5P	100	0	2.86	0.76	M	M
	5M	100	0	3.78	1.02	H	H
	5D	100	0	4.33	1.28	H	H
Ruby-crowned kinglet ( <i>Regulus calendula</i> )	5S	11	19	0.04	0.06	-	L*
	5P	4	8	0.03	0.08	H	L*
	5M	6	11	0.02	0.04	H	L*
	5D	0	0	0.00	0.00	M	.*
Western bluebird ( <i>Sialia mexicana</i> )	5S	28	25	0.19	0.25	L	L
	5P	25	33	0.18	0.30	L	L
	5M	19	13	0.07	0.11	-	L
	5D	8	14	0.03	0.06	-	L
Mountain bluebird ( <i>Sialia currucoides</i> )	5S	11	10	0.04	0.09	-	L
	5P	4	8	0.01	0.04	-	L
	5M	0	0	0.00	0.00	-	-
	5D	0	0	0.00	0.00	-	-
Townsend's solitaire ( <i>Myadestes townsendi</i> )	5S	83	17	0.57	0.34	M	M
	5P	88	13	0.47	0.23	M	M
	5M	69	13	0.49	0.32	L	M
	5D	58	14	0.39	0.29	-	M
Swainson's thrush ( <i>Catharus ustulatus</i> )	5S	0	0	0.00	0.00	-	-
	5P	4	8	0.01	0.04	M	L
	5M	0	0	0.00	0.00	M	-
	5D	0	0	0.00	0.00	M	-
Hermit thrush ( <i>Catharus guttatus</i> )	5S	89	10	1.46	0.75	-	M
	5P	100	0	1.61	0.38	-	M
	5M	96	7	1.81	0.83	L	M
	5D	92	14	1.92	1.07	M	M



Table 1. Continued.

Species	Structural <sup>1</sup> class	Frequency		Abundance		Predictions <sup>2</sup>	
		mean	SD	mean	SD	WHR	HV <sup>3</sup>
Green-tailed towhee ( <i>Pipilo chlorurus</i> )	5S	28	19	0.33	0.52	M	L
	5P	17	19	0.06	0.06	-	L
	5M	12	11	0.10	0.26	-	L
	5D	8	14	0.03	0.06	-	L
Chipping sparrow ( <i>Spizella passerina</i> )	5S	72	25	0.72	0.71	H	M*
	5P	38	13	0.24	0.21	M	L*
	5M	48	28	0.26	0.18	L	L*
	5D	8	14	0.03	0.06	-	L*
Fox sparrow ( <i>Passerella iliaca</i> )	5S	78	9	2.11	2.56	M	H
	5P	38	21	0.21	0.30	M	M
	5M	40	8	0.51	0.89	L	M
	5D	33	14	0.81	1.47	-	M
Lincoln's sparrow ( <i>Melospiza lincolni</i> )	5S	6	10	0.02	0.05	-	L
	5P	4	8	0.01	0.04	-	L
	5M	8	10	0.03	0.08	-	L
	5D	17	14	0.14	0.28	-	L
Dark-eyed junco ( <i>Junco hyemalis</i> )	5S	100	0	4.54	1.34	H	H
	5P	100	0	4.49	1.53	H	H
	5M	100	0	5.10	1.19	M	H
	5D	100	0	4.17	1.03	L	H
Brown-headed cowbird ( <i>Molothrus ater</i> )	5S	6	10	0.02	0.05	L	L
	5P	4	8	0.01	0.04	L	L
	5M	31	7	0.18	0.23	L	L
	5D	8	14	0.03	0.06	L	L
Pine grosbeak ( <i>Pinicola enucleator</i> )	5S	33	34	0.24	0.29	M	M
	5P	13	22	0.06	0.08	M	M
	5M	13	7	0.06	0.15	M	M
	5D	17	14	0.14	0.28	L	M
Purple finch ( <i>Carpodacus purpureus</i> )	5S	6	10	0.02	0.05	-	L
	5P	17	19	0.07	0.08	-	L
	5M	4	3	0.01	0.04	-	L
	5D	0	0	0.00	0.00	-	-
Cassin's finch ( <i>Carpodacus cassinii</i> )	5S	100	0	2.67	1.08	M	H
	5P	96	7	1.60	0.78	M	M
	5M	81	11	1.19	0.92	M	M
	5D	92	14	1.03	0.43	L	M
Red crossbill ( <i>Loxia curvirostra</i> )	5S	50	33	0.78	0.88	L	M
	5P	25	22	0.25	0.33	L	L
	5M	21	7	0.14	0.24	L	L
	5D	42	29	0.17	0.14	L	L

Table 1. Continued.

