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Jock S. Young

The University of Montana

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Nonlinear bird-habitat relationships in managed forests of the Swan Valley, Montana

by

Jock S. Young

B.S. Oregon State University, 1983

M.S. University of California, San Diego, 1987

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Approved by:

Chairperson

Dean, Graduate School

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Nonlinear bird-habitat relationships in managed forests of the Swan Valley, Montana.

Director: Richard L. Hutto

Abstract:

The development of empirical models that describe bird-habitat relationships involves the search for important habitat variables that are associated with the distribution or abundance of particular bird species. The interpretation of such relationships depends on the statistical model used in the analyses. The responses of bird species to habitat variables are usually analyzed using linear regression, even though the responses of species to many important environmental factors are expected to be unimodal. In a review of recent literature, I found that, of 34 papers that used regression approaches, only 4 (12%) considered nonlinear relationships. It is possible that traditional modeling approaches have provided misleading conclusions about the nature of bird-habitat relationships. To examine this problem, I conducted a 2-year study (1993-94) in mixed-conifer forests of the Swan Valley of western Montana, where varied silvicultural practices had left a diversity of vegetation structures within this general vegetation type. I used point counts to sample birds on 86 sites, which were chosen to represent a gradient of tree density. I used logistic regression to model the responses of 18 common species to several vegetation variables that represented habitat structure and tree species composition. I compared linear vs. nonlinear approaches to modeling the habitat relationships of these species. Of 144 significant univariate relationships, about 45% included a quadratic term. Most importantly, of those relationships that were significant with a quadratic term in the model, 63% were not significant when only the linear term was included; these variables would not have been considered important using traditional methods that only examined linear relationships. Multivariate logistic regression models also included quadratic terms for about half of the component variables. Models for 14 of the 18 species showed significant improvement when quadratic terms were included, relative to models that included only linear terms. Nonlinear responses of birds to habitat variables appear to be common and should be routinely examined in studies of bird-habitat relationships. Because I was comparing bird distributions along gradients representing large changes in vegetation density, erroneous relationships could have resulted from a detectability bias caused by the song attenuation in dense vegetation. However, I found that the mean detection distance for all individuals of all species was uncorrelated with tree or shrub density.

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INTRODUCTION

A fundamental challenge in both ecology and conservation biology is to predict the abundance and distribution of animals in both natural and human-altered landscapes. The study of wildlife-habitat relationships approaches this task by asking the question: "Are variations in the distribution or abundance of particular species closely associated with habitat characteristics?" (Wiens 1989). And if so, can we predict a species' distribution and abundance based on measured habitat variables? Steps involved in answering these questions include: selecting variables of possible biological relevance to the species; constructing empirical, statistical models relating the occurrence of a species to these variables; and testing or validating these predictive models with new data. There is an implicit assumption that the distribution of birds is predictable across habitats because birds are free to settle in any habitat and are likely to engage in the process of habitat selection.

Habitat selection

In natural landscapes, it is generally assumed that animals choose to live in habitats to which they are best adapted (Grinnell 1917, Rotenberry 1981). Mobile species, such as birds, are especially likely to be able to find and settle in appropriate habitats (Cody 1985). The proximate cues they use to choose a habitat, however, may not be the factors most directly responsible for their fitness in the habitat (Hilden 1965). The cues must be readily assessible at the time of settling, and must be predictably correlated with factors that affect fitness more directly (Partridge 1978), under the conditions in which the species was adapted. If habitats are altered so these cues are no longer correlated with fitness, the species would still be expected to choose habitats based, in the short term, on the evolved cues.

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.

Animals may assess habitat cues independently, or they may respond to several variables at once, which act synergistically to produce some type of "gestalt" (James 1971, Cody 1985). If some of the habitat variables are dependent on each other, or if there are interactions between them relative to a species' response, then a multivariate analysis will be required for any accurate prediction of such a response.

Multivariate approach

The idea that many environmental variables act simultaneously to determine the distribution and abundance of animals was not new when Hutchinson (1957) formulated the concept of the niche as an n-dimensional hypervolume, but it was this formulation that has inspired many studies of habitat relationships from a multivariate niche perspective. The n-dimensional concept of the niche is analogous to the n-dimensional sample space of multivariate statistical methods, and it was inevitable that these methods would be applied to the study of wildlife-habitat relationships (Shugart 1981). Multivariate methods help us determine how many cues a species seems to be using to select a habitat (the number of variables required for good prediction), and whether these cues seem to be assessed independently, or if there are interactions among them, such that habitat selection can only be understood in terms of a multidimensional "gestalt" vegetation configuration (James 1971).

