

Multivariate bird-habitat relationships models for some Northern Region bird species

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INTRODUCTION

The study of wildlife-habitat relationships involves the search for habitat characteristics that are closely associated with variations in the distribution or abundance of particular species. We would like to be able to predict a species' distribution and abundance based on measured habitat variables. Steps involved in this type of study include: selecting variables of possible biological relevance to the species; measuring these variables at locations where bird data are also collected; constructing empirical, statistical models relating the occurrence of a bird species to these variables; and testing or validating these predictive models with new data.

For birds, the physical structure of the habitat has long been considered to provide important proximate cues for habitat selection (Rotenberry 1981). Foliage volume in different layers of vegetation provides nesting substrate, protection from predators, and foraging opportunities for various bird species. Species composition of the vegetation may also be important for many species (Holmes 1981, Rotenberry 1985) because foliage distribution and resource availability differ among plant species, which may influence foraging opportunities or nest sites for birds (Robinson and Holmes 1984). We can never really know how an animal perceives its environment, or how it bases decisions on that perception. The variables we measure may only be correlated with the actual cues used by animals, but a significant relationship suggests that there is a response to the measured habitat feature. Validation of a predictive model would help confirm that the correlation is meaningful.

For predictive models to be accurate, data must be collected from many stands representative of the existing variation within the target habitat types (Balda et al. 1983). Complete sampling along the full range of a habitat gradient is necessary if we are to determine the form of species responses as accurately as possible (Best and Stauffer 1986).

The responses of species to habitat variables are often analyzed using multiple linear regression (e.g. Maurer 1986, Morrison et al. 1987). This procedure tests only for linear relationships between variables. Curvilinear relationships may often be transformed to approximate linear ones, but only for monotonically increasing or decreasing relationships. However, there is no reason to assume that such a relationship will be maintained through the entire range of a habitat attribute (Meents et al. 1983). If the response curve is unimodal (with a single maximum along the gradient), then linear regression may be unable to detect the relationship (Young 1996).

Unimodal, curvilinear response functions have long been used in niche theory. This is based on the fundamental assumptions that there is a single optimal environmental condition to which a species is best adapted, and that the fitness of the animal decreases gradually as the environment changes from this optimum toward either extreme of any important niche dimension. If we also assume that animals will be most abundant under environmental conditions in which they "expect" the highest fitness, then we would predict a unimodal relationship of a species' abundance as a function of each important variable (Young 1996).

The Northern Region Landbird Monitoring Program provides a tremendous opportunity to study bird-habitat relationships, because it provides a very large number of point counts across a wide spectrum of habitats. This report presents results of multivariate analyses relating the presence of several bird species to continuous vegetation variables. These variables describe the structure and species composition of the vegetation, and were chosen because of their potential importance for bird species.

The general distribution pattern of birds among a broad range of cover types has already been presented by Hutto (1997). Here, we seek to explain the occurrence of species in greater detail, using the continuous vegetation variables collected in the field. Although many of these variables covary with cover type designation, because they are part of the definition of those types, examination of their multivariate effects in continuous form allows a more detailed understanding of the apparent habitat selection responses of the bird species. This method should be most effective within a subset of cover types, because an analysis of the entire data set would still be dominated by broad differences in habitat structure associated with the cover type.

We have restricted these analyses to conifer forests, because we are interested in more specific distribution patterns within the set of conifer forest cover types that should potentially be usable by a bird species that forages or nests in conifer trees. This information is of special relevance to forest managers who wish to better understand tradeoffs associated with alternative harvesting methods.

Furthermore, much of this detail is unavailable through remote sensing, so it is important to determine if field data are necessary for classifying each point according to elements that are important to bird species and, thus, in explaining any observed changes in density over time.

METHODS

In this type of study, the abundance or frequency of occurrence of a given bird species is correlated with average habitat characteristics. At this scale, a "habitat" can be considered "a spatially contiguous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types" (Hutto 1985). This scale is appropriate for assessing the impact of logging practices, because such habitat alterations usually occur over entire forest stands. The presence or absence of a bird species within 100 m of each point was determined during a single 10-minute count. As in the cover type models, points with more than one cover type within 100 m were excluded, so that the estimates of vegetation structure could reasonably be expected to represent the entire area of bird sampling. Thus, both the bird and vegetation data were samples intended to represent the 3.14 ha (100-m radius) area around the point.

General measures of vegetation structure were recorded at each count point along a transect, after the bird counts were completed, as described in Hutto and Hoffland (1996). All vegetation variables included in this report were estimated within 30 m of the point (excluding

the road corridor), except for counts of trees within 11.3 m of the bird count point (excluding the road corridor). Two variables were derived from these tree counts: 1) LGTREE: the number of large-dbh (> 40 cm) trees; and 2) AVGSIZE: the average size category of trees within 11.3 m (where 1=trees between 5 and 10 cm dbh; 2 = trees between 10 and 40 cm dbh; 3 = trees > 40 cm dbh).