Species	Structural <sup>1</sup> class	Frequency		Abundance		Predictions <sup>2</sup>	
		mean	SD	mean	SD	WHR	HV <sup>3</sup>
Pine siskin ( <i>Carduelis pinus</i> )	5S	94	10	1.48	0.73	M	M
	5P	100	0	1.78	0.62	M	M
	5M	98	3	1.81	0.78	L	M
	5D	92	14	1.25	0.55	-	M
Evening grosbeak ( <i>Coccothraustes vespertinus</i> )	5S	33	29	0.31	0.26	-	M
	5P	29	8	0.17	0.22	M	M
	5M	31	13	0.21	0.18	H	M
	5D	33	14	0.22	0.24	M	M

<sup>1</sup> Structural classes are S = medium/large trees for size class and, for canopy-closure classes, S (sparse) = 10-24%, P (open) = 25-39%, M (moderate) = 40-59%, and D (dense) = 60-100%.

<sup>2</sup> Habitat ratings are low (L), medium (M), high (H), historically present in much higher numbers (\*), and none of this species breeds in this structural class (-). Number of study sites in each structural class was 5S = 6, 5P = 8, 5M = 16, and 5D = 4.

<sup>3</sup> Historic ratings were based on information from Beedy (1982).

such as latilongs as a basis for predictive models may lead to errors. For example, an area in a certain habitat type on the east slope of the Sierra Nevada may have a somewhat different avifauna from that of an area in the same habitat on the west slope. Thus conclusions from our data, which were collected in red fir habitats on the west slope, do not necessarily apply to similar habitats on the east slope.

Because our frequency and abundance estimates were most likely lower than during average years, we recommend that most of the bird species that were present on our sites but not predicted in the matrices (the most serious type of matrix error from the manager's standpoint) should now be included in the WHR models. We agree with Raphael and Marcot (1986) that adjustments in the matrix are clearly needed for marked differences in habitat suitability. For example, the CDFG matrix did not predict Hammond's flycatcher in 5P, but we rated the habitat suitability of 5P as high for that species. However, whether adjustments should be made for species with small changes in habitat suitability or those detected in low abundance or frequency is not clear. Those species that were encountered on only a few sites or in only one year (for example, calliope hummingbird and Swainson's thrush) may not be present often enough to be included in the matrices. Vagaries in habitat selection of individual birds could lead to misinterpretations of habitat suitability. However, evidence from other researchers

can supplement information for decisions about habitat value. Calliope hummingbirds were also found during the breeding season in red fir by Beedy (1982) and Granholm (1982), and we believe that they should be included in a revised WHR. Whether all additional species that were detected in our study will continue to breed in red fir forests is unknown, but we expect that those in high numbers will use the habitat in future years.

We reluctantly decreased ratings of species from those of CDFG, and we do not necessarily recommend changes in the WHR matrix data base for those species. Sampling error (low number of study sites in a category) as well as population fluctuations could have caused our lower ratings. It is highly likely that some species, such as the hermit warbler, were in the trough of a short-term population fluctuation during the period of our study. Hermit warblers increased slightly during the years of our study (from nine detections in 1983 to 15 in 1985 over all 34 sites), and continued to increase on the only two of our sites that were sampled in 1986 (nine total detections for the two sites) and 1987 (ten total detections for the two sites). These increases paralleled those of two more intensively studied populations that have been documented on research areas near the geographic center of our 34 sites: hermit warbler numbers increased from 20 to 24.5 to 43.5/42 ha during the summers of 1985, 1986, and 1987 at a site supporting old-growth mixed-coniferous/

Table 2. Comparison of CDFG's WHR predictions to those of Hejl and Verner (HV) for the 52 species listed in Table 1. Values represent the number of species in each category.

