EVALUATING AVIAN-HABITAT RELATIONSHIPS MODELS IN MIXED-CONIFER FORESTS OF THE SIERRA NEVADA

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Abstract: Using data from two studies in the southern and central Sierra Nevada, we compared the presence and abundance of bird species breeding in mixed-conifer forests during 1978-79 and 1983-85 to predictions from the California Wildlife Habitat Relationships (WHR) System. Twelve percent of the species observed in either study were not predicted by the WHR database to occur in mixed-conifer vegetation (errors of omission). Twenty-eight percent of the species predicted by the database were not observed in either study (errors of commission). We suggest several corrections to the WHR database and discuss the problems of classifying stands, predicting the effects of management activities, evaluating habitat quality, and regional differences in habitat suitability. Because California is a large and diverse state, geographic differences in habitat suitability within a species' range need to be considered by biologists using the WHR database. We suggest subdividing the database into several bioregional zones.

The California Wildlife Habitat Relationships (WHR) system was developed cooperatively by federal, state, academic, and private organizations to organize and summarize existing wildlife information for the state (Mayer and Laudenslayer 1988). Information on the distribution, habitat requirements, life histories, and status of all terrestrial vertebrates that occur regularly in the state are accessible through a computerized database. The WHR database was designed to aid wildlife managers in making land management decisions and in evaluating the impacts of vegetation change on individual species and on entire wildlife communities. In developing the WHR database, information on the occurrence of wildlife species in specific vegetation types was provided by wildlife biologists who made predictions based on literature reviews, their professional field experience, and the opinions of other naturalists. The vegetation classification system is described in Mayer and Laudenslayer (1988). Tree-dominated vegetation types are divided into discrete structural classes based on tree size and canopy closure.

The value of the WHR database depends on the accuracy of its predictions. Predictive models need to be tested, refined, and updated to be useful. Few tests of the WHR database have been reported to date and none have tested the mixed-conifer vegetation type (e. g., England and Anderson 1985, Hejl and Verner 1988, Avery and Van Riper 1990).

Underlying assumptions are inherent in any model. For the WHR database these include: (1) a species' distribution and likelihood of occurrence can be predicted by vegetation type, (2) habitats can be described by simple and easily measured structural characteristics such as tree size and canopy cover, (3) habitat quality can be determined for each species and suitability for reproduction reflects reproductive success and ultimately population density, and (4) the value of a vegetation type is uniform throughout a species' range (Airola 1988).

When using or testing a predictive database, a lack of correspondence between predictions and observations can occur in two ways. The first is called an error of omission and occurs when a species is detected in the field but not predicted to occur by the database. The second is an error of commission and occurs when a species is predicted by the database and not observed in the field. Minimizing errors of omission will affect errors of commission and vice versa. Errors of omission are potentially more serious than errors of commission in a predictive database because these may result in inadequate attention to species during management actions. Inadequate sampling, including sampling too few sites over too few seasons, or poor latitudinal or elevational coverage often mistakenly indicates errors of commission. When testing WHR, however, suggested corrections should be based on many site/year combinations and a close correspondence between predictions and observations is expected.

Our objective is to evaluate the WHR database for bird species breeding in mixed-conifer forests using data from two studies (Larson 1981, Hejl 1987) in the central and southern Sierra Nevada. We compare the WHR database predictions with field data from these studies and suggest corrections to the database to increase the reliability and usefulness of the model.

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STUDY AREAS

Larson Study

Forty-nine sites were sampled during the 1978 and 1979 breeding seasons in mixed-conifer forests of the Sierra National Forest. Three sites were virgin forest and forty-six had been subjected to various logging treatments, from clearcutting to selective overstory removal. Logged sites had been subjected to various postlogging treatments such as shrub removal, slash burning, thinning, and planting of seedlings. All logged sites were surrounded by forest. Stand sizes were measured using timber sale maps and aerial photographs, and ranged from 1-80 ha. Elevations ranged from 1646-2316 m.

Hejl Study

Seventeen sites in white fir (*Abies concolor*) forests, a subcategory of mixed-conifer forests (Airola 1988) were sampled in Sequoia National Park (8 sites), Sierra National Forest (8 sites), and Yosemite National Park (1 site) during the 1983-1985 breeding seasons. All sites had 50% or more of total foliage volume consisting of white fir, were situated in mature to old-growth stands of trees homogeneous in size class and canopy-closure class, and were located in stands at least 10 ha in size. An attempt was made to find stands that represented the full range of canopy closures. One site was located within each stand. Five sites had been partially logged. All sites were at least 400 m apart and most were 800 m apart, in an attempt to assure independent measurements.

METHODS

Bird Observations

Larson Study.--Birds were counted on 7 days at each site by the same observer during the 1978 and 1979 breeding seasons (mid-May to mid-July). Seven to 10 sites were sampled each day from about 1/2 to 4-1/2 hours after sunrise. Sampling order of sites was rotated over the 7 count days to standardize potential time-of-day bias. All birds detected within the stand during a 10-minute period were recorded. *Empidonax* flycatchers were not identified to species and were excluded from this analysis. See Verner and Larson (1989) for more details on study design.