Ocular estimates of the following variables were conducted within a 30-m-radius circle centered on the count point:

HEIGHT: the average height of the tree canopy layer.
CANOPY: the percent cover of canopy trees (larger than saplings)
SAPLING: the percent cover of sapling trees (between 5 and 10 cm dbh)
SEEDLING: the percent cover of seedling trees (< 5 cm dbh)
SHRUB: the percent cover of tall shrubs (multi-stemmed woody plants greater than 1 m)
BUSH: the percent cover of low shrubs (less than 1 m tall)
GROUND: the percent cover of grasses and forbs

For tree species composition, the total canopy cover made up by each of the tree species indicated (with some lumping):

PIPO: Percent of total canopy cover made up by ponderosa pine (*Pinus ponderosa*)
PSME: Percent of total canopy cover made up by Douglas-fir (*Pseudotsuga*)
LAOC: Percent of total canopy cover made up by Western Larch (*Larix*)
PICO: Percent of total canopy cover made up by lodgepole pine (*Pinus contorta*)
SPRUCFIR: Percent of total canopy cover made up by spruce/fir (*Picea*, *Abies lasiocarpa*)
MESIC: Percent of total canopy cover made up by cedar (*Thuja*), hemlock (*Tsuga*) and Grand Fir (*Abies grandis*).
STONPINE: Percent of total canopy cover made up by whitebark pine (*Pinus albicaulis*) or limber pine (*Pinus flexilis*)
DECID: Percent of total canopy cover made up by deciduous trees (*Betula*, *Populus*)

We included only conifer forest cover types, and only those points with canopy cover greater than zero. Clearcuts with no trees at all were excluded because they were basically unavailable to most conifer 'specialist' bird species, and because several variables would be undefined for these points (species composition and canopy height). We did include older clearcuts with pole-sapling regrowth, and some newer clearcuts with a few scattered trees remaining. However, we excluded all points with canopy height less than 5 m, because trees this size should not be considered canopy. This left all points with some conifer trees, ranging from 5-35 m tall and 1-80% canopy coverage.

The resulting data set included a total of 2292 points, including 1669 on 12 National Forests plus Potlatch Corp. lands, and 623 of the extra points visited in 1993 and 1994.

Statistical analyses

We used logistic regression to model the habitat relationships of all 24 species of birds that were present on at least 5 percent of the points. For less common species, the imbalance of presence and absence may provide statistical problems (Mills et al. 1993). For each common bird species, a multiple logistic regression model was constructed that best predicted the presence or absence of the species on individual points, using the vegetation variables in this data set. The binary outcome variable used by logistic regression -- in this case the presence or absence of a particular species -- is appropriate to the data set generated in this study. In general, even the most common species are detected on fewer than half of the counts during point-count studies in this region (e.g. Hutto, in press). The preponderance of zeroes strongly skewed the outcome variable and violated the normality assumption of a simple regression model. Furthermore, 23 of the 24 analyzed species were represented by either zero or one detection on 85-99% of the points, so reduction of the data to presence or absence did not sacrifice much explanatory power. Also, I expected biases due to detectability and animal movement to be less pronounced in presence/absence data than in abundance data, because there is no need to determine which songs are from separate individuals, and only one individual must be detected. Logistic regression is preferable to linear discriminate analysis of binary data when the explanatory variables are nonnormal (Press and Wilson 1978), which is true of most of the continuous habitat variables in this study.

As a first step in selecting variables for each species model, we fit separate univariate logistic regression equations for each variable (Hosmer and Lemeshow 1989). For each variable, we considered the two alternatives of linear and unimodal relationships. We used the simplest method of modeling a unimodal relationship: adding a quadratic term to an equation that already included the first-order term of the variable in question. If the coefficient of the first-order term is positive and that of the quadratic term is negative ($aX-bX^2$), then the equation describes a unimodal curve (an inverted U, highest in the middle). However, depending on the range of the variable, X, that is used, the entire unimodal curve may not be present in a study, and the relationship may appear exponential or sigmoidal. In this case both of the models (with and without the quadratic term) should be significant. If the signs of the coefficients are reversed ($-aX+bX^2$), then the equation describes an upright U, or whatever part of it is in the variable range used. To test for a quadratic relationship, the statistical modeling program must evaluate both terms together, and must not allow an equation with the quadratic term alone (which would not be a unimodal curve).

Variables considered for entry into a multivariate model were those for which the univariate test indicated potential significance. Hosmer and Lemeshow (1989) suggested a p-value < 0.25 as a criterion for consideration of a variable. However, most of the species in this study had so many significant univariate relationships that this criterion would have produced a numerically unstable model that could not be trusted. Therefore, I used $p < 0.15$ for the model with the linear term only, and $p < 0.10$ for the addition of the quadratic term. The high power of the analyses resulted in most variables satisfying these criteria (82% of the possible 408 (17 variables x 24 species) relationships), and any relationship with a higher p-value would probably be very weak or specious.

I used stepwise variable selection by backward elimination to build the models. The criteria for removal of a term from the model were the effect of removing the quadratic term or

the effect of removing both terms. I also ran forward selection procedures to examine consistency of variable selection.

RESULTS

Regression models were developed for the 24 species of birds that were present on at least 5 percent of the points (Table 1). Most of these species were conifer specialists, which is why they were common in these habitats, but some birds of shrubby habitats were included that also occurred in riparian areas.

Most species were significantly related to a majority of the 17 habitat variables. The occurrence of each species showed significant univariate relationships with between 6 and 16 variables (22 of the 24 bird species had at least 9). Overall, 74% of the possible variable-species combinations produced significant relationships (either linear or quadratic; $p < 0.05$). Even when reduced by multivariate analyses, the percentage was still high (50%; with between 4 and 12 variables per species).