Numerous researchers have used a multivariate approach to explore avian use of habitats and to quantify the habitat as niche (e.g. Hespenheide 1971, James 1971, Martinka 1972, Anderson and Shugart 1974, Whitmore 1975, and many later studies). Most of these studies have dealt with individual microhabitat choice by measuring vegetation in occupied territories or around singing or foraging individuals. This may be the best way to study habitat selection as a behavioral phenomenon on the microhabitat scale (Noon 1981, Shugart 1981), but it gives no indication of the population-level consequences of habitat selection (Shugart 1981). For this, it is more appropriate to compare avian abundance and vegetation measurements on the scale of a homogeneous area of land (i.e. habitat). 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). In this type of study, the abundance or frequency of occurrence of a given bird species is correlated with average habitat characteristics. This scale is also appropriate for assessing the impact of logging practices, because such habitat alterations usually occur over entire forest stands. A study of habitat selection at this scale should reveal the proximate cues each species uses to select appropriate habitats in which to search for the best available territory.

Gradient analysis

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 nature of nonlinear species responses as accurately as possible (Best and Stauffer 1986).

The determination of individual species' responses to one or a few habitat axes (selected a priori) is termed direct gradient analysis (Whittaker 1967, Ter Braak and Prentice 1988). This general procedure can involve a wide variety of statistical methods, however, and the choice of methods to be used in building an empirical model depends in part on the expected shape of the species response curves.

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.

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. Therefore, Gaussian curves are a standard assumption for all niche dimensions (e.g. MacArthur 1972, and most ecology textbooks). Although this specific mathematical model may have been used for computational convenience, some type of smooth, unimodal response curve does make ecological sense, as long as individuals are mobile enough to find and choose the best habitat, and as long as habitats have been constant for long enough for adaptations to occur.

There is no conceptual reason why such unimodal species responses to environmental gradients should fit symmetrical Gaussian curves (Austin 1980). Physiological response curves are often skewed, at least in plants (Austin 1980), and any response may be altered by competition (Giller 1984, Mueller-Dombois and Ellenberg 1974). There is also no reason to expect that the two sides of a species' response curve should be shaped or limited by the same environmental factors, so symmetry may not be common (Austin 1976). Bimodal response curves may be due to unsatisfactory distribution of observations and/or unrecognised environmental factors (Austin et al. 1984). The shape of response curves may also be altered by other correlated environmental factors (Westman 1980), or simply by the measurement units or the scaling chosen for the environmental variables or the species importance values (Austin 1976). In short, "species response curves for indirect environmental gradients may be expected to have at least one maximum, but little else is certain" (Austin 1980).

Empirical evidence for the shapes of species response curves has come mostly from the field of plant community ecology. Gauch and

Whittaker (1972) first put forth the generalization that the abundance of most plant species along environmental gradients tend to fit Gaussian curves. They cited several empirical studies, involving direct gradient analysis of vegetation, to support this claim (Curtis and McIntosh 1951, Brown and Curtis 1952, Whittaker 1951, 1956, 1967). Westman (1980) developed this idea further, and cited several similar studies (Curtis 1959, Monk 1965, Noy-Meir 1974, Whittaker 1956, 1960). Austin (1976) surveyed 135 response curves from these same 5 studies and concluded, through visual inspection, that 73% of the curves were unimodal, although usually not Gaussian, and only 5% were linear. Although there has been controversy surrounding the exact model underlying these distributions (Austin 1980), it is generally agreed that the overwhelming majority of response curves are nonlinear.

Although unimodal relationships have been commonly studied in the botanical literature, few researchers in avian ecology have taken this phenomenon seriously. Even after Meents et al. (1983) used second- and third-order polynomials to demonstrate many biologically interesting nonlinearities that would not otherwise have been discovered, most studies continue to use simple linear methods. This is both a matter of convenience and an assumption that nonlinear relationships are either rare or unimportant, and should be addressed only if compelling evidence exists (Morrison et al. 1992, p. 312). Rarely have nonlinear responses been routinely addressed in a study of bird-habitat relationships (but see Green et al. 1994, Heglund et al. 1994, Hansen et al. 1995).

Because we have theoretical reasons to expect unimodal relationships, such relationships should be examined as part of any study. The exact model to be used in testing significance, however, could be Gaussian or quadratic, with the realization that part of the unexplained variation could be due to an inappropriate model. With the lack of any theoretical or empirical basis for expecting any particular model, it is best to make as few assumptions as possible, so only the simpler curvilinear relationships (such as quadratic) should be investigated. Although real ecological relationships may be more complex, these simple models are nevertheless useful for statistical analysis of data showing mostly unimodal responses (Ter Braak and Prentice 1988).