Hejl Study.--Counting was conducted at each site on a randomly placed transect 200 m long. Counting points were located at the beginning, middle, and end of each transect; birds were also counted along the transect between the three counting points.

Hejl counted birds 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. All birds detected during an 8-minute period were recorded at each of the three counting stations, with two transect counts interspersed between the three points. Observers recorded each bird using the stand, regardless of its distance from the observer, and attempted to avoid double-counting individuals as they proceeded from point count to transect to point count. All counts were conducted between 0530 and 1130 PDT.

Site Classification

Sites were categorized using WHR's criteria for structural classes according to tree size and canopy closure (Mayer and Laudenslayer 1988:16). Tree size classes include (1) seedling (dbh <1"), (2) sapling (dbh 1-6"), (3) pole (dbh 6-11"), (4) small (dbh 11-24"), (5) medium-large (dbh > 24"), and (6) multi-layered (medium-large trees over a distinct layer of small or pole-sized trees). Canopy-closure classes are defined as: sparse (S) = 10 to 24% cover, open (P) = 25 to 39% cover, moderate (M) = 40 to 59% cover, and dense (D) = 60 to 100% cover.

Larson Study.--Canopy cover was measured using a point intercept method at 50-100 points (depending on the size and shape of the site) placed at 20-m intervals. Sites were classified into size-classes using on-the-ground knowledge of the sites and vegetation data. Three of the 49 sites were too heterogeneous to classify, containing all sizes of trees in a patchy distribution: these were excluded from the analysis. Two sites were multi-layered stands that had been thinned, resulting in an estimated canopy cover of 46% for both. According to the WHR classifications, multi-layered stands have greater than 60% total canopy cover. For this reason, these 2 sites were excluded from analysis. Thirteen sites had been clearcut but had residual patches of trees of varying sizes which we believed would affect bird species composition and richness. These sites were examined as separate categories but were excluded from analysis.

The remaining 31 stands were classified into 13 categories: seedling ($n = 5$), sapling sparse ($n = 3$), pole-sized open ($n = 5$), pole-sized moderate ($n = 2$), pole-sized dense ($n = 1$), small tree sparse ($n = 2$), small tree open ($n = 3$), small tree moderate ($n = 3$), medium-large tree sparse ($n = 1$), medium-large tree open ($n = 1$), medium-large tree moderate ($n = 1$), medium-large tree dense ($n = 1$), and multi-layered tree ($n = 3$).

Hejl Study.--Canopy closure estimates for each site were based on the presence or absence of canopy above ten randomly located points in each of six randomly located 15x15-m quadrats on each site (Hejl 1987). Size classes were based on visual examination and vegetation data. All sites were in the medium-large tree size-class and included one sparse site, 13 moderate sites, and three dense sites.

Evaluating the WHR Model

We evaluated all detections of adult birds that were determined to be using the stand. Raptors, ducks, ravens, crows, and aerial feeders were excluded from the analysis, as our methods precluded adequate counts of them. Because counts were done during the breeding season and we included only species believed to be breeding on the sites, only the "reproduction" column of the WHR matrix was examined. Breeding status on the sites was determined from the presence of nests, fledglings, or frequently singing males found on or near the study sites.

The WHR model was first tested at the general level of presence/absence over all size class/cover categories represented in the mixed-conifer vegetation type in each study. Individual categories were not examined, as many of the categories were represented by fewer than 4 sites, and several by only one site. "Present" species were defined as those species predicted (or observed) in at least one of the categories represented; "absent" species were defined as those not predicted (or observed) in any of the categories represented.

We arbitrarily accepted sample sizes of ≥ 5 sites to examine habitat suitability ratings, representing an effort of 70 minutes per site in each of two breeding seasons in the Larson study and more than 72 minutes in each of three breeding seasons in the Hejl study. Habitat suitability ratings were examined for two vegetation categories in the Larson study (seedling and pole-sized open) and one category in the Hejl study (medium-large moderate). Average frequency was calculated for each bird species as the mean percent of sites with detections in a year, averaged over years. Average abundance was calculated from the mean number of detections per visit to a stand, averaged over years. Standard deviations for both parameters were computed over years.

We evaluated habitat suitability for each species according to the criteria described in Airola (1988:19) relative to other habitats in California and throughout its range. WHR habitat ratings are defined as: high = habitat that can support a high population density (as implied by probability of occurrence), medium = habitat that can support a moderate population density (as implied by probability of occurrence), low = habitat that can support a low population density (as implied by probability of occurrence), and not used = the species is not expected to occur in the habitat.

Our predictions for habitat suitability ratings were necessarily somewhat subjective. We could not rigorously quantify criteria for assigning ratings because territories differ in size between species, show different degrees of saturation, and detectability varies between species. Therefore, we examined each species individually, relative to its suitability in all other vegetation types, as does WHR. We used our knowledge from field experience in other locations and vegetation types, consulted the literature, and solicited the opinions of other naturalists. We generally weighted frequency more heavily than abundance, except when the standard deviation was high. We compared frequencies and abundances for that species to other categories and from other studies to obtain an estimate of the ranges in frequency and abundance encountered. For example, dark-eyed junco (*Junco hyemalis*) is a widespread, easily-detected species which often reaches a frequency of 1.0, with variable abundance. Therefore the quality of a given vegetation type for juncos is better reflected by abundances across vegetation types.