All species showed at least one significant quadratic relationship, and most species had more than 4 such relationships. In fact, of 298 significant univariate relationships, 151 (51%) included a quadratic term. In 52 (34%) of these cases (with significant quadratic relationships), the model with only the linear term was not significant (Table 2). The latter cases are especially important; not only would the variables have been overlooked using conventional linear methods, but these are the only relationships that can safely be considered non-monotonic. A nonlinear but monotonic curve (such as sigmoidal or exponential) would be represented a quadratic relationship with a significant linear term. All but 5 of the 52 non-monotonic relationships were unimodal, rather than U-shaped. There is little biological reason to expect a U-shaped relationship, and these cases may have been due to other variables influencing the relationship in some way, if they were not chance effects (Type I errors).

Each habitat variable had a significant univariate relationship with at least nine species (range 9-23; all physiognomic variables with at least 13 species). In the multivariate models the total number of significant relationships was reduced from 298 to 202 (Tables 2-4). The variables were affected differently, however. Variables representing coverage of the lowest understory layer were eliminated most often, with SEEDLING being eliminated from all but one of the multivariate models. CANOPY cover was still present in all models, however, and tall SHRUB cover was retained in 75%.

Table 1. Frequency of occurrence for all bird species detected on more than 15 of the 2304 points in coniferous habitats (1992-1994). Species are listed in descending order of abundance.

SPECIES	Number of points detected	Proportion of points detected
Dark-eyed Junco	1354	.588
Yellow-rumped Warbler	1118	.485
Red-breasted Nuthatch	1092	.474
Swainson's Thrush	783	.340
Western Tanager	769	.334
Chipping Sparrow	721	.313
Ruby-crowned Kinglet	662	.287
Townsend's Warbler	645	.280
American Robin	498	.216
Mountain Chickadee	486	.211
MacGillivray's Warbler	472	.205
Warbling Vireo	402	.174
Golden-crowned Kinglet	397	.172
Cassin's Vireo	366	.159
Townsend's Solitaire	294	.128
Pine Siskin	247	.107
Dusky Flycatcher	234	.102
Orange-crowned Warbler	232	.101
Northern Flicker	222	.096
Varied Thrush	200	.087
Gray Jay	175	.076
Brown-headed Cowbird	172	.075
Hammond's Flycatcher	170	.074
Hermit Thrush	142	.062
Winter Wren	106	.046
Chestnut-backed Chickadee	92	.040
Clark's Nutcracker	90	.039
Olive-sided Flycatcher	89	.039
Red Crossbill	86	.037
Red-naped Sapsucker	84	.036
Fox Sparrow	81	.035
Black-capped Chickadee	81	.035
Cassin's Finch	74	.032
Pileated Woodpecker	73	.032
Hairy Woodpecker	69	.030

Table 1, continued

SPECIES	Number of points detected	Proportion of points detected
Steller's Jay	67	.029
Common Raven	64	.028
Wilson's Warbler	59	.026
Ruffed Grouse	51	.022
Black-headed Grosbeak	50	.022
Evening Grosbeak	46	.020
Mountain Bluebird	45	.020
Nashville Warbler	36	.016
Brown Creeper	33	.014
Williamson's Sapsucker	30	.013
Rufous Hummingbird	30	.013
White-breasted Nuthatch	28	.012
Red-tailed Hawk	23	.010
Lazuli Bunting	23	.010
House Wren	23	.010
Pine Grosbeak	23	.010
Calliope Hummingbird	22	.010
Yellow Warbler	22	.010
Spotted Towhee	22	.010
Song Sparrow	20	.009
Three-toed Woodpecker	17	.007
Black-backed Woodpecker	1	.000

Table 2. The occurrence of vegetation variables in habitat-relationships models across the assemblage of 24 species. Under “Univariate relationships” are the number of species for which the linear univariate relationship with the specified variable was significant ($p < 0.05$; column 1), the linear and quadratic relationships were significant (column 2), or only the quadratic relationship was significant (column 3). Under “Multivariate relationships” are the number of species for which each variable was retained in the multivariate models, tallied by the form of relationship (linear or quadratic) and the sign of the coefficient for the specified term ("Positive" or "Negative").

Variable	Univariate relationships			Multivariate relationships			
	Only	Linear +	Only	Linear		Quadratic	
	Linear	Quadratic	Quadratic	Pos	Neg	Pos	Neg
CANOPY	12	6	5	7	8	1	8
SAPLING	10	2	2	3	2	2	1
SEEDLING	5	4	4	1	0	0	0
SHRUB	6	12	2	0	5	2	11
BUSH	3	7	8	1	3	0	3
GROUND	19	2	0	14	0	1	0
HEIGHT	7	4	10	0	6	0	10
LGTREE	7	6	1	3	3	0	2
SIZE	10	3	5	4	2	1	0
PIPO	6	12	3	6	5	0	6
PSME	5	12	3	5	3	1	4
LAOC	10	5	2	5	2	0	4
PICO	11	6	3	4	7	1	1
SPRUCFIR	16	1	1	6	7	0	0
MESIC	8	13	0	0	5	5	3
STONPINE	7	1	2	1	6	0	2
DECID	5	3	1	5	1	0	3
Totals:	147	99	52	65	65	14	58

Table 3. The inclusion of structural (physiognomic) vegetation variables in the multivariate models for each species. The first column under each variable shows the sign of the coefficient. If 2 signs are shown, this indicates a significant quadratic relationship; shown are the signs of the coefficients for the linear term and the quadratic term, respectively. The second column under each variable is the chi-square statistic for the inclusion of that variable in the model; a larger number indicates a greater improvement of the model due to the inclusion of the variable. Tree species composition variables are shown in Table 4.