Objectives

The present study was conducted in western Montana, where varied silvicultural practices had created forest stands with a diversity of vegetation structures that may not have occurred naturally in unaltered forests. This provided an opportunity to tease apart the importance of several structural habitat variables within a single cover type. If birds respond to the same habitat cues in altered habitats that they respond to in naturally occurring habitats, then an empirical model based on bird responses in altered habitats will be applicable to either altered or unaltered areas. However, if the combinations of habitat variables in logged stands are outside the evolutionary experience of a species, the birds may not respond in a predictable fashion. It is important to determine if bird occurrence can be predicted in altered landscapes, and, if so, which variables, or combinations of variables ("gestalt"), the birds appear to be using as proximate cues.

Toward this end, I conducted a study in the Swan Valley of western Montana, using point counts to sample birds on many sites chosen to represent a gradient of tree densities (which included a wide variety of silvicultural practices). My objectives were to:

1. Determine the response curves of all common species of birds to a variety of vegetation variables using both univariate and multivariate statistical techniques.

2. Determine the prevalence of unimodal relationships along gradients that span a sufficient range of potential habitat variation.

3. Develop predictive models that can be tested with monitoring data collected in the region, and can be subsequently used by managers to help predict the consequences of habitat alteration for a wide variety of bird species.

METHODS

Description of study

Silvicultural practices in the Swan Valley of western Montana have produced forest stands with a wide variety of vegetation structures. The present study was conducted within the mixed-conifer cover types of the valley floor below 5000 feet (mostly Douglas-fir and western larch, with varying amounts of spruce/fir, pine, cedar, and deciduous elements). Eighty-six sites were located all along the valley for 55 kilometers, between Holland Lake and Swan Lake (Figure 1).

It was not possible to take extensive vegetation measurements in potential stands prior to choosing study sites. Therefore, to assure a useful range of variation within the mixed-conifer cover type, one gradient was chosen that could be estimated beforehand, was biologically meaningful to the birds, and represented a major axis of silvicultural habitat alteration. Tree density, or canopy cover--a closely correlated variable, could be roughly estimated from aerial photos and quick ground inspections. Tree density was also expected to be very important to most forest birds because trees provide foraging or nesting opportunities to almost all forest-dwelling species, and the total volume of tree foliage should, in turn, have a major influence on their abundance. Basal area is a better estimator of total foliage volume than is tree density (Verner and Larson 1989), and I chose to use this measure instead of tree density. All three measures of canopy density

