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DEVELOPMENT AND TESTING OF LINEAR REGRESSION MODELS PREDICTING BIRD-HABITAT RELATIONSHIPS

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Abstract: We used an existing forest inventory data base to develop models predicting the abundance of birds collected during the summers of 1983-85 in a mixed-conifer forest of the western Sierra Nevada. Stepwise multiple linear regression was used to develop models for 21 species of birds. Adjusted coefficients of multiple determination (R^2) were low, ranging from 0.02 to 0.24. We used 1984 count data to validate models developed during 1983 ("same place, different time" validation). Most predictions ranged from 25-50% underestimates of observed values. We combined 1983 and 1984 data to produce models used to predict count data collected during 1985 from different locations ("different place, different time" validation). Predictions were about 50-75% underestimates of observed values. Most observed values were, however, within the confidence intervals generated from the predictive equations. Although our final regression models were successful in predicting presence-absence of most species, it is doubtful that forest inventory systems can be used to predict bird abundance.

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The development of easily interpretable models that predict the distribution and abundance of wildlife is necessary for decisions regarding the management of natural resources. Such models can be developed using literature sources and/or expert opinion, such as the Habitat Suitability Index Model Series of the U.S. Fish and Wildlife Service (U.S. Fish. and Wildl.

Serv. FWS/OBS-82/10) and from empirical data that has biological importance to the animal. In either case the models may, or may not, be subjected to a validation procedure. Validation allows confidence levels of model predictions and use for management decisions, testing of the adequacy of available habitat inventory procedures for predicting species' re-

sponses to management activities, refining of habitat inventory procedures to increase model reliability, and identification of fallacious model assumptions (Marcot et al. 1983).

The intent of our study was to develop and test, through multiple linear regression analysis, bird-habitat models that serve as descriptors of the ability of a habitat variable to predict the abundance of a species. We used a previously existing vegetation data set, which was collected to predict and guide timber harvest operations, to determine if such data sets can be successfully used to analyze bird abundances and habitat relationships.

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STUDY AREA

The study area was the Blodgett Forest Research Station, El Dorado County, California. The 1,200-ha forest is located at about 1,400 m elevation in the mixed-conifer zone of the western Sierra Nevada (see Griffin and Critchfield [1972]). The forest is predominated by California incense-cedar (*Libocedrus decurrens*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa (*Pinus ponderosa*) and sugar (*P. lambertiana*) pines, and California black oak (*Quercus kelloggii*). The study area was described by Airola and Barrett (1985) and Morrison et al. (1985, 1986).

The forest was demarcated into compartments, for management purposes, of about 5–40 ha. Within each compartment, a growth-stocking grid (at about 120- × 120-m spacings) was previously established to serve as the basis for a forest inventory system. During 1983, we randomly selected 120 of these points from 24 compartments (total area = 420 ha); these same 120 points were used during 1984. During 1985, we randomly selected 43 points from 7 different compartments (total area = 137 ha).

METHODS

Vegetation Analysis

The growth-stocking points in each compartment are surveyed on 5–10-year intervals based

on management or research needs. These surveys were used to describe current stand condition and to project future growth for silvicultural and harvesting purposes. Except as noted, data were collected in 0.047-ha circular plots. Here we briefly summarize the variables we used: number of seedlings/0.01 ha; diameter at breast height (dbh), total height, length of the live crown, and basal area (m²/ha) of trees by species; and number of snags/ha. The total height and live crown data were used to calculate foliage volume for each conifer species, using equations developed by Van Deusen and Biging (1984); foliage volume could not be determined for California black oak. Foliage volume was calculated for total volume and volume by tree species for height intervals <5, 5–10, 10–15, 15–20, and >20 m, and all heights combined. Shrub and forb data were not in a form we could use in our analyses.

Bird Abundance

Bird abundance was determined by counting all birds seen or heard during a 5-minute period in a 30-m-radius plot centered on each vegetation sampling point; observations for males and females were combined in this analysis. Each plot was visited on 4 occasions at 1–2-week intervals between early May and early July. An index of abundance was calculated simply as the number of birds counted/visit. The index, and how we used it to compare species and sites, thus assumed equal detectability of all birds within the 30-m radius and across sites. This assumption was probably not completely valid (see Discussion).

Regression Model Development

Stepwise multiple linear regression (Draper and Smith 1981) was used to develop equations predicting bird abundances for each bird species from the habitat variables. Separate models were developed for 1983, 1984, 1985, and a combined 1983–84 data set. The stepwise procedure was used to identify a subset of habitat variables that accounted for the majority of explainable variation in the bird abundance data. Because of the prevalence of 0 values, all variables were transformed ($\ln[\text{variable} + 1]$) prior to statistical analyses. All calculations were performed using the SPSSX statistical package (SPSS 1983).