HV Predictions	Structural class <sup>1</sup>	WHR predictions			
		Absent	Low	Medium	High
Absent	5S	4	1	0	0
	5P	2	1	0	0
	5M	2	1	1	0
	5D	5	3	2	0
Low	5S	12	7	1	0
	5P	11	8	3	1
	5M	13	6	1	1
	5D	10	4	1	0
Medium	5S	4	4	6	2
	5P	3	2	9	2
	5M	0	7	8	2
	5D	3	6	4	1
High	5S	1	2	2	6
	5P	1	2	1	6
	5M	0	1	4	5
	5D	0	4	3	6

<sup>1</sup> Size class 5 = medium/large trees. Canopy closure: S (sparse) = 10-24%, P (open) = 25-39%, M (moderate) = 40-59%, and D (dense) = 60-100%.

red fir forest transition (Labinger et al. 1985, Lovio et al. 1986, Suydam et al. 1987) and increased from 29 to 34.5 to 40/42 ha at a site supporting mature upper mixed-coniferous forest-montane chaparral during the same summers (Lovio et al. 1985, Milne et al. 1986, Milne et al. 1987).

Dilemmas in predicting the suitability of a particular habitat also stem from long-term population changes of individual species. Dedon et al. (1986) noted that WHR models were designed conservatively. Accordingly, if experts believed that a species could breed in a given habitat, it was so coded. In the early 1900s, ruby-crowned kinglets commonly bred in red fir of the Yosemite region (Grinnell and Storer 1924). This fact is a possible reason for high habitat ratings in the WHR system. Today, in the western Sierra Nevada, ruby-crowned kinglets breed mostly (although uncommonly) in subalpine forests, especially in lodgepole pine (*Pinus contorta*) (Beedy 1982, Gaines 1988). No one knows whether the abundance of ruby-crowned kinglets will increase in the future in red fir habitat. Contrarily, golden-crowned kinglets uncommonly bred in red fir in the early 1900s but they are abundant there today (Beedy 1982).

We do not know if some of the marked differences in CDFG's and our predictions are due to incorrect estimates of habitat suitability or to problems associated with long-term population changes. We do not understand why Swainson's thrushes were given a high rating, as they were not listed in red fir by Verner and Boss (1980) and they were not found breeding in red fir by Beedy (1981, 1982) or Granholm (1982). Historically, they were documented as uncommon breeders in low-elevation ponderosa pine (*Pinus ponderosa*) forests, rare breeders in mid-elevation mixed-conifer forests, and absent from upper-elevation red fir forests in the central Sierra Nevada (Beedy 1982). Recently, Swainson's thrushes have bred rarely, if at all, in the central and southern Sierra Nevada: one record in this paper, one observed by us in 1982, and detections at three localities reported by Beedy and Granholm (1985) and Gaines (1988). Marshall (1988) estimated 12 pairs per km<sup>2</sup> in Whitaker's Forest in the southern Sierra Nevada in the 1930s, but none was detected in the 1960s or in 1986. However, it is possible that their numbers are currently increasing in the northern Sierra Nevada (several detections per summer at University of California's Blodgett Experimental Forest during the summers of 1982-1984,

Table 3. Summary of severity of prediction differences between CDFG's WHR predictions to those of Hejl and Verner. Values are number of species in each category, with percent in parentheses.

Class	Severity of prediction differences			
	None	Low <sup>1</sup>	Moderate <sup>2</sup>	Great <sup>3</sup>
5S	23 (44)	22 (42)	6 (12)	1 (2)
5P	25 (48)	20 (38)	6 (12)	1 (2)
5M	21 (40)	28 (54)	3 (6)	0
5D	19 (37)	24 (46)	9 (17)	0

<sup>1</sup> Low difference = absent to low, low to medium, medium to high.

<sup>2</sup> Moderate difference = absent to medium, low to high.

<sup>3</sup> Great difference = absent to high.

S. A. Laymon, pers. comm.) and may increase in the southern Sierra Nevada in the future. We believe that the models should (1) reflect current numbers in the low, medium, and high habitat ratings, (2) at least include a historic designation for the indication of a long-term population decrease, and (3) be updated periodically.