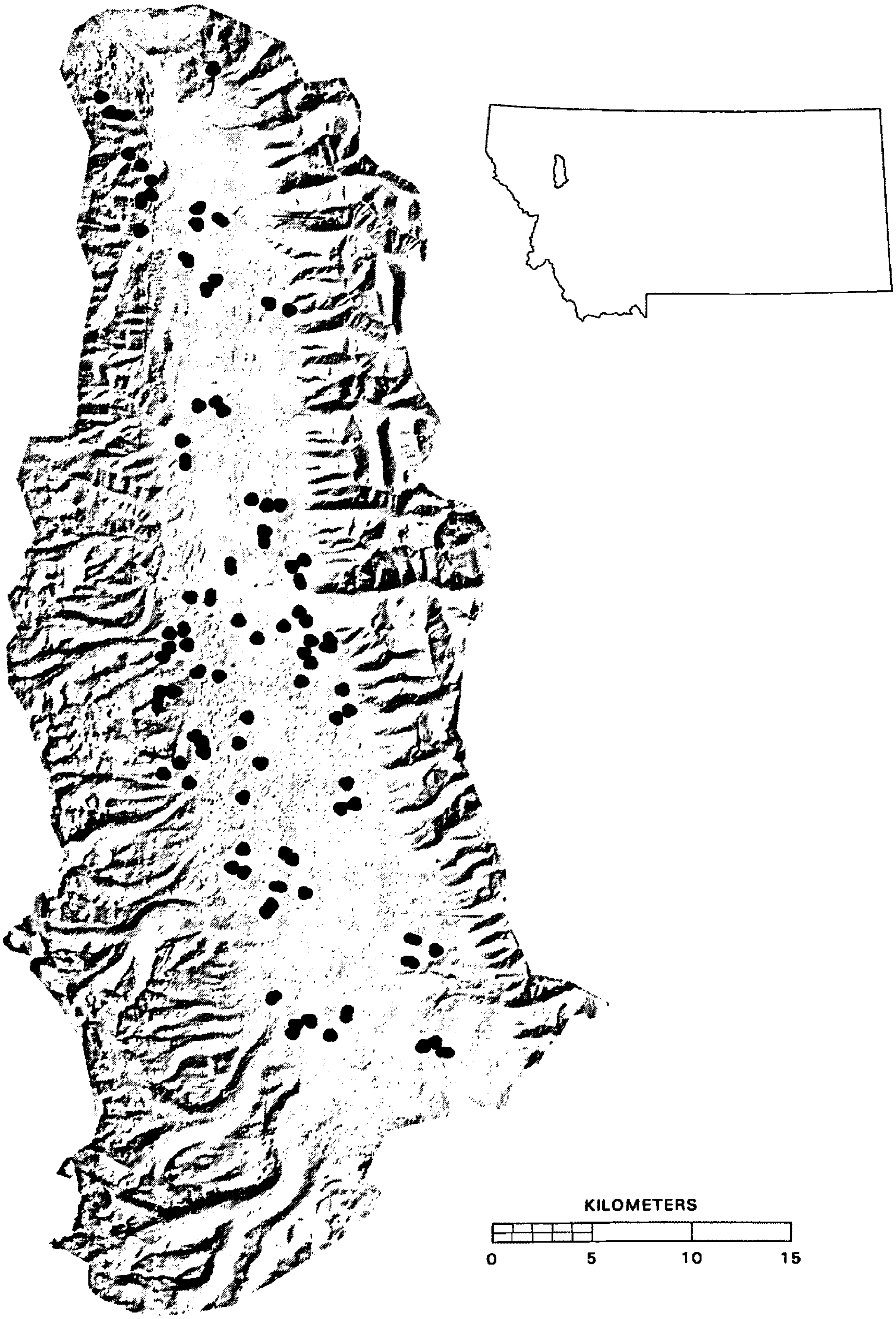


Figure 1. Location of study sites in the Swan Valley of western Montana.

(basal area, mature tree density, and canopy cover) were very closely correlated in this study ($r > 0.95$).

Tree density is also the major axis of human-induced disturbance, since logging practices manipulate this variable directly. Increasingly varied silvicultural practices have provided both an opportunity and a necessity for studying the effects of such habitat alteration on the distribution and abundance of forest birds (Hansen and Hounihan 1996).

Site selection

Study sites were chosen to assure a range of tree densities that was as complete and uniform as possible (based on canopy cover estimates from aerial photos). Logistical constraints allowed for the sampling of three sites per day that were near enough to one another to be reached during the morning period of bird singing activity. To select these sites, section corners were chosen at random, and aerial photos were used to pick three forest stands from the surrounding four square-mile sections. These stands had to be large enough to contain the sample design discussed below, and homogeneous enough to provide meaningfully consistent data. Every effort was made to select a low, medium, and high tree density stand each day, in order to block for daily effects due to weather (Robbins 1981), season (Best 1981) and location. However, it was sometimes impossible to meet all of these criteria simultaneously, and priority was given to distributing tree densities evenly with respect to season, because seasonal effects were thought to be especially significant.

Sampling methods

Within each site, birds were counted at three separate points during the spring of 1993, and these same points were revisited in 1994. These points were positioned 200 m apart, usually in an equilateral triangle (Figure 2; although other configurations had to be used at times). Only those bird detections within 100 m of each point were used in the analyses. For each species, detections were summed over all three points in each site.

Habitat variables thought to be biologically meaningful to the birds (Table 1) were measured in 15 circular sample plots per site. Each plot enclosed 100 sq m, with one plot positioned at each bird point and one randomly located within in each quadrant of the surrounding 100-m-radius circle (Figure 2). All variables were reported as means per plot (100 sq m), averaged over all 15 plots at each site.

The density, 10-cm size class, and species of all trees with dbh over 10 cm were recorded. "Mature" trees were defined, for this study, as those over 20 cm dbh. At this size, most trees were part of the overstory canopy and were potentially harvested under most silvicultural treatments. Smaller trees (dbh < 20 cm) usually represented a subcanopy layer. The average size of mature trees was estimated by assigning the midpoint of the appropriate 10-cm size class to each tree (e.g. 25, 35, 45, and 55 for all trees greater than 50 cm) and averaging over all trees on the site.

Basal area was estimated from the center of each vegetation plot by counting trees that were displaced by less than their own diameter in a standard basal area prism [and multiplying by the Basal Area Factor of the prism (10) to get basal area in square feet per acre]. This "plotless" sampling method is standard forestry practice (Husch et al. 1982). I then partitioned the total basal area values into the basal area due to mature trees (dbh > 20 cm; BAMAT; see Table 1) and that due to small trees (dbh = 10-20 cm; BASM). For an estimate of large trees (dbh > 50 cm) on the sites, I did not use the basal area because this would have been a component of BAMAT. Instead I used the density of

Table 1. Main vegetation variables and descriptions.