One member of a pair of highly intercorrelated ($r > 0.8$) habitat variables was removed

from consideration for inclusion in the regression procedure. The variable (in an intercorrelated pair) retained was the one judged to be the most biologically meaningful and easiest to measure. Most variable-pairs had either high (>0.8) or low (<0.5) r -values. If the X 's are highly intercorrelated, use of the final model for prediction for values of X 's that do not follow the past pattern of multicollinearity (e.g., as may arise from different environmental conditions) is highly suspect (Neter and Wasserman 1974:388)—this is important given our desire to develop predictive models (see below). Our original set of 56 variables was reduced to 14 variables with low intercorrelations (Table 1). The lowest 2 height intervals of foliage volume (<5 and $5-10$ m) were combined to simplify the analysis; the upper intervals were removed from further analysis because of high intercorrelations with other variables; e.g., dbh.

We set the significance value necessary for an independent variable to enter (P -to-enter) in the stepwise procedure at ≤ 0.15 so as not to exclude any variable that might be biologically important to the species. The final regression model was determined, however, by examining the change in the adjusted R^2 (Norusis 1985) after each step in the procedure—a variable was included in the final model if it was accompanied by a significant ($P < 0.1$) change in the F -value associated with the overall regression. Models were evaluated by examining prediction error, calculated as $SS_{res}/n - 2$, where SS_{res} = sums of squares residuals and n = number of bird counts from which individual estimates of bird abundances were calculated (Marcot 1984:table 12; see also Draper and Smith [1981:20 and 34]). Small prediction errors meant that abundance of a given species was tightly associated with the given habitat variables, whereas large prediction errors suggested a loose association.

We evaluated prediction bias (Neter and Wasserman 1974:388) by determining the predictive power of the final models on a new set of data. First, we used the 1983 models to determine their ability to predict 1984 bird abundances ("same place, different time" validation) by comparing (% difference) the actual abundances obtained during 1984 to those predicted using the 1983 bird-vegetation models. Second, we used the combined 1983–84 models to predict 1985 bird abundances ("different place, different time" validation) by comparing

Table 1. Variables from the forest inventory system at Blodgett Forest, California, used to develop the final regression models for birds during summer.

Variable	Units	Mnemonic
Snags	N/ha	SNAGS
\bar{x} canopy ht	m	MEANH
Foliage vol	m ³ /ha	
Total (all species, all ht)		TOTCRVOL
By species, <10 m in ht		
Ponderosa pine		PPVOLI
Sugar pine		SPVOLI
Douglas-fir		DFVOLI
California incense-cedar		ICVOLI
White fir		WVOLI
dbh, by species	cm	
Ponderosa pine		PPDBH
Sugar pine		SPDBH
Douglas-fir		DFDBH
California incense-cedar		ICDBH
White fir		WFDBH
California black oak		BODBH

the abundances obtained during 1985 with those predicted using the 1983–84 models. As a final examination of model performance, we used the 95% confidence intervals generated from the predictive equations as the acceptable interval in which an observed value must fall to qualify as a valid model (see Balda et al. [1983]).

RESULTS

Twenty-one species of birds were included in this analysis (Table 2). The bird species were diverse in that they included bark-foragers (gleaners and drillers), salliers, foliage gleaners, and ground-foragers; but except for the dark-eyed junco (*Junco hyemalis*), the most numerous species were foliage-gleaners (Table 2). Although the total index of abundance declined across all 3 years of study, the relative order of abundance among species was very similar between years (Spearman's rank correlation, r_s : 1983 vs. 1984 = 0.96, 1983 vs. 1985 = 0.86, and 1984 vs. 1985 = 0.81, all at $P < 0.001$).

The P -to-enter limits were reached by the inclusion of ≤ 5 variables for the bird species analyzed by stepwise multiple regression analysis (Table 3). The coefficient of multiple correlation (R) ranged from 0.17 for the chestnut-backed chickadee (*Parus rufescens*) to 0.53 for the dusky flycatcher (*Empidonax oberholseri*).

Table 2. Index of abundance (No./count) of birds breeding at Blodgett Forest, California, during summer 1983–85. Indices were scaled by multiplying the original values by 100 and then rounding (for ease of presentation).