We acknowledge that our decisions were subjective, as were those of the creators of the CDFG matrices. Our two major difficulties were assessing the likelihood that a species actually bred in a habitat and estimating the relative probability of its occurrence (habitat rating) from our data. Breeding status of a species was inferred from the literature as well as from field evidence, because we could not find nests of all species on each site. For example, although we repeatedly detected them on many sites, we did not include the house wren (*Troglodytes aedon*) and orange-crowned warbler (*Vermivora celata*) in our analysis of breeders, because they are known to breed downslope and move into red fir forests in late summer (Verner and Boss 1980, Gaines 1988). Our greatest doubt concerned whether or not the Clark's nutcracker breeds in these forests. We do not know whether this species regularly breeds in red fir forests or moves into them after breeding in the eastern Sierra Nevada (see Verner and Boss 1980, Beedy and Granholm 1985, Gaines 1988). However, we have winter records of nutcrackers on one Yosemite study site, indicating that these early spring breeders may indeed breed on the west slope, and not all move over to the east slope for the winter and spring breeding.

The most difficult step in our work was evaluating the relative probabilities of occurrence and deriving habitat suitability ratings from these probabilities. Each species was separately rated for a habitat by comparing data from our field detections to its presence and abundance in all

other habitats in the state and throughout its range, in a manner similar to that used by authors of CDFG's WHR predictions. One way to determine these categories objectively would be to obtain counts and breeding-success information for all habitats for many years throughout a species' range. Because such data do not exist, we used our knowledge from field experience in other habitats, consulted the literature, and used the opinions of other naturalists to arrive at proposed changes in species-habitat ratings. These are simply our best estimates and should be treated as such. We expect further refinements as others gather data in red fir and other habitats in the future.

Surprisingly, canopy cover was not an obviously important predictor of the presence and/or abundance of many species in our red fir sites. Our ratings for 54 percent of the species were the same for all canopy-closure classes, even though the existence of predetermined canopy-closure classes caused us to try to differentiate our ratings among these classes. Some species showed differences, but we lacked objective criteria for deciding what level of difference was sufficient to distinguish between low and medium, or between medium and high habitat capabilities. Moreover, some of the observed differences may have resulted from sampling error. We preferred to use subjective judgment based on frequency and abundance data for our ratings, because we had neither large nor even sample sizes. We doubt that statistics could really help in these assessments unless we had large and fairly even samples from throughout the range of each species.

Canopy cover was an important correlate for a few species, such as the golden-crowned kinglet (Hejl 1987), but it was not for most species. Many species that were not listed by CDFG in the more open structural

classes are widely recognized as typical forest species, and many that were not listed in the more closed structural classes were typical open-area species. For example, Hammond's flycatchers are described as inhabiting shady forests and dusky flycatchers as inhabiting sunny, open forests, forest edges, and shrub-covered slopes (Beedy and Granholm 1985, Gaines 1988). Dusky flycatchers were predicted by the CDFG system to occur only in sparse and open classes of younger stands, and Hammond's flycatchers were predicted only in moderate and dense classes of the small and medium/large-tree classes. Although dusky flycatchers were more abundant in our open stands and Hammond's flycatchers were more abundant in closed ones, both species occurred in all classes. We attribute these results to the fact that even fairly homogeneous stands in our study were actually mixtures of open areas and trees, and we believe this to be typical throughout red fir forests of the Sierra Nevada. Similarly, the obligate shrub-nesting fox sparrow might be expected to be more abundant in stands with less tree canopy. Fox sparrow numbers were correlated with shrub species richness (Hejl 1987), and one might expect greater shrub richness in open stands. Although fox sparrow counts were highest in our more open stands, shrub richness did not correlate with canopy cover (SJH, pers. obs.), and fox sparrows occurred in all classes because shrubs occurred in all.

Perhaps the poor predictability of canopy cover arises not from its lack of predictive power but, instead, from the chosen levels of canopy-closure classes. We attempted to find equal numbers of large stands in all canopy classes when we defined our study, but we found few stands with canopy cover exceeding 60 percent. As our sites were randomly drawn from a large sample of suitable sites, we believe that they accurately represented older red fir stands in the central and southern Sierra Nevada. Dense-canopied, older stands of red fir are probably rare or nonexistent. A simple scheme based on just two canopy-closure classes, open and moderate, might function better for the WHR system in older red fir forests, as dense stands do not exist and few bird species seem to correlate with small differences in canopy cover.