BAMAT	Basal area (sq ft/acre) of 'mature' trees (dbh > 20 cm)
BASM	Basal area (sq ft/acre) of small trees (1 - 20 cm dbh)
LARGE	Density of large trees; stems/plot(100 sq m), dbh > 50 cm
GROUND	Percent cover of ground vegetation (all plants < 3 dm tall, and all forbs and grasses)
BUSH	Percent cover of low bushes (all woody plants less than 1 m)
SHRUB	Percent cover of tall shrubs (all woody plants, 1 - 10 m tall, including conifers)
SHRDEC	Percent cover of deciduous shrubs; component of SHRUB
SAP	Percent cover of conifer saplings; component of SHRUB
AVGSIZE	Average size of mature trees (by midpoint of size classes: dbh = 25, 35, 45, or '55' cm for all large trees)
PSME	Proportion of mature trees that were Douglas-fir (*Pseudotsuga*)
LAOC	Proportion of mature trees that were Western Larch (*Larix*)
PINE	Proportion of mature trees that were pine (*Pinus*: Lodgepole, ponderosa and western white pines)
MESIC	Proportion of mature trees that were mesic-associated species: spruce/fir (*Picea*, *Abies*), cedar (*Thuja*), and deciduous (*Betula*, *Populus*)
SPFIR	Proportion of mature trees that were spruce (*Picea engelmanni*) or fir (*Abies lasiocarpa* and *Abies grandis*)
CANHT	Typical height of forest canopy (in meters)
SNAGBA	Basal area of snags with dbh > 20 cm
DECPRES	Categorical variable for presence or absence of deciduous trees on sample plots (coded 1 or 0).

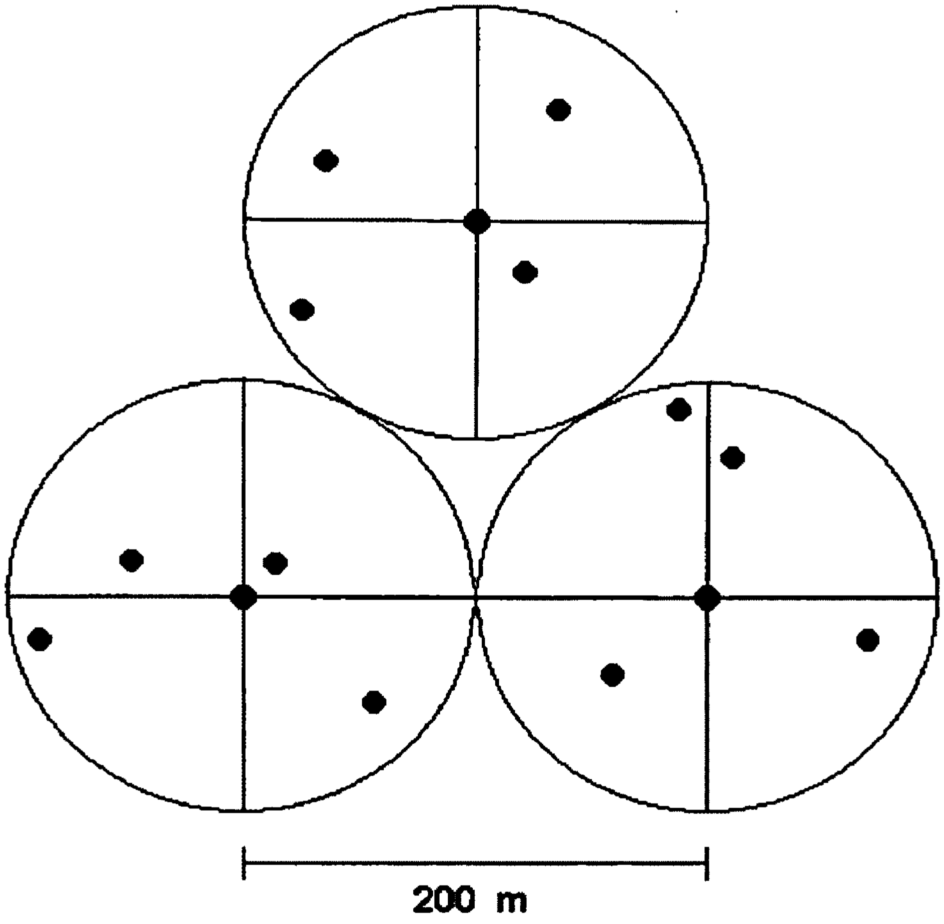


Figure 2. Sampling design within each site. The three point counts were conducted at the centers of the large circles, and all birds observed within that circle (100-m radius) were used in the analyses. The 15 associated vegetation plots (dark dots) were positioned at each bird point and at random locations in each surrounding quadrant.

large trees (LARGE), so that the estimate would be less dependent on BAMAT.