<u>Species</u>	<u>Variable:</u>	Canop y	Sapling	Tall Shrub	Low Bush	Groun d	Canop y Height	Large Trees	Average Size
Northern Flicker		- 28			- 5	+ 19			-/+ 11
Hammond's Flycatcher		+ 5	- 7			+ 16	- 4	+ 6	
Dusky Flycatcher		- 99	+/- 16		+/- 10	+ 14		- 6	
Gray Jay		+ 8				+ 6	+/- 11		
Mountain Chickadee		+/- 6		- 11			+/- 7		
Red-breasted Nuthatch		+ 24		+/- 9			+/- 15	+ 9	
Golden-crowned Kinglet		+/- 66	- 5	+/- 13	- 7			+ 5	
Ruby-crowned Kinglet		+/- 12		- 12	+/- 15	+ 15	+/- 6		+ 8
Townsend's Solitaire		+/- 32		- 9	+/- 9	+ 33			+ 5
Swainson's Thrush		+ 51	+ 12	+/- 98	- 4			- 21	- 5
Hermit Thrush		+/- 11		-/+ 40			+/- 6		
American Robin		- 12	-/+ 16	-/+ 9		+ 20	- 7		
Varied Thrush		+ 14	+ 6	+/- 10				+/- 11	
Solitary Vireo		+ 25		+/- 19			+/- 14		
Warbling Vireo		- 33	+ 9	+/- 88		+ 11	- 18		
Orange-crownd Warbler		- 10		+/- 38		-/+ 40	- 17		
Yellow-rumped Warbler		+/- 15		- 6			+/- 22		+ 8
Townsend's Warbler		+ 53		+/- 39			+/- 27	+/- 7	- 9
MacGillivray's Warbler		-/+ 16		+/- 92	+ 18	+ 5	- 12	- 14	
Western Tanager		+/- 12		+/- 10		+ 11			
Chipping Sparrow		- 42		+/- 11		+ 93	- 6		
Dark-eyed Junco		- 21		- 11		+ 18			
Brown-headed Cowbird		- 4				+ 11	+/- 7		
Pine Siskin		+/- 10	-/+ 6			+ 8	+/- 7		+ 6

Table 4. The inclusion of floristic (tree species composition) variables in the multivariate models for each species. The first column under each variable shows the sign of the coefficient. If 2 signs are shown, this indicates a significant quadratic relationship; shown are the signs of the coefficients for the linear term and the quadratic term, respectively. The second column under each variable is the chi-square statistic for the inclusion of that variable in the model; a larger number indicates a greater improvement of the model due to the inclusion of the variable. Structural vegetation variables are shown in Table 3.

<u>Species</u>	<u>Variable:</u>	Pond- erosa pine	Dougla s -fir	Larch	Lodge- pole pine	Spruc e- fir	Cedar/ Hemloc GrandF	Stone pines	Decid- uous
Northern Flicker									- 5
Hammond's Flycatcher		+ 21			- 15	- 6			+/- 12
Dusky Flycatcher		+/- 14			- 18	- 32	- 10		
Gray Jay		- 13				+ 4	- 7	- 7	
Mountain Chickadee							-/+ 66		
Red-breasted Nuthatch		+/- 72	+ 21	+ 21			+/- 35	- 4	
Golden-crowned Kinglet		- 26		+/- 13		+ 62	+/- 27		
Ruby-crowned Kinglet		+ 9		- 14	+/- 26	+ 4	-/+ 96		
Townsend's Solitaire		+ 18	+ 16		+ 22				
Swainson's Thrush		+/- 20	- 34	+/- 27	- 34			- 8	+ 6
Hermit Thrush				- 17		+ 11			
American Robin		+ 47	+ 30		+ 10		+ 11		+ 12
Varied Thrush		- 36	- 43		- 16	+ 14		+/- 9	
Solitary Vireo		+/- 44	+/- 17	+ 10		- 13	-/+ 23		
Warbling Vireo			+/- 10			- 5	- 12		+/- 25
Orange-crownd Warbler		+ 19	+ 23	+/- 47	+ 7		-/+ 6		+/- 14
Yellow-rumped Warbler		+ 6	+ 14	+ 8			- 14	+/- 11	
Townsend's Warbler		- 37	+/- 11	+/- 7	- 35		+/- 16	- 15	
MacGillivray's Warbler			- 19		- 34			- 6	+ 5
Western Tanager		+ 19	+/- 13		- 30	- 34		- 9	
Chipping Sparrow		+/- 75	-/+ 37	+ 18		- 4	- 4	+ 6	
Dark-eyed Junco				+ 19	+ 6				+ 5
Brown-headed Cowbird		+/- 35			-/+ 14	- 8			
Pine Siskin							-/+ 16		+ 4

DISCUSSION

The habitat relationships of these bird species were diverse and complex. All species were dependent on several variables. Although some relationships may have been spurious or weak, because of the high power and the diversity of habitats included, it is clear that bird species were influenced by many aspects of their environment. Even so, some patterns showed up repeatedly and have significant management implications.