We compared our results with predictions from the August 1990 version of the WHR database for the Yosemite latilong in the Sierra Nevada. All of Larson's sites were within 7 km of the latilong. Hejl's eight sites in Sequoia National Park were approximately 22 km southeast of the latilong. All categories for seasons in location and seasons in habitat were included. No habitat elements were specified in the habitat reports.

RESULTS

Presence/Absence

Larson Study.--Forty-two bird species were detected as probable breeders on the 31 sites examined in the 13 categories (Table 1, following Literature Cited section). Three of these species were not predicted by the WHR habitat reports to occur in mixed-conifer stands.

Sixty-two species were predicted to occur in at least one of the 13 mixed-conifer categories by the habitat reports (Table 1). Twenty-three of these predicted species were not detected on any site in either year. Western bluebirds occurred only on the unclassified clearcut sites that had residual trees, although they were predicted to occur in all vegetation categories. Observed and predicted categories matched for only two species: hermit warbler and western tanager.

Hejl Study.--Forty-eight bird species bred in the 17 white fir sites in the three categories of medium-large trees (Tables 2, 3). Seven species present in white fir forests were not predicted by the habitat reports to occur in any of the three mixed-conifer structural categories examined. Of these species, all seven occurred in the moderate, and four in the dense canopy-closure classes.

Fifty-eight species were predicted by the WHR habitat reports to occur in one or more of the three categories examined. Seventeen of these species were not detected on any site in any year. Eleven additional species were predicted but not detected in the sparse structural class and seven additional species were predicted but not detected in the dense structural class.

Habitat Suitability Ratings

Larson Study.--Twenty-nine percent (21 of 73) of our assigned habitat suitability ratings were higher than those predicted by the database, 15% (11 of 73) matched those of the database, and 56% (38 of 73) were lower (Table 4). In cases where our ratings were higher than those predicted by the database, 76% were not predicted by WHR to be present in that vegetation category and 38% of the differences were substantial (i.e. differed by 2 or more abundance categories). Of those ratings that we reduced, 83% of the species were absent in our data and 37% were substantial reductions.

Hejl Study.--Thirty-one percent (18 of 59) of our predicted habitat suitability ratings were higher than WHR's, 27% (16 Of 59) matched WHR's, and 42% (25 of 59) were lower (Table 3). Fifty percent of our higher ratings were for species we detected that were not predicted by the database, and 28% of our higher ratings were substantial. Of our reduced ratings, 75% were for species absent in our data and 30% involved substantial changes.

DISCUSSION

The usefulness of the California Wildlife Habitat Relationships database depends on how accurately it predicts habitat suitability based on structural vegetation classes. Combining the results of both studies, 12% (6 of 52) of the bird species observed in mixed-conifer forests in either study were not predicted to occur by the WHR database (errors of omission). Twenty-eight percent (18 of 64) of the species predicted by the database to occur in mixed-conifer forests were not observed (errors of commission).

We emphasize that the basis for our predictions of species' presence/absence and habitat suitability in mixed-conifer forests is limited. Both studies were done over a short time period (2 or 3 years) on only a few sites in any one structural class (from 1-13 study sites in any class, 13 categories represented) in only a portion of the habitat (48 study sites on the west slope in central and southern Sierra Nevada). Bird populations are known to fluctuate widely in mixed-conifer forests in the Sierra Nevada (Beedy 1982, Granholm 1982, Morrison et al. 1987, Hejl et al. 1988). During the white fir study, populations of many species were very low in 1983 and increased in 1984 and 1985 (Hejl et al. 1988). Consequently, our frequency and abundance estimates may be low. Low populations are a possible reason that we did not encounter some of the species listed in the WHR habitat matrix. However, heavy winter years occur on average at 5-year intervals in the Sierra Nevada (Hejl et al. 1988), and we suspect that our population estimates are representative.

Three of the six observed species not predicted by WHR (black-backed woodpecker, Clark's nutcracker, and pine grosbeak) typically occur in subalpine forests. These boreal birds may move downslope to breed in certain years. Similarly, DeSante (1990) found rosy finches (*Leucosticta arctoa*) moving downslope from alpine forests to breed in subalpine forests. Because these matrices are intended to be conservative (Dedon et al. 1986), we believe it is appropriate to include these species in an updated matrix.

Three other species we observed were omitted by WHR. MacGillivray's warblers are known to nest in mixed-conifer forests in the Sierra Nevada (Verner and Boss 1980). Wilson's warblers and Lincoln's sparrows find mixed-conifer forests with shrubs near water or wet meadows suitable to optimum for breeding (Verner and Boss 1980). We recommend that MacGillivray's warblers, Wilson's warblers and Lincoln's sparrows be added to the database.

Errors of commission may have occurred for several different reasons. We do not suggest removing species from the WHR matrices based solely on our data, especially for those categories for which we had few sites, but suggest reconsideration of each species in future matrices. Eighteen species predicted to occur in mixed-conifer vegetation by the database were not detected in either study.