Species	1983 index		1984 index		1985 index		Foraging mode
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
Red-breasted sapsucker	8	20.2	1	5.2	4	10.3	Bark driller
Hairy woodpecker	4	11.2	6	16.1	2	6.4	Bark driller
White-headed woodpecker (<i>Picoides albolarvatus</i>)	7	15.5	3	9.6	3	8.1	Bark driller
Pileated woodpecker	3	11.5	2	9.1	0	0.0	Bark driller
Hammond's flycatcher (<i>Empidonax hammondi</i>)	23	33.1	12	24.4	33	30.7	Sallier
Dusky flycatcher	16	24.2	9	22.5	19	31.9	Sallier
Mountain chickadee (<i>Parus gambeli</i>)	13	29.6	4	16.3	6	15.5	Foliage gleaner
Chestnut-backed chickadee	21	31.5	15	31.1	11	35.5	Foliage gleaner
Red-breasted nuthatch (<i>Sitta canadensis</i>)	34	38.8	17	27.6	18	25.2	Bark gleaner
Brown creeper (<i>Certhia americana</i>)	14	33.2	6	13.9	12	22.7	Bark gleaner
Golden-crowned kinglet	45	53.1	47	66.7	23	28.0	Foliage gleaner
American robin	0	0.0	1	7.1	0	0.0	Ground forager
Solitary vireo (<i>Vireo solitarius</i>)	43	39.2	26	32.3	12	21.4	Foliage gleaner
Warbling vireo	39	49.8	27	41.4	12	24.6	Foliage gleaner
Nashville warbler (<i>Vermivora ruficapilla</i>)	52	44.5	28	33.8	13	22.1	Foliage gleaner
Yellow-rumped warbler (<i>Dendroica coronata</i>)	32	36.9	18	25.3	9	16.4	Foliage gleaner
Hermit warbler	86	52.8	47	46.0	35	33.7	Foliage gleaner
Western tanager (<i>Piranga ludoviciana</i>)	52	47.1	36	38.6	19	24.3	Foliage gleaner
Black-headed grosbeak (<i>Pheucticus melanocephalus</i>)	22	38.6	17	31.2	6	21.7	Foliage gleaner
Dark-eyed junco	65	60.3	78	59.9	41	45.7	Ground forager
Purple finch (<i>Carpodacus purpureus</i>)	5	13.4	4	10.8	1	3.8	Foliage gleaner

In most species R ranged from 0.3 to 0.4. The (adjusted) coefficient of multiple determination (R^2) patterned the results for R , being lowest in the chestnut-backed chickadee (0.02) and highest in the dusky flycatcher (0.24); most species ranged from 0.1 to 0.2 (Table 3). Prediction errors were small (i.e., <0.2) for all species except the golden-crowned kinglet (*Regulus satrapa*), warbling vireo (*Vireo gilvus*), and dark-eyed junco (Table 3).

The standardized regression coefficients that comprised the final regression models indicated the relative importance of each variable to the model. For example, the abundance of red-breasted sapsuckers (*Sphyrapicus ruber*) increased with an increasing number of snags, but decreased with an increase in the dbh of California incense-cedar, ponderosa pine, and California black oak (Table 3). The abundance of hermit warblers (*Dendroica occidentalis*) increased with an increase in total cover and the size of Douglas-fir. Therefore, the habitat-relationships for each species can be deciphered in a similar manner.

The 1983 models underestimated 17 of the 19 species analyzed when used to predict the 1984 abundances (Table 4). Predictions ranged from an 85% underestimate for the sapsucker to a 63% overestimate for the hairy woodpecker

(*Picoides villosus*). Estimates for the remaining species were usually 25–50% underestimates of observed values. All except 1 of the observed values were within the predicted confidence intervals (Table 4).

The combined 1983–84 models underestimated 17 of the 21 species analyzed when used to predict the 1985 abundances (Table 4). Predictions ranged from a 100% underestimate for the pileated woodpecker (*Dryocopus pileatus*) to a 194% overestimate for the hairy woodpecker; the American robin (*Turdus migratorius*) was overestimated by 100%. All of these 3 species had low abundances during all years of study, however. Predictions for the remaining species were about 50–75% underestimates of observed values. All except 3 of the observed values were within the predicted confidence intervals (Table 4). We also conducted other validations (e.g., using 1984 to predict 1983) and combinations of data (e.g., 1983 plus 1985), but these examinations did not differ substantially from the analyses reported herein.