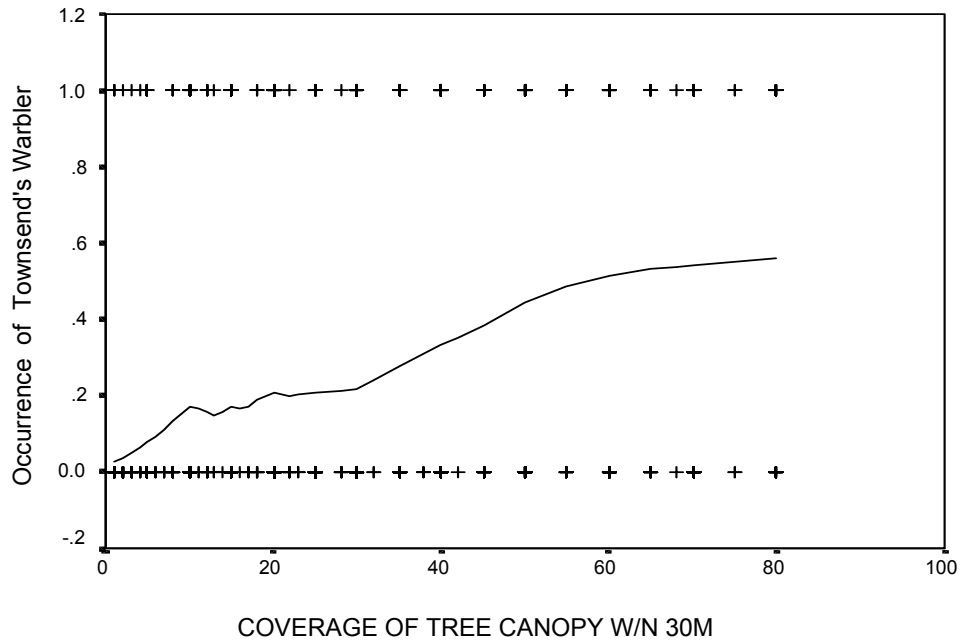
Canopy cover was a significant component of every model, and this relationship was usually among the strongest. This fundamental component of habitat selection is also the fundamental component of habitat change due to logging. Removal of trees would result in significant changes in the bird community. Such species as Golden-crowned Kinglet and Townsend's Warbler (Figure 1) would become less frequent, whereas Dark-eyed Juncos, Chipping Sparrows and Dusky Flycatchers would become more frequent. Species more frequent in intermediate harvests included the Yellow-rumped Warbler, Ruby-crowned Kinglet, and Mountain Chickadee (Figure 2). These changes depended on other aspects of the habitat, of course. Juncos preferred open habitats with fewer shrubs, for example, whereas many open forest species such as Dusky Flycatcher, Warbling Vireo, and MacGillivray's Warbler require shrubby habitats. Tall shrub cover was present in most models, although it was only strong in five.

Although the frequency of occurrence of each species changed with canopy cover, the number of species or the total abundance did not (Figure 3). Such summary indices completely obscured important habitat relationships in this case. The question is not one of changes in diversity or productivity, but in the makeup of the assemblage of bird species. It is likely that any change in habitat will be good for some species and detrimental for others. This reiterates the need to retain the full variety of cover types throughout the landscape, in order to maintain healthy populations of all bird species on a region-wide scale.

Stepwise procedures are often criticized for being unable to produce the best fitting model for the data (e.g., James and McCulloch 1990). The decision to include a variable depends on the variables that are already in the model, and these may not necessarily be the most important. Although I report the backward-elimination results as the chosen model, I also tried forward selection in an attempt to examine the effects of the order of variable entry. In most cases (11 of 18) the forward and backward procedures produced the same model, but in other cases the results showed very different conclusions regarding the importance of particular variables. The variable subset representing tree species composition was more prone to such inconsistencies, perhaps because the inherent interdependencies among these variables resulted in greater effects of the order of variable entry. Thus, it may be better to use some type of ordination procedure to reduce the number of species composition variables.

Even when both methods produce the same model, it may not be the best biological model. One variable that by chance has an inflated relationship can mask intercorrelated variables that may be more meaningful biologically. For example, the Dusky Flycatcher is related to the cover of both tall shrubs and low bushes in the univariate case, but since the relationship with bush cover is stronger, this variable is always included in the model, and the residual relationship with shrub becomes non-significant. It may be that the cover of tall shrubs, or perhaps a combination of the two, is the more meaningful variable.

a.



b.