Six of these species were perhaps missed because of sampling error. Mourning doves and acorn woodpeckers are known to breed in low elevation mixed-conifer forests (Verner and Boss 1980, Beedy and Granholm 1985, Gaines 1988). Mourning doves nest in openings in mixed-conifer forests and acorn woodpeckers breed in mixed-conifer stands where oaks are abundant. Lazuli buntings occasionally breed in open timbered areas at low elevations (Verner and Boss 1980, Beedy and Granholm 1985). Song sparrows are expanding their range to higher elevations in the southern Sierra Nevada (Beedy and Granholm 1985). They require wet meadows, rivers, streams, ponds, or lakes. Brewer's blackbirds breed in all vegetation types near water or human use areas in the western Sierra Nevada, although they find mixed-conifer forests marginal (Verner and Boss 1980). Lesser goldfinches have been documented to breed in the mixed-conifer vegetation type (J. Verner, unpublished data) and habitat suitability ratings for reproduction in the database are all low. We do not recommend changes for any of these species.

Some errors are likely due to geographic differences in habitat suitability within a species' range. The model assumption of uniform value of a habitat throughout a species' range is clearly violated in certain cases. Because there can be only one habitat suitability rating for a given vegetation type throughout a species' range, we do not recommend changes in the database that will affect its performance for other locations. Biologists using the

WHR database need to be aware of these potential discrepancies and knowledgeable of species' distributions and habitat use in their area. For example, wild turkeys occur in the Yosemite latilong, but not in mixed-conifer forests. Since they occur in the latilong, the model predicts that they also occur in the mixed-conifer vegetation type and assigns them habitat suitability ratings that reflect the few scattered populations where they do utilize mixed-conifer forests. Four other species are included in the reproductive matrix for mixed conifer for the east side of the Sierra Nevada, but occur rarely if at all on the west slope: broad-tailed hummingbirds (Gaines 1988), Lewis' woodpeckers (Verner and Boss 1980), Virginia's warblers (Beedy and Granholm 1985), and pygmy nuthatches (Verner and Boss 1980). Broad-tailed hummingbirds and Virginia's warblers do not breed on the west slope and are rare and local breeders on the east slope (Gaines 1988). Distributional differences on east and west slopes for these four species illustrate the problem with the use of large heterogeneous areas such as latilongs.

We believe that other differences in species predicted by the model, but which we did not observe, are a result of errors in the WHR database. Bewick's wrens and western meadowlarks breed at low elevations and do not use the mixed-conifer zone (Verner and Boss 1980). We believe that their inclusion in the database in mixed-conifer forests by the database is erroneous.

California quail, Anna's hummingbirds, downy woodpeckers, European starlings, and house finches may breed at least locally in low-elevation mixed-conifer forests and may require special habitat elements (Airola and Barrett 1981, Granholm, pers. commun.). We recommend further study for these species.

What are the appropriate threshold criteria for including or excluding a species in the WHR matrix for a habitat? This is a problem for rare or uncommon species, species that don't occur every year, and local species that occur in only a few discrete locations. Perhaps a species should be included if it occurs in a certain percentage of sampled sites or over a certain percentage of the area of the vegetation type. Or, perhaps an additional habitat suitability rating could be added for rare or local species. We suggest that threshold criteria or additional habitat ratings would be a valuable addition to the WHR model and supporting literature.

Habitat elements were neither included or excluded in the habitat reports, although inclusion is the default. Habitat elements are important in predicting species' occurrences on a specific site. Averaging across sites over a relatively large scale, as we have done, increases the likelihood that many of the essential and preferred habitat elements were present.

Managers should be aware that predicting the results of management activities will be problematic when the resulting stands do not fit neatly into the vegetation categories. Three sites from the Larson study were too heterogeneous to classify. The 13 clearcut sites in the Larson study that had residual patches of standing trees could not be assigned a vegetation category, and therefore could not be compared to the WHR predictions. This is an increasingly common (and presumably beneficial) forestry practice and biologists need to be able to predict species' occurrences in such stands. Although also unclassifiable, the multi-layered stands in the Larson study which had been thinned generally complemented our results for multi-layered stands with a canopy cover of 60 percent or more, except the thinned stands also included species that prefer more open habitat and shrub-nesting species. We suggest the addition of canopy closure classes to the multi-layered tree category to accomodate thinned stands and uneven-aged management systems.

The subcategory of white fir in mixed-conifer forests and the category of red fir in Mayer and Laudenslayer (1988) are described as being essentially monotypic. Although Hejl selected study sites from 161 examined in the southern and central Sierra Nevada, she did not find many monotypic white fir and red fir stands. Data showed a gradation from mostly white fir to mostly red fir trees. Mixed stands exhibiting more than 50% red fir foliage volume were classified "red fir" and used to test red fir WHR models (Hejl and Verner 1988). For this study, stands with greater than 50% white fir were used to examine the mixed-conifer models (of which white fir is a subcategory and has no separate predictions). Shimamoto (1988) described white fir stands as consisting of more than 80% white fir. Following the WHR vegetation descriptions, Hejl's ten sites which had > 50% but < 80% white fir would not fall into any category.