DISCUSSION

The coefficients of multiple determination (R^2) indicated that the vegetation variables available through the forest inventory system we used accounted for a low amount of the

Table 3. Multiple regression models (stepwise inclusion of variables) predicting bird abundance, based on bird-vegetation relationships for birds breeding at Blodgett Forest, California, 1983–85. Regression coefficients are based on transformation ($\ln[\text{index} + 1]$) of unscaled indices of abundance given in Table 2, and transformed vegetation variables. Mnemonics for models given in Table 1.

Species (No./count)	Model	R	Ad-justed R ²	Pre-diction error ^a
Red-breasted sapsucker	0.009(SNAGS) - 0.016(ICDBH) - 0.008(PPDBH) - 0.006(BODBH) - 0.002(WFVOLI) + 0.093	0.44	0.15	0.003
Hairy woodpecker	0.011(BODBH) - 0.011(SPVOLI) + 0.022	0.28	0.06	0.012
White-headed woodpecker	-0.006(DFVOLI) - 0.019(WFDBH) - 0.013(BODBH) - 0.010(PPVOLI) + 0.014	0.42	0.13	0.019
Pileated woodpecker	-0.018(WFDBH) + 0.022(ICDBH) - 0.005(PPVOLI) + 0.015	0.34	0.09	0.012
Hammond's flycatcher	0.072(WFDBH) - 0.024(WFVOLI) + 0.071	0.41	0.15	0.090
Dusky flycatcher	0.022(PPVOLI) - 0.034(DFDBH) + 0.031(WFDBH) - 0.019(PPDBH) + 0.031(ICDBH) - 0.027	0.53	0.24	0.042
Mountain chickadee	0.023(SPVOLI) - 0.012(PPDBH) - 0.022(SNAGS) + 0.061	0.39	0.12	0.024
Chestnut-backed chickadee	0.145(MEANH) - 0.310	0.17	0.02	0.084
Red-breasted nuthatch	0.052(SNAGS) - 0.025(SPVOLI) + 0.113	0.27	0.06	0.078
Brown creeper	0.052(SNAGS) - 0.025(BODBH) - 0.011(WFVOLI) + 0.157	0.36	0.10	0.104
Golden-crowned kinglet	0.072(SPDBH) + 0.227	0.40	0.15	0.247
American robin	0.015(SNAGS) + 0.003(WFVOLI) - 0.017	0.22	0.03	0.006
Solitary vireo	0.026(SPDBH) + 0.033(BODBH) + 0.191(MEANH) - 0.429	0.39	0.12	0.090
Warbling vireo	-0.014(PPVOLI) + 0.039(BODBH) + 0.029(SPDBH) + 0.038(WFDBH) + 0.095	0.38	0.11	0.224
Nashville warbler	0.037(PPVOLI) - 0.046(PPDBH) - 0.016(DFVOLI) - 0.039(WFDBH) + 0.582	0.47	0.19	0.161
Yellow-rumped warbler	-0.027(BODBH) - 0.071(SNAGS) + 0.026(SPDBH) + 0.300	0.33	0.08	0.126
Hermit warbler	0.153(TOTCRVOL) + 0.047(DFDBH) - 0.876	0.45	0.19	0.184
Western tanager	0.050(DFDBH) - 0.019(PPVOLI) + 0.200	0.42	0.16	0.132
Black-headed grosbeak	-0.041(PPDBH) - 0.013(WFVOLI) + 0.034(DFDBH) + 0.088(ICDBH) - 0.071(TOTCRVOL) + 0.461	0.48	0.18	0.127
Dark-eyed junco	-0.029(PPDBH) - 0.082(TOTCRVOL) + 1.218	0.25	0.05	0.319
Purple finch	-0.015(PPDBH) + 0.036(TOTCRVOL) + 0.009(SPDBH) - 0.206	0.40	0.13	0.011

^a Values are SE's of predicted bird abundances (SSE), based on nontransformed abundance values.

variation in bird abundance; the amount of prediction error was generally low, however. Our results indicated that variables describing the size (dbh or ht) of trees by species, the foliage volume in the subcanopy (i.e., lower ht intervals), and number of snags were important predictors of bird abundance. In a related study, Morrison et al. (1986) found that tree size and subcanopy development were important components of the habitat of many forest birds; seasonal variation in habitat use also was noted.

The models developed during 1983 and tested for predictive power with the 1984 data—the “same place, different time” validation—were

usually able to predict within 50% of the observed value. The predictions generated using the 1983–84 models—the “different place, different time” validation—were usually able to predict only within 50–75% of observed. However, most of the abundance values we observed fell within the confidence intervals generated from the predictive models. Therefore, we concluded that the final models presented herein (Table 3) successfully predicted presence or absence (except for several rare species) but did not clearly track the variation in abundance between years. Remember that abundance generally declined across all years of study

Table 4. Index (No./count) of bird abundance ($\ln[\text{index} + 1]$) using combined 1983–84 and 1983 (alone) multiple regression models to predict 1985 and 1984 abundance, respectively, difference between predicted and observed abundance, and fit (yes or no) of observed value to confidence interval (CI) calculated from predictive equation, for birds at Blodgett Forest, California, during summer. Indices were scaled by multiplying by 100 and rounding; % difference based on original, unscaled values.