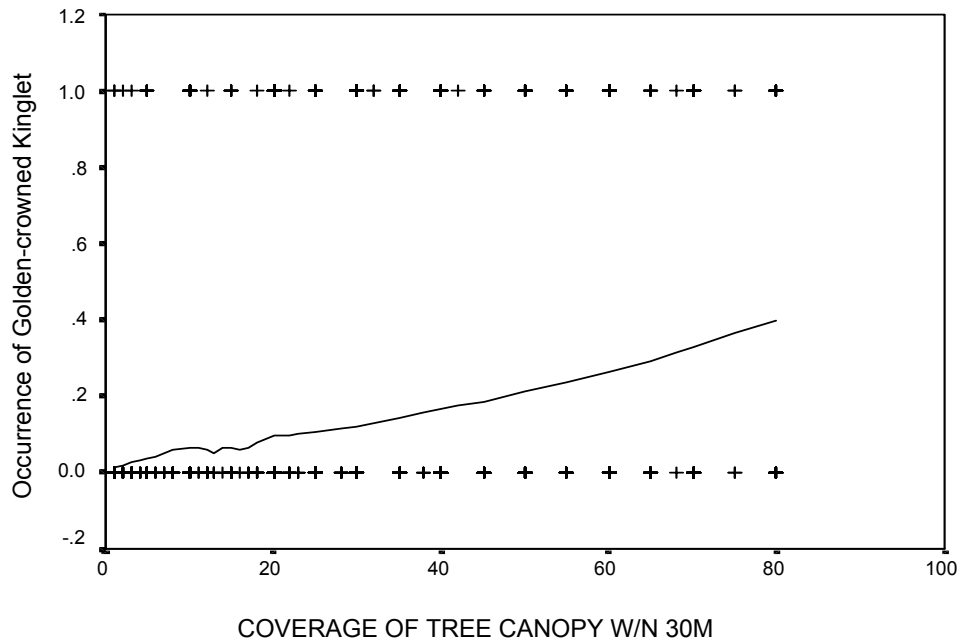
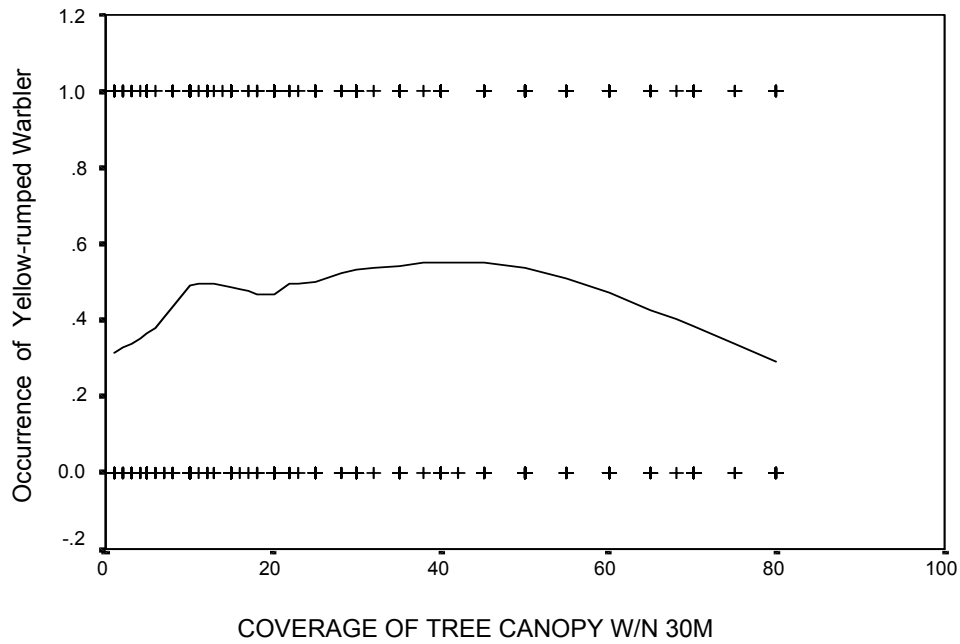


Figure 1. Univariate relationships of two species with the estimated percent cover of tree canopy. a) Townsend's Warbler, and b) Golden-crowned Kinglet. Both these species were detected more frequently in denser forests. Presence/absence data (coded 1 or 0, respectively) are depicted by plus signs (plus signs may represent multiple sites). A smoothed curve is drawn for easier visualization, using LOWESS smoothing.

a.



b.

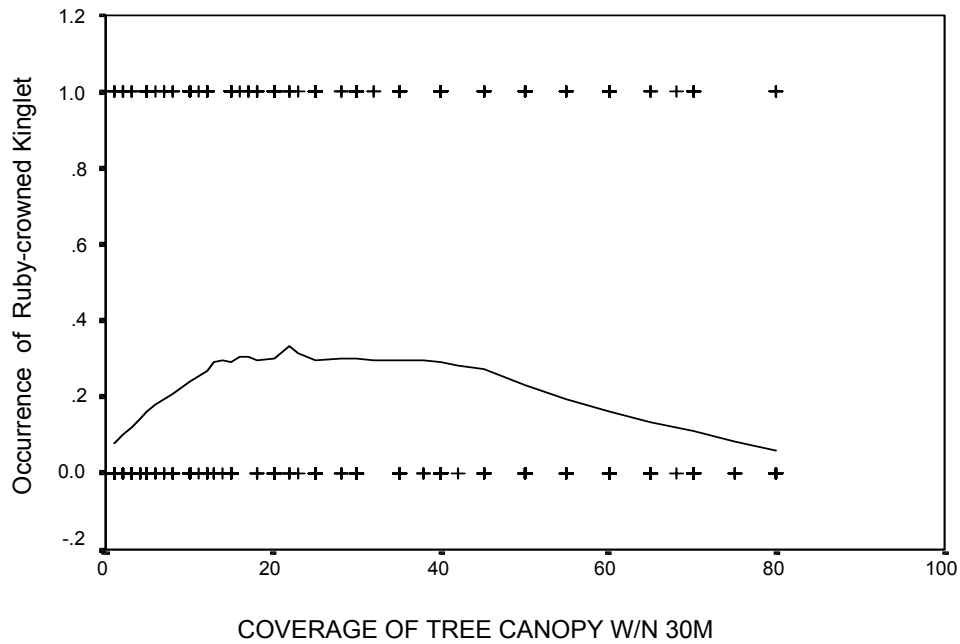
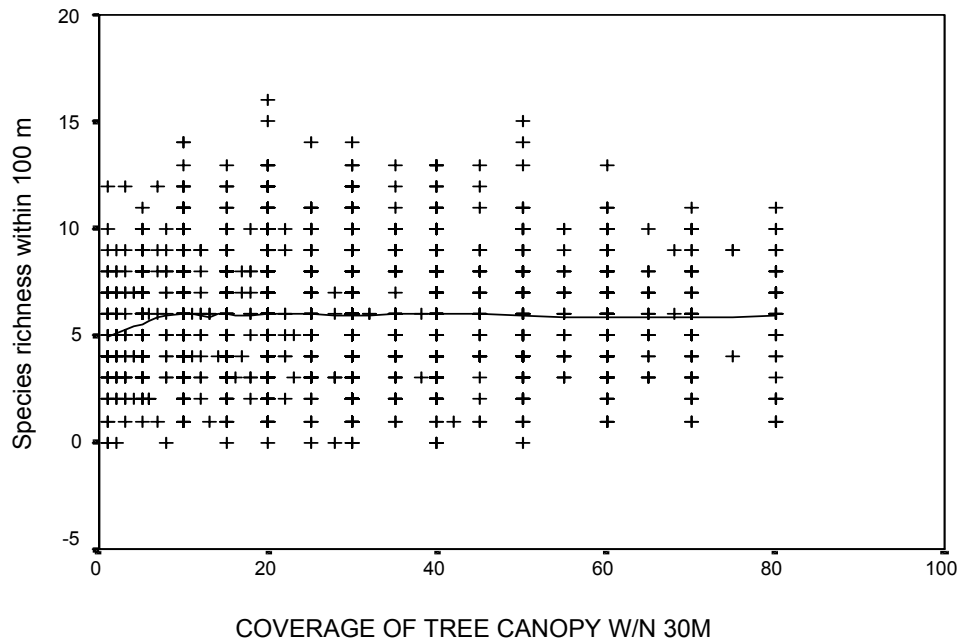