Less than half of the WHR habitat suitability ratings agree with our assigned ratings. No specific recommendations for changes in the WHR database are suggested. Our results are meant for comparison only and as an overall appraisal of the model's performance. However, we do suggest that changes should be considered for species in vegetation categories with substantial differences.

Our habitat suitability ratings are subjective, as are those of the WHR matrices. At least two other methods that are not based on subjective decision-making have been used. W. Block (pers. commun.) plotted cumulative frequencies of all species and used two significant inflections in the resulting curve to partition low, medium, and high habitat suitability. Beedy (1982) used a modified form of Gaines' (1977) classifications in which abundance is based on the number of individuals observed per hour of field time. This method is particularly well-suited to comparing data from studies using different methods (if information is given on individuals/unit of time). A major problem, that some species have inherently low detectability because of large home ranges (e.g., woodpeckers) or secretive habits (e.g., owls) is not solved with either method. In addition, all the methods described, including ours, are based on the probability of occurrence, not true habitat value. As Van Horne (1983) has shown, populations with high densities, and thus high frequencies and probabilities of occurrence, may not always have high reproductive success and recruitment.

The vegetation surrounding a site may also be important in determining abundance or frequency of birds in a stand. Many eastern U.S. songbirds have been affected by habitat fragmentation (Askins et al. 1990), and so could western species (see Rosenberg and Raphael 1986). Edge effects and the amount of interior forest can also be important in small stands: some species decrease with increasing fragmentation, while those species with edge affinities increase. Nest predation and parasitism are often higher in edge situations (Wilcove 1985). In the Larson study, mountain chickadees and white-headed woodpeckers bred in stumps in clearcuts (seedling and sapling categories) and were not predicted by the model. We believe these two species would not have bred in these vegetation types had they not been surrounded by forest.

The fact that there cannot be different ratings within a vegetation type between various geographic areas is a potentially limiting factor in the use of the WHR database. California is a large and diverse state and the assumption that habitat use and suitability will not change throughout a species' distribution is clearly unrealistic. The habitat requirements of a species at the edge of its range may well differ from those near the center of its distribution. Biologists using the database should consult the species distribution maps and species reports for each species and should be aware of special requirements (habitat elements) and elevational affinities for each species.

Finally, we suggest a change from the use of large, nonbiologically based areas such as latilongs and counties to the use of bioregional zones as a basis for the WHR matrix. A regional model with several, separate databases would be more appropriate. Many of the incorrect predictions of the WHR matrix resulted from differences in species' habitat preferences on the east and west slopes of the Sierra Nevada. We suggest the eastern Sierra Nevada and western Sierra Nevada as appropriate bioregional zones.

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Table 1. Number of vegetation categories (out of 13) in which a breeding bird species was observed or predicted to occur. Predictions are based on California Wildlife Habitat Relationships (WHR) reports. Under type of error, C = error of commission, O = error of omission. Based on data from Larson (1981).

Species	Observed	Predicted by WHR	Type of Error
Blue grouse *Dendragapus obscurus*	1	13	–
Wild turkey *Meleagris gallopavo*	0	13	C
California quail *Callipepla californica*	0	12	C
Mountain quail *Oreortyx pictus*	6	13	–
Band-tailed pigeon *Columba fasciata*	3	11	–
Mourning dove *Zenaida macroura*	0	8	C
Anna's hummingbird *Calypte anna*	0	8	C
Calliope hummingbird *Stellula calliope*	4	6	–
Broad-tailed hummingbird *Selasphorus platycerus*	0	9	C
Lewis' woodpecker *Melanerpes lewis*	0	8	C
Acorn woodpecker *Melanerpes formicivorus*	0	7	C
Red-breasted sapsucker *Sphyrapicus ruber*	7	8	–
Williamson's sapsucker *Sphyrapicus thyroideus*	1	4	–
Downy woodpecker *Picoides pubescens*	0	9	C
Hairy woodpecker *Picoides villosus*	5	11	–
White-headed woodpecker *Picoides albolarvatus*	11	11	–
Northern flicker *Colaptes auratus*	6	11	–
Pileated woodpecker *Dryocopus pileatus*	4	7	–
Olive-sided flycatcher *Contopus borealis*	8	8	–
Western wood-pewee *Contopus sordidulus*	10	11	–
Steller's jay *Cyanocitta stelleri*	10	6	–
Mountain chickadee *Parus gambeli*	13	11	–
Red-breasted nuthatch *Sitta canadensis*	10	8	–
White-breasted nuthatch *Sitta carolinensis*	0	11	C
Pygmy nuthatch *Sitta pygmaea*	0	7	C
Brown creeper *Certhia americana*	7	6	–
Bewick's wren *Thryomanes bewickii*	0	6	C
Winter wren *Troglodytes troglodytes*	1	9	–
Golden-crowned kinglet *Regulus satrapa*	9	11	–
Ruby-crowned kinglet *Regulus calendula*	0	12	C
Western bluebird *Sialia mexicana*	0	6	C
Mountain bluebird *Sialia currucoides*	2	4	–
Townsend's solitaire *Myadestes townsendi*	10	11	–
Hermit thrush *Catharus guttatus*	10	9	–

Table 1. (cont.)