An important management consideration in the use of WHR is that naturally sparse or open stands may not have the same assemblages of bird species or individuals as managed stands. The goals of CDFG's WHR System include helping wildlife management decisions by providing predictive models of habitat value and being used to predict changes in wildlife that accompany habitat change (Salwasser and Laudenslayer 1982). Most of our stands had not obviously been disturbed by man. We suggest the creation of separate categories for managed and unmanaged stands. The effects of natural or man-

caused disturbances on habitat suitability probably differ, are species specific, and depend on factors other than canopy cover, such as size of a stand, foliage volume, the density and dbh of snags, the decay state of snags, shrub foliage volume, the extent of herbaceous understory, and the juxtaposition of different habitat types.

Finally, we believe that the habitat-rating designations (high, medium, and low) used in the CDFG system are ambiguous. They could be correctly understood to designate habitat capability for a given species, or they could be misinterpreted to designate simply abundance or density classes for a given species in a structural class. We recommend a return to the designations (optimum, suitable, and marginal) used earlier in Forest Service documents (Marcot 1979, Verner and Boss 1980, Laudenslayer and Airola 1982). These designations convey the same basic notions about habitat capability as high, medium, and low but could not easily be misinterpreted to refer to species' abundances. For example, we speculate that our disagreement with the CDFG's ratings for the black-backed woodpecker resulted from confusion over the intended meanings of the high, medium, and low classes. When compiling the data for the CDFG system, contractors were instructed to rate each species independently of others. The black-backed woodpecker had low ratings in CDFG's WHR predictions for red fir 5S through 5D habitats, but optimum ratings in Verner and Boss's predictions for the same habitats. We rated them as medium to high, depending on canopy closure. We suspect that the low rating on the CDFG printout resulted erroneously from the fact that black-backed woodpeckers are low in numbers in red fir, in spite of the fact that red fir is probably suitable to optimum (CDFG's medium to high) breeding habitat for this species in comparison to other habitats throughout its range. Unfortunately, as Van Horne (1983) emphasized, density can be a misleading indicator of habitat quality. However, until we have reproductive data for each species throughout its range, decisions about habitat suitability will be based on relative frequency and abundance.