Figure 2. Univariate relationships of two species with the estimated percent cover of tree canopy. a) Yellow-rumped Warbler, and b) Ruby-crowned Kinglet. Both these species were detected more frequently in forests with intermediate canopy cover. Presence/absence data (coded 1 or 0, respectively) are depicted by plus signs (plus signs may represent multiple sites). A smoothed curve is drawn for easier visualization, using LOWESS smoothing.

a.



b.

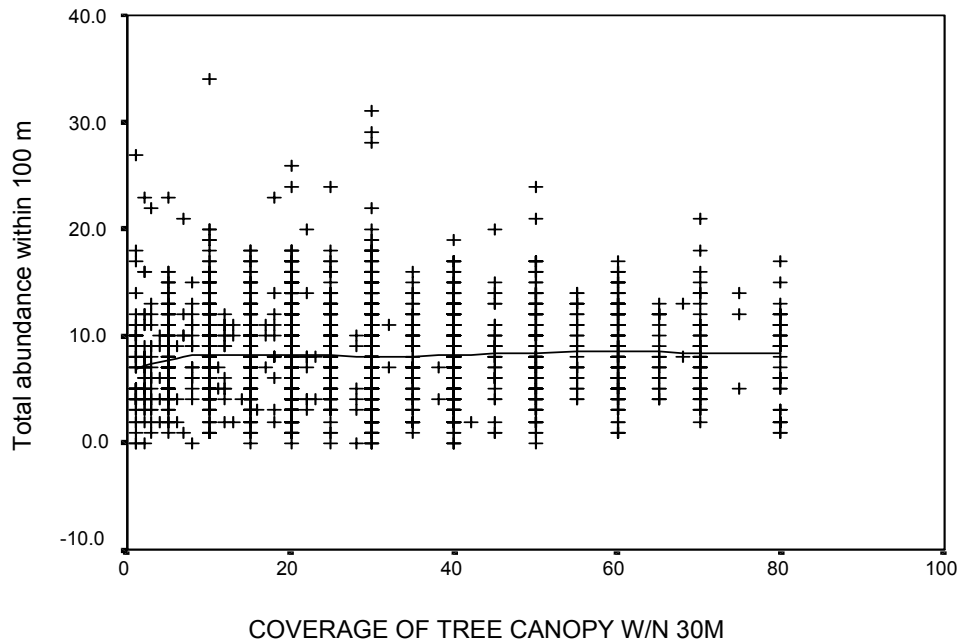


Figure 3. Univariate relationships of two bird community indices with the estimated percent cover of tree canopy. a) the total number of species detected within 100 m, and b) the total number of individuals of all species. Neither of these indices are significantly related to canopy cover. Plus signs may represent multiple sites. A smoothed curve is drawn for easier visualization, using LOWESS smoothing.

The large number of significant relationships suggests the possibility of Type I errors or confounding effects. Because of the high sample size, there was a great deal of power to detect nonrandom patterns in the data, even if small. A measured variable could have shown a significant pattern if it was even mildly correlated with one or more unmeasured variables that affected the distribution of the species. Because of the complexity and diversity of habitats throughout the region, it is not surprising that many nonrandom patterns emerged, whether or not they were biologically meaningful. We assumed that the stronger relationships did reflect biological responses that were consistent across the diversity of habitats.

As in all resource selection studies, conclusions are dependent on the set of resources that are considered available to the species. If a species does not occur in a cover type, we may want to see this reflected in the habitat relationships. On the other hand, we may consider this obvious or unimportant, and eliminate that part of the data set as "unavailable", thus changing the question to one of habitat relationships within some subset of cover types. This restriction could still be performed even if a species occurs in other habitats, if the question of most interest is relevant to the restricted data set. This is what we have done in this report, with a data set including only coniferous habitats. It is important to remember that different conclusions may be drawn from different subsets of the data, and that a complete picture of habitat relationships for a species may require several sets of analyses, depending on the question of interest.