For most sites, the understory vegetation was measured by ocular estimates of percent cover for three vertical strata of vegetation in each plot: ground cover (all plants less than 3 cm tall, and all forbs and grasses), low "bush" cover (all woody plants, including conifers, less than 1 m), and tall "shrub" cover (all woody plants, including conifers, between 1 and 10 m). Field estimates of percent cover were based on the Braun-Blanquet system (Mueller-Dombois and Ellenberg 1974), then converted to mean percentages for analysis. (Understory cover on about 20 sites was estimated by counting 'hits' at 10 points, positioned at 1-meter intervals across each plot.)

Shrub cover was estimated in the field as the total cover of all plants (conifer and broadleaf) that had a maximum height between 1 and 10 m. I did not differentiate between conifer saplings and deciduous shrubs in this quantitative estimate, but I additionally described each plot fairly well, in terms of species, heights and relative cover. From these descriptions I was able to reconstruct what the Braun-Blanquet scores would probably have been for conifer (SAP) and broadleaf (SHRDEC) elements in each plot. Pacific yew was included in SAP as a conifer, even though it generally has a multi-stemmed, "shrubby" growth form in this region. These estimates were more crude than the direct field estimates of total shrub cover (SHRUB), but when averaged over each site they seemed to partition the total shrub component consistently (SHRUB vs. SAP + SHRDEC were correlated with $r = .99$). At the very least, they gave a good indication of which elements the birds were more likely responding to.

Since there were 12 species of trees sampled in this study, and several were on only a small proportion of sites, I combined tree species into four categories for use in the analyses. The two most common tree species, Douglas-fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*), were still represented by separate variables (PSME and LAOC, respectively). I combined all three species of PINE together--lodgepole pine (*Pinus contorta*) was very common, western white pine (*Pinus monticola*) was uncommon, and ponderosa pine (*Pinus ponderosa*) was intermediate. Englemann spruce (*Picea engelmannii*) and the two fir species--grand (*Abies grandis*) and subalpine fir (*Abies lasiocarpa*)--were combined (SPFIR). Western redcedar (*Thuja plicata*) and the three deciduous species--paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*), in decreasing order of importance--were added to SPFIR to create an optional category of MESIC species.

Statistical analyses

For each common bird species, a multiple logistic regression model was constructed that best predicted the presence or absence of the species on the study sites, using the vegetation variables in this data set. A detection on any of the three point counts on a site constituted a presence for the bird species on that site. In most analyses (see Results), the bird data from both years of the study were combined, so that a detection in either year constituted a presence for a species.

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). Even when I combined results from the three points on each of my study sites, most species were absent on 35-75% of the sites in a single visit. The preponderance of zeroes strongly skewed the outcome variable and violated the normality assumption of a simple regression model.

Furthermore, most species were represented by either zero or one detection on 72-92% of the sites, 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.

I chose logistic regression over linear discriminant analysis because logistic regression is preferable when the explanatory variables are nonnormal, especially when any are categorical (Press and Wilson 1978). Although I had only one categorical variable, most of the continuous habitat variables in this study were nonnormal.

Variable selection

I measured too many vegetation variables to be included in a single logistic regression model. Not only do too many variables make a model numerically unstable, and sometimes impossible to calculate, but a more parsimonious model is more easily generalizable (Hosmer and Lemeshow 1989), and is easier to interpret biologically. Furthermore, if future prediction is desired, fewer variables are easier and more economical to measure on new sites. If we want to know which variables are most important in explaining the distribution of a species in the study area, then we should include only the subset of variables that most effectively combine to explain the data.