Species	Observed	Predicted by WHR	Type of Error
American robin *Turdus migratorius*	13	12	–
European starling *Sturnus vulgaris*	0	9	C
Solitary vireo *Vireo solitarius*	3	11	–
Warbling vireo *Vireo gilvus*	10	10	–
Nashville warbler *Vermivora ruficapilla*	4	7	–
Virginia's warbler *Vermivora virginiae*	0	7	C
Yellow-rumped warbler *Dendroica coronata*	11	12	–
Hermit warbler *Dendroica occidentalis*	11	11	–
Yellow warbler *Dendroica petechia*	2	7	–
MacGillivray's warbler *Oporonis tolmiei*	8	0	O
Wilson's warbler *Wilsonia pusilla*	4	0	O
Western tanager *Piranga ludoviciana*	11	11	–
Black-headed grosbeak *Pheucticus melanocephalus*	6	11	–
Lazuli bunting *Passerina amoena*	0	4	C
Green-tailed towhee *Pipilo chlorurus*	3	4	–
Rufous-sided towhee *Pipilo erythrophthalmus*	2	4	–
Chipping sparrow *Spizella passerina*	9	8	–
Fox sparrow *Passerella iliaca*	11	10	–
Song sparrow *Melospiza melodia*	0	7	C
Dark-eyed junco *Junco hyemalis*	13	12	–
Western meadowlark *Sturnella neglecta*	0	4	C
Brewer's blackbird *Euphagus cyanocephalus*	0	11	C
Brown-headed cowbird *Molothrus ater*	3	12	–
Pine grosbeak *Pinicola enucleator*	1	0	O
Purple finch *Carpodacus purpureus*	2	8	–
Cassin's finch *Carpodacus cassinii*	9	8	–
House finch *Carpodacus mexicana*	0	6	C
Red crossbill *Loxia curvirostra*	0	8	C
Pine siskin *Carduelis pinus*	0	8	C
Lesser goldfinch *Carduelis psaltria*	0	6	C
Evening grosbeak *Coccothraustes vespertinus*	1	6	–

Table 2. Presence (+) or absence (-) of breeding bird species in mixed-conifer forest structural classes medium-large sparse (5S) (1 site) and medium-large dense (5D) (3 sites), and predictions from WHR reports. WHR habitat ratings are low (L), medium (M), high (H), and not observed or predicted to breed in this structural class (-). Based on data from Hejl (1987).

Species	Structural Class	Presence/ Absence	WHR Rating
Blue grouse	5S	+	H
	5D	-	H
Wild turkey	5S	-	M
	5D	-	L
California quail	5S	-	M
	5D	-	L
Mountain quail	5S	+	H
	5D	-	M
Band-tailed pigeon	5S	-	H
	5D	+	H
Mourning dove	5S	-	M
Anna's hummingbird	5S	-	M
Calliope hummingbird	5S	-	H
Broad-tailed hummingbird	5S	-	M
Lewis' woodpecker	5S	-	H
	5D	-	L
Acorn woodpecker	5S	-	L
Red-breasted sapsucker	5S	+	H
	5D	+	L
Williamson's sapsucker	5S	-	L
Downy woodpecker	5S	-	L
Hairy woodpecker	5S	+	H
	5D	+	M
White-headed woodpecker	5S	+	H
	5D	+	M
Black-backed woodpecker *Picoides arcticus*	5D	+	-
Northern flicker	5S	+	H
	5D	+	M
Pileated woodpecker	5S	-	L
	5D	-	H

Species	Structural Class	Presence/ Absence	WHR Rating
Olive-sided flycatcher	5S	+	H
	5D	+	H
Western wood-pewee	5S	+	H
	5D	+	H
Hammond's flycatcher	5S	+	-
Empidonax hammondii	5D	+	H
Dusky flycatcher	5S	+	M
Empidonax oberholseri	5D	+	L
Steller's jay	5S	+	-
	5D	+	H
Mountain chickadee	5S	+	H
	5D	+	M
Red-breasted nuthatch	5S	+	H
	5D	+	H
White-breasted nuthatch	5S	-	H
	5D	+	H
Pygmy nuthatch	5S	-	H
	5D	-	H
Brown creeper	5S	+	-
	5D	+	H
Bewick's wren	5S	-	L
Winter wren	5D	+	H
Golden-crowned kinglet	5S	+	M
	5D	+	H
Ruby-crowned kinglet	5S	-	H
	5D	-	M
Western bluebird	5S	-	M
Mountain bluebird	5S	+	-
Townsend's solitaire	5S	+	H
	5D	+	L
Hermit thrush	5S	+	-
	5D	+	H

Table 2. (cont.)