Species	Using 1983–84 to predict 1985 abundance				Using 1983 to predict 1984 abundance			
	Predicted	Observed	% difference	Within CI	Predicted	Observed	% difference	Within CI
Red-breasted sapsucker	4	4	-29	Yes	7	1	-85	(Yes) ^a
Hairy woodpecker	5	2	194	No	3	5	63	Yes
White-headed woodpecker	4	3	-37	Yes	5	2	-55	Yes
Pileated woodpecker	3	0	-100	(Yes) ^a	2	2	-35	Yes
Hammond's flycatcher	16	26	68	Yes	17	10	-42	Yes
Dusky flycatcher	9	14	53	Yes	13	7	-46	Yes
Mountain chickadee	6	5	-12	Yes	11	3	-68	Yes
Chestnut-backed chickadee	12	7	-93	Yes	16	11	-32	Yes
Red-breasted nuthatch	21	15	-32	Yes	SA ^b	13	SA ^b	NC ^c
Brown creeper	10	10	-3	Yes	11	51	-53	Yes
Golden-crowned kinglet	31	19	-41	Yes	34	31	-8	Yes
American robin	<1	0	100	Yes	SA ^b	1	SA ^b	NC ^c
Solitary vireo	28	10	-64	Yes	31	20	-36	Yes
Warbling vireo	27	9	-67	Yes	27	19	-29	Yes
Nashville warbler	32	11	-67	Yes	38	22	-42	Yes
Yellow-rumped warbler	20	8	-60	Yes	25	15	-41	Yes
Hermit warbler	42	27	-35	Yes	60	34	-43	Yes
Western tanager	35	16	-55	No	38	27	-28	Yes
Black-headed grosbeak	19	4	-77	Yes	16	13	-18	Yes
Dark-eyed junco	53	29	-45	Yes	45	52	16	Yes
Purple finch	4	1	-87	Yes	4	3	-11	Yes

^a Observed value = lower bound of CI.

^b SA = species absent.

^c NC = could not be calculated.

(for reasons unknown to us). Further, confidence in the models must decline as one moves (geographically and floristically) away from the sites used to develop them. Models developed on the same sites but in different years may provide improvements over those developed from different sites because of site tenacity of some birds and sameness of the vegetation.

In summary, the models presented herein failed to adequately predict bird abundance. Our models did indicate, however, that most species will not disappear given subtle changes to their habitat (e.g., moderate thinning). It appears, therefore, that more intensive studies of individual species, including the addition of species-specific variables, will be required to predict bird abundance—our models can be used to guide such studies. The data contained in the forest inventory system we used was apparently inadequate to track bird abundances.

Observer variability likely accounted for some of the prediction error we noted—different observers were used during each year of our study. Even trained observers vary in their ability to count birds, especially between years and habitats; e.g., Ralph and Scott (1981). Such error

cannot be eliminated but must be minimized through careful selection and training (Kepler and Scott 1981). Our counting technique was simple and should be easy to duplicate. Alternate techniques, especially the variable circular-plot method (Reynolds et al. 1980), usually sample birds from wide radii around a point (i.e., detection distances of >50 m), and thus can be only loosely related to forestry inventories that sample in small radii around a point. Unfortunately, we do not know how strongly the occurrence of a bird within a 30-m-radius plot is related to the vegetation in that area. Although we assumed equal detectability of birds within and between plots, it is doubtful that this assumption was fully met. Given the similarity in vegetation among plots (i.e., all mature mixed-conifer), however, the error introduced into the models through violation of this assumption probably accounted for a small part of the overall variation.

A model is adequate if it supplies the level of resolution required by the user. It is extremely expensive, in terms of the number of observers required, to develop models to predict bird abundance that are within (say) 10%

of observed values (see Verner [1983]). Exploratory models (those that search for general bird-habitat relationships), and those that seek only presence-absence resolution, are far less costly and are probably adequate in many situations. It is doubtful, however, if pre-existing forest inventories will supply the resolution needed to develop models capable of predicting more than presence-absence of birds on a local scale—such inventories are simply not designed to analyze wildlife populations.

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