Another way of restricting the data set would be to eliminate a geographic region where a species is rare or absent. For example, the Townsend's Warbler did not occur in the southeastern part of the region. This absence may have been due in part to a lack of appropriate habitat in this region, but it may have been more complex, involving landscape, climate, or even historical changes. If the distribution was not due to habitat differences, then overall analyses of habitat variables may be misleading. It may not always be clear which is the case. For example, the strong positive relationships of the Townsend's Warbler with tall shrub and low bush cover in the overall data set may have been due to the species' abundance in mesic forests, which only occur in the northwestern areas and which typically have more shrubs, rather than a preference of the species for shrubs per se. In fact, these relationships were much weaker in a restricted data set including only the northwestern forests. Another species of the northwestern mesic forests, the Varied Thrush, showed an even stronger shift in relation to these variables, with most becoming nonsignificant within the northwestern forests. Therefore, it is important to keep the framework of the analyses in mind in any discussion of habitat relationships.

An alternative method of controlling for such distributional complications is to include only those transects with at least one point occupied by the species. This eliminates points that are unoccupied due to landscape or geography, as well as many inappropriate habitats, and it changes the scope of the question. It may be assumed that all occupied transects were in at least marginally appropriate landscapes. The discrimination of individual points of use and nonuse by birds within occupied transects (which were less than 3 km in length) would likely be due to local factors.

The latter method would also help the statistical analysis of less common species. Less common species have large imbalances between the sizes of the presence and absence groups that the analyses are comparing, with many times more unoccupied than occupied points. Mills et al. (1993) suggested that this could cause problems when fitting regression models. One problem is again the inclusion of many points that are unoccupied for a variety of reasons, thus diluting any one particular effect. The exclusion of unoccupied transects would eliminate much

of this dilution as well as improving the numerical balance between occupied and unoccupied points. There were 45 species that were detected on at least 20% of the points within occupied transects.

If entire transects were unoccupied due to inappropriate landscapes (e.g., habitat fragmentation), then this can be discovered only by using the entire data set. It may be important to include landscapes in analyses of bird distributions, because good habitat in the wrong landscape may be unoccupied. We hope to be able to incorporate these into future analyses, as we have done in the specific case of the Brown-headed Cowbird (Young and Hutto, in review).

Like all models, those reported here need validation with new data. We will repeat this analysis process with 1995 and 1996 data. General habitat relationships studies will be less comprehensive in these latter years, because we did not repeat the 'extra' points visited in 1992-1994. However, there were still a sufficient number of points in conifer habitats to perform analyses within those cover types, as in this report. In fact, there were 1700 points in both 1995 and 1996 that are usable for modeling. Unfortunately, quantitative data on tree species composition were not collected after 1994, so models using only the structural habitat variables may be constructed.

LITERATURE CITED

- Balda, R. P., W. S. Gaud, and J. D. Brawn. 1983. Predictive models for snag nesting birds. Pp. 216-22 in (J. W. Davis, G. A. Goodwin, and R. A. Ockenfels, eds.). Snag habitat management: proceedings of the symposium. USDA For. Serv., Gen. Tech. Rep. RM-99.
- Best, L. B., and D. F. Stauffer. 1986. Factors confounding evaluation of bird-habitat relationships. Pp. 209-16 in (J. Verner, M. L. Morrison, and C. J. Ralph (Eds.). *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates*. Univ. Wisc. Press.
- Holmes, R. T. 1981. Theoretical aspects of habitat use by birds. Pp. 33-37 in (D. E. Capen, Ed.). *The use of multivariate statistics in studies of wildlife habitat*. USDA Forest Serv., Gen. Tech. Rep. RM-87.
- Hosmer, D. W., Jr., and S. Lemeshow. 1989. *Applied Logistic Regression*. John Wiley and Sons, New York.
- Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pp. 455-76 in (M.L. Cody, ed.). *Habitat selection in birds*. Academic Press, New York.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (U.S.A.) conifer forests. *Conservation Biology* 9: 1041-58.
- Hutto, R. L. (in review). Distribution and habitat relationships of landbirds in the USFS Northern Region. USDA Forest Serv., Gen. Tech. Rep. INT-
- Hutto, R.L. and J. R. Hoffland. 1996. USDA Forest Service Northern Region Landbird Monitoring Project: Field Methods. In-house report.

- James, F. C., and C. E. McCulloch. 1981. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annu. Rev. Ecol. Syst.* 21: 129-66.
- Maurer, B. A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. *J. Wildl. Manage.* 50: 556-66.
- Meents, J. K., J. Rice, B. W. Anderson, and R.D. Ohmart. 1983. Nonlinear relationships between birds and vegetation. *Ecology* 64: 1022-27.
- Mills, L.S., R.J. Fredrickson, and B.B. Moorhead. 1993. Characteristics of old-growth forests associated with Northern Spotted Owls in Olympic National Park. *J. Wildl. Manage.* 57:315-321.
- Morrison, M. L., I. C. Timossi, and K. A. With. 1987. Development and testing of linear regression models predicting bird-habitat relationships. *J. Wildl. Manage.* 51: 247-53.
- Press, S. J., and S. Wilson. 1978. Choosing between logistic regression and discriminant analysis. *Journal of the Amer. Statistical Assoc.* 73: 699-705.
- Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101: 672-84.
- Rotenberry, J. T. 1981. Why measure bird habitat? Pp. 29-32 in (D.E. Capen, Ed.). *The use of multivariate statistics in studies of wildlife habitat.* USDA Forest Serv., Gen. Tech. Rep. RM-87.
- Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? *Oecologia* 67: 213-17.
- Young, J.S. 1996. Nonlinear bird-habitat relationships in managed forest of the Swan Valley, Montana. M.S. Thesis, Univ. of Montana.
- Young, J.S. and R.L. Hutto. In review. Habitat and landscape factors affecting cowbird distribution in the northern Rockies. *Studies in Avian Biology.*