Species	Structural Class	Presence/ Absence	WHR Rating
American robin	5S	+	H
	5D	+	L
European starling	5S	-	L
Solitary vireo	5S	-	L
	5D	-	L
Warbling vireo	5S	+	L
	5D	+	-
Nashville warbler	5D	+	-
Yellow-rumped warbler	5S	+	H
	5D	+	M
Hermit warbler	5S	-	M
	5D	+	H
MacGillivray's warbler	5D	+	-
Wilson's warbler	5D	+	-
Western tanager	5S	+	H
	5D	+	H
Black-headed grosbeak	5S	-	L
	5D	-	L
Lazuli bunting	5S	-	L
Green-tailed towhee	5S	+	M
Chipping sparrow	5S	+	H
	5D	+	-
Fox sparrow	5S	+	H
	5D	+	-
Song sparrow	5S	-	L
Dark-eyed junco	5S	+	H
	5D	+	L
Western meadowlark	5S	-	L
Brewer's blackbird	5S	-	L
	5D	-	M
Brown-headed cowbird	5S	-	M
	5D	-	L
Purple finch	5S	-	L
	5D	+	M
Cassin's finch	5S	+	H
	5D	+	-
House finch	5S	-	M
Red crossbill	5S	+	L
	5D	-	L
Pine siskin	5S	+	M
	5D	+	-
Lesser goldfinch	5S	-	L
Evening grosbeak	5D	+	H

Table 3. Frequency and abundance of birds breeding in the medium-large moderate structural class (5M) (13 sites), and predictions of habitat suitability ratings from WHR reports and Hejl's study (Hejl 1987). Predicted WHR habitat ratings are low (L), medium (M), high (H), and not observed or predicted to breed in this structural class (-).

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Blue grouse	5M	77	8	0.03	0.03	H	H
Wild turkey	5M	0	-	0	-	L	-
California quail	5M	0	-	0	-	M	-
Mountain quail	5M	46	8	0.21	0.04	M	M
Band-tailed pigeon	5M	41	12	0.21	0.09	H	M
Mourning dove	5M	0	-	0	-	M	-
Anna's hummingbird	5M	0	-	0	-	L	-
Broad-tailed hummingbird	5M	0	-	0	-	L	-
Lewis' woodpecker	5M	0	-	0	-	M	-
Acorn woodpecker	5M	0	-	0	-	L	-
Red-breasted sapsucker	5M	85	0	0.70	0.32	M	H
Williamson's sapsucker	5M	23	23	0.16	0.20	L	M
Downy woodpecker	5M	0	-	0	-	L	-
Hairy woodpecker	5M	38	16	0.22	0.16	H	M
White-headed woodpecker	5M	46	16	0.38	0.31	H	M
Black-backed woodpecker	5M	3	5	0.01	0.01	-	L
Northern flicker	5M	72	29	0.56	0.30	H	M
Pileated woodpecker	5M	31	8	0.19	0.04	H	M
Olive-sided flycatcher	5M	54	8	0.30	0.09	H	M
Western wood-pewee	5M	95	9	1.82	0.47	H	H
Hammond's flycatcher	5M	80	24	1.48	1.03	M	H
Dusky flycatcher	5M	54	35	0.48	0.45	M	M
Steller's jay	5M	92	8	1.24	0.33	H	H
Clark's nutcracker (*Nucifraga columbiana*)	5M	21	12	0.11	0.11	-	L
Mountain chickadee	5M	100	0	2.10	0.67	H	H

Table 3. (cont.)

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Red-breasted nuthatch	5M	100	0	3.31	1.60	H	H
White-breasted nuthatch	5M	39	28	0.26	0.21	H	M
Pygmy nuthatch	5M	0	-	0	-	H	-
Brown creeper	5M	92	8	1.15	0.32	H	H
Winter wren	5M	56	25	0.43	0.14	M	M
Golden-crowned kinglet	5M	100	0	3.78	0.40	H	H
Ruby-crowned kinglet	5M	3	5	0.02	0.03	H	L
Western bluebird	5M	21	29	0.07	0.10	L	L
Townsend's solitaire	5M	67	4	0.35	0.08	M	M
Hermit thrush	5M	100	0	1.73	0.55	H	H
American robin	5M	100	0	1.80	0.26	M	M
European starling	5M	0	-	0	-	L	-
Solitary vireo	5M	0	-	0	-	M	-
Warbling vireo	5M	74	5	1.34	0.45	L	H
Nashville warbler	5M	41	36	0.44	0.39	-	M
Yellow-rumped warbler	5M	100	0	7.98	1.90	H	H
Hermit warbler	5M	49	19	0.48	0.28	H	M
MacGillivray's warbler	5M	28	5	0.25	0.19	-	L
Wilson's warbler	5M	49	25	0.32	0.25	-	M
Western tanager	5M	100	0	3.21	0.43	H	H
Black-headed grosbeak	5M	21	12	0.15	0.14	M	L
Green-tailed towhee	5M	46	34	0.30	0.25	-	L
Chipping sparrow	5M	77	8	0.87	0.07	-	M
Fox sparrow	5M	92	0	2.53	0.50	L	H
Lincoln's sparrow (*Melospiza lincolnii*)	5M	5	5	0.02	0.01	-	L

Table 3. (cont.)