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## LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Allen Press, Inc., Lawrence, Kans. 877pp.
- \_\_\_\_\_. 1985. Thirty-fifth supplement to the American Ornithologists' Union check-list of North American birds. *Auk* 102:680-686.
- BEDDY, E.C. 1981. Bird communities and forest structure in the Sierra Nevada of California. *Condor* 83:97-105.
- \_\_\_\_\_. 1982. Bird community structure in coniferous forests of Yosemite National Park, California. Unpubl. Ph.D. Dissertation, University of California, Davis. 167pp.
- \_\_\_\_\_, and S.L. GRANHOLM. 1985. Discovering Sierra birds. Yosemite Natural History Association and Sequoia Natural History Association, USA. 229pp.
- DEDON, M.F., S.A. LAYMON, and R.H. BARRETT. 1986. Evaluating models of wildlife-habitat relationships of birds in black oak and mixed-conifer habitats. Pages 115-119 in J. Verner, M.L. Morrison, and C.J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- DESANTE, D.F. 1985. Births, deaths, or immigration: what controls the numbers of subalpine birds? *Point Reyes Bird Observatory Newsletter* 71:1-5.
- GAINES, D. 1988. Birds of Yosemite and the east slope. Artemisia Press, Lee Vining, Calif. 352pp.
- GRANHOLM, S.L. 1982. Effects of surface fires on birds and their habitat associations in coniferous forests of the Sierra Nevada, California. Unpubl. Ph.D. Dissertation, University of California, Davis. 130pp.
- GRINNELL, J., and A.H. MILLER. 1944. The distribution of the birds of California. *Pacific Coast Avifauna* 27:1-608.
- \_\_\_\_\_, and T.I. STORER. 1924. Animal life in the Yosemite: an account of mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada. University of California Press, Berkeley. 741pp.
- HEJL, S.J. 1987. Bird assemblages in true fir forests of the western Sierra Nevada. Unpubl. Ph.D. Dissertation, Northern Arizona University, Flagstaff. 144pp.
- \_\_\_\_\_, J. VERNER, and R.P. BALDA. 1988. Weather and bird populations in true fir forests of the Sierra Nevada, California. *Condor* 90:561-574.
- LABINGER, Z., T.E. HOSLER, M.A. FLETT-LAMBERT, and S.J. KUPFERBERG. 1985. Breeding bird census: old-growth mixed-coniferous/red fir forest transition. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.
- LAUDENSLAYER, W.F., JR., and D.A. AIROLA, eds. 1982. Northeast interior zone, vol. 1, introduction and species-habitat relationships matrix. U.S. Forest Service, Pacific Southwest Region, San Francisco. 161pp.
- LOVIO, J.C., C.R. CUTLER, B.R. NORTH, and J.L. SEAY. 1986. Breeding bird census: old-growth mixed-coniferous/red fir forest transition. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.
- \_\_\_\_\_, K.A. MILNE, R.S. SUYDAM, and C.R. CUTLER. 1985. Breeding bird census: mature upper mixed-coniferous forest—montane chaparral. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.
- MARCOT, B.G., ed. 1979. California wildlife/habitat relationships program: north coast/Cascades zone. Volumes 1-4. U.S. Forest Service, Six Rivers National Forest, Eureka, Calif. 899pp.
- MARSHALL, J.T. 1988. Birds lost from a giant sequoia forest during fifty years. *Condor* 90:359-372.
- MEWALDT, L.R., and S.G. TORRES. 1982. Bird species-habitat relationships matrix. Pages 45-123 in W.F. Laudenslayer, Jr., and D.A. Airola, eds. Northeast interior zone, vol. 1, introduction and species-habitat relationships matrix. U.S. Forest Service, Pacific Southwest Region, San Francisco.
- MILNE, K.A., W.R. MAYNARD, and B.R. NORTH. 1987. Breeding bird census: mature upper mixed-coniferous forest—montane chaparral. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.
- MILNE, K.A., R.S. SUYDAM, and R.J. REYNOLDS. 1986. Breeding bird census: mature upper mixed-coniferous forest—montane chaparral. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.

- RAPHAEL, M.G., and B.G. MARCOT. 1986. Validation of a wildlife-habitat-relationships model: vertebrates in a Douglas-fir sere. Pages 129-138 in J. Verner, M.L. Morrison, and C.J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison.
- RUNDEL, P.W., D.J. PARSONS, and D.T. GORDON. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. Pages 559-599 in M.G. Barbour and J. Major, eds. *Terrestrial vegetation of California*. John Wiley and Sons, New York.
- SALWASSER, H., J.C. CAPP, H. BLACK, JR., and J.F. HURLEY. 1980. The California wildlife habitat relationships program: an overview. Pages 369-378 in R.M. DeGraaf, tech. coord. *Management of western forests and grasslands for nongame birds: proceedings of the workshop*. U.S. Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-86, Ogden, UT.
- \_\_\_\_\_, and W.F. LAUDENSLAYER, JR. 1982. *California wildlife and fish habitat relationships (WFHR) system: products and standards for wildlife*. Photocopy from California Interagency Wildlife Task Group, through U.S. Forest Service, Pacific Southwest Region. 125pp.
- SUYDAM, R.S., K.M. BURTON, J. SEAY, C. STEGALL, D.M. TAYLOR, and E.D. WHISLER. 1987. Breeding bird census: old-growth mixed-coniferous/red fir forest transition. Manuscript and data stored in data base management system at Cornell Laboratory of Ornithology, Ithaca, NY.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47:893-901.
- VERNER, J. 1980. Bird communities of mixed-conifer forests of the Sierra Nevada. Pages 198-223 in R.M. DeGraaf, tech. coord. *Management of western forests and grasslands for nongame birds: proceedings of the workshop*. U.S. Forest Service, Intermountain Forest and Range Experiment Station, General Technical Report INT-86, Ogden, UT.
- \_\_\_\_\_, and A. S. BOSS. 1980. *California wildlife and their habitats: western Sierra Nevada*. U.S. Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-37, Berkeley, Calif. 439pp.