As a first step in selecting variables for each species model, I fitted separate univariate logistic regression equations for each variable (Hosmer and Lemeshow 1989). For each variable, I considered the two alternatives of linear and unimodal relationships. I used the simplest method of modeling a unimodal relationship: adding a quadratic term to an equation that already includes 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). If these signs are reversed ($-aX+bX^2$), then the maximal values are at the extremes of the variable range (an upright U). I was primarily interested in unimodal relationships, but I allowed the coefficients to vary freely, so there were quadratic relationships of both types (there were no cases where the signs of both coefficients were either positive or negative, which would describe some type of exponential curve). To test for a unimodal relationship, the statistical modeling program must evaluate both terms together, and not allow an equation with the quadratic term alone (which would not be a unimodal curve). I was able to program this in BMDP (Dixon 1990) by using the interaction of the variable with itself (X*X) as the quadratic term, and invoking the heirarchical rule that the component variables (in this case X) must be moved with the interaction term if the latter is entered or removed from the model. The criterion for evaluation of a term was the likelihood ratio test for the improvement of the log likelihood between models with and without the variable. In the case of the quadratic relationship, I used the p-value for the improvement of the model when the quadratic term was added to an equation that already included the first-order term.

Model building

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. In practice, I used $p < 0.15$ for the model with only the linear term, and $p < 0.10$ for the addition of the quadratic term, with some adjustment based on the number of significant variables and the biological relevance of some variables for particular species.

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. The backward elimination method is usually considered to be more appropriate than forward selection. Most potentially confounding variables (of those available) are contained in the model when each variable is evaluated, whereas forward selection evaluates early variables without the benefit of information from potentially confounding variables. In forward selection, variables entered early will later be reevaluated, but decisions are made on most variables when few other variables are controlled for. It is possible for a potentially important variable to be kept out of a model if a correlated variable happens to have a stronger univariate relationship.

Stepwise procedures are often criticised for being unable to produce the best fitting model for the data (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, in some cases I also tried forward selection and all-possible-subsets model-building methods, in an attempt to examine the effects of the order of variable entry. There were two cases in which I felt these alternative methods indicated a model that was clearly superior to that produced by backward elimination, so I reported the alternative model in Table 5 (Hairy Woodpecker and Gray Jay; see Appendix for discussion). Otherwise, these alternative models are only discussed in the Appendix. For the all-possible-subsets regression I used the method described by Hosmer and Lemeshow (1989, pp. 118-126), which allowed the use of a "best subsets" linear regression procedure (which is available in BMDP) to perform "best subsets" logistic regression. Because I was uncertain about the accuracy of this method, I did not use it as the primary method for building multivariate models.

All model-building procedures can still produce models with irrelevant variables. They require examination for biological plausibility and future study.

During model building I used the total understory cover (SHRUB) in the initial phase, unless any relationship was clearly due to only one of the separate understory elements (SAP or SHRDEC), in which case I included only that element from the beginning. For some species, I then tried alternative models with the conifer and deciduous elements separately, in place of total understory cover, to see if either gave a superior improvement to the multivariate model.

I never entered all four tree species composition categories into any model, because the fourth category was fully dependent on the others (PSME + LAOC + PINE + MESIC = 1). Since SPFIR comprised the bulk of the MESIC category, only one or the other of these variables was included in any model. I usually chose the one with the best improvement in the univariate case, although, if they were both significant as well as DECPRES, I used MESIC as a way of including all mesic elements.

Goodness-of-fit

After the variables were chosen for the model, the model was tested to determine how well it explained the data. This was done by comparing observed and expected values for each site, and summarizing the deviations in a measure of goodness-of-fit. I used the Hosmer-Lemeshow test (1989), which is available in BMDP (Dixon 1990). This is based on a chi-square test, with the data grouped into 10 equal quantiles ($p < 0.05$ recommends rejection of the habitat model as an explanation of the data). This is preferable to a classification table as a measure of fit, because a classification table is sensitive to the relative sizes of the component groups, and a binary classification table carries less information than a continuous probabilistic model.

The assessment of fit is separate from the issue of variable selection, because all measures of goodness-of-fit, or predictability, increase with the number of variables in the model and cannot, therefore, be used as criteria for selection of variables.

All p-values are reported in unadjusted form. I used $\alpha = 0.05$ as the final criterion for including a variable in a model. Hosmer and Lemeshow (1989) caution that the p-values from stepwise selection procedures should be thought of only as indicators of relative importance among variables, rather than as strict criteria for significance. As long as we keep this in mind, I think that Bonferroni adjustment of the p-values is unnecessary, even though I conducted many tests. In addition, I was interested in examining each potential relationship to determine if there was evidence for something worth investigating; therefore, I wanted to use a p-value that reflected the nature of the data directly, not a number that was dependent on how many other tests I happened to do. Bonferroni adjustment of the p-values would be necessary if I wanted to pick out the significant relationships from my study and report them as final conclusions. This was not my intention, however; all apparent relationships should be considered as hypotheses for further study.

RESULTS

Habitat variables

The study sites represented a fairly uniform coverage of the tree density gradient (as measured by the basal area of mature trees, BAMAT), except for the relatively large number of sites with low values of BAMAT (Figure 3); sites with BAMAT greater than about 90 square feet per acre (arrow in figure) were in unlogged forests. Furthermore, the tree density gradient was fairly evenly distributed across the breeding season (Figure 4), although the correlation between BAMAT and Julian date was marginally significant in 1994 ($r=.21$, $p=.05$). The frequency distributions of other major habitat variables were more uneven, as expected from the study design (Figures 5-6), but they still showed a large amount of useful variation to work with in developing models of habitat relationships (Table 2). Furthermore, less than half of the variable pairs were significantly correlated (Table 3); only 10 of 120 variable pairs had $r^2 > 0.25$, which was good for separating their effects statistically.

The study sites ranged from very sparse seed tree cuts to very dense, closed-canopy forests. Four seed tree cuts contained only western larch (LAOC) as mature trees (dbh about 40-50 cm and evenly spaced). These 4 sites with LAOC = 1.0 strongly influenced the results of bird relationships with that variable. Most of these cuts were relatively recent, with limited understory, but there were a few older cuts with few mature trees and very dense shrubs (Figure 7a). Many other sites with low tree density were probably overstory removals or some type of "release" cut (dense stands of low diameter trees were severely thinned for competitive release of the remaining trees). The trees left on these sites were usually small (most 10-20 cm dbh; Figure 7b), and they were often aggregated, with open areas between.

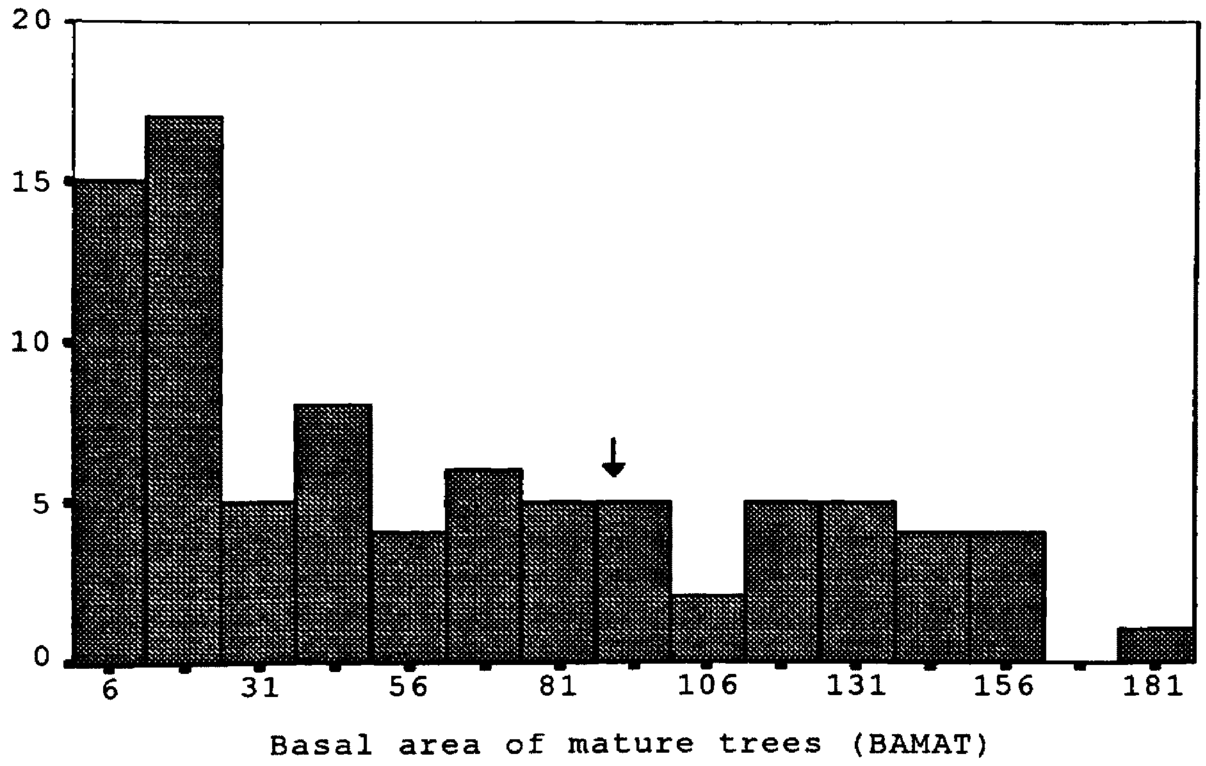