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Dark-eyed junco	5M	100	0	5.96	0.32	M	H
Brewer's blackbird	5M	0	-	0	-	M	-
Brown-headed cowbird	5M	49	9	0.53	0.22	L	M
Pine grosbeak	5M	3	5	0.03	0.04	-	L
Purple finch	5M	54	8	0.73	0.24	H	M
Cassin's finch	5M	87	16	1.11	0.41	L	M
Red crossbill	5M	3	5	0.01	0.01	M	L
Pine siskin	5M	90	18	1.51	0.38	L	M
Evening grosbeak	5M	56	12	0.46	0.27	H	M

Table 4. Frequency and abundance of birds breeding in seedling (structural class 1) (5 sites) and pole open (structural class 3P) (5 sites) categories, and predictions of habitat suitability ratings from WHR reports and Larson's study (Larson 1981). WHR habitat ratings are low (L), medium (M), high (H), and not observed or predicted to breed in this structural class (-).

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Blue grouse	1	0	-	0	-	L	-
	3P	0	-	0	-	L	-
Wild turkey	1	0	-	0	-	L	-
	3P	0	-	0	-	M	-
California quail	1	0	-	0	-	L	-
	3P	0	-	0	-	M	-
Mountain quail	1	0	-	0	-	M	-
	3P	0	-	0	-	H	-
Band-tailed pigeon	3P	10	14	0.01	0.02	L	L
Mourning dove	3P	0	-	0	-	L	-
Anna's hummingbird	3P	0	-	0	-	M	-
Calliope hummingbird	1	10	14	0.01	0.02	-	L
	3P	0	-	0	-	H	-
Broad-tailed hummingbird	3P	0	-	0	-	M	-
Red-breasted sapsucker	3P	10	14	0.01	0.02	-	L
Downy woodpecker	3P	0	-	0	-	L	-
Hairy woodpecker	1	10	14	0.07	0.10	-	L
	3P	10	14	0.01	0.02	L	L
White-headed woodpecker	1	50	14	0.33	0.14	-	M
	3P	50	14	0.11	0.00	L	L
Northern flicker	3P	0	-	0	-	L	-
Pileated woodpecker	3P	10	14	0.03	0.04	-	L
Olive-sided flycatcher	3P	40	0	0.14	0.08	-	M
Western wood-pewee	3P	90	14	0.54	0.08	M	H
Steller's jay	3P	80	0	0.37	0.08	-	M
Mountain chickadee	1	40	0	0.23	0.12	-	L
	3P	100	0	0.94	0.00	L	H
Red-breasted nuthatch	3P	100	0	0.69	0.04	-	H
White-breasted nuthatch	3P	0	-	0	-	L	-

Table 4. (cont.)

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Brown creeper	3P	50	14	0.21	0.02	-	L
Bewick's wren	3P	0	-	0	-	L	-
Winter wren	3P	0	-	0	-	L	-
Golden-crowned kinglet	3P	40	0	0.09	0.04	L	L
Ruby-crowned kinglet	3P	0	-	0	-	H	-
Mountain bluebird	1	30	14	0.27	0.06	-	M
	3P	0	-	0	-	M	-
Townsend's solitaire	3P	40	0	0.26	0.04	H	M
Hermit thrush	3P	20	0	0.11	0.12	M	L
American robin	1	40	0	0.17	0.04	-	L
	3P	100	0	0.50	0.02	H	H
European starling	3P	0	-	0	-	L	-
Solitary vireo	3P	0	-	0	-	M	-
Warbling vireo	3P	90	14	0.73	0.02	L	H
Nashville warbler	3P	10	14	0.01	0.02	H	L
Virginia's warbler	1	0	-	0	-	L	-
	3P	0	-	0	-	L	-
Yellow-rumped warbler	3P	100	0	0.83	0.00	H	H
Hermit warbler	3P	80	0	0.43	0.28	M	M
Yellow warbler	3P	0	-	0	-	H	-
MacGillivray's warbler	1	50	14	0.23	0.12	-	M
Wilson's warbler	3P	30	14	0.20	0.00	-	L
Western tanager	3P	100	0	1.24	0.34	M	H
Black-headed grosbeak	3P	10	14	0.01	0.02	L	L
Green-tailed towhee	1	60	0	0.86	0.53	M	M
Lazuli bunting	3P	0	-	0	-	L	-
Rufous-sided towhee	1	0	-	0	-	L	-
	3P	0	-	0	-	M	-

Table 4. (cont.)

Species	Structural Class	Frequency		Abundance		Predictions	
		Mean	SD	Mean	SD	WHR	Hejl Study
Chipping sparrow	1	10	14	0.03	0.04	-	L
	3P	40	0	0.19	0.06	H	L
Fox sparrow	1	60	0	2.06	0.32	H	H
	3P	50	14	0.81	0.02	H	M
Song sparrow	1	0	-	0	-	L	-
	3P	0	-	0	-	L	-
Dark-eyed junco	1	80	0	0.71	0.77	H	L
	3P	100	0	1.81	0.71	H	H
Western meadowlark	1	0	-	0	-	L	-
Brewer's blackbird	3P	0	-	0	-	L	-
Brown-headed cowbird	1	10	14	0.03	0.04	-	L
	3P	30	14	0.06	0.00	M	L
Cassin's finch	3P	70	70	0.36	0.10	L	M
House finch	3P	0	-	0	-	L	-
Pine siskin	3P	0	-	0	-	L	-
Lesser goldfinch	3P	0	-	0	-	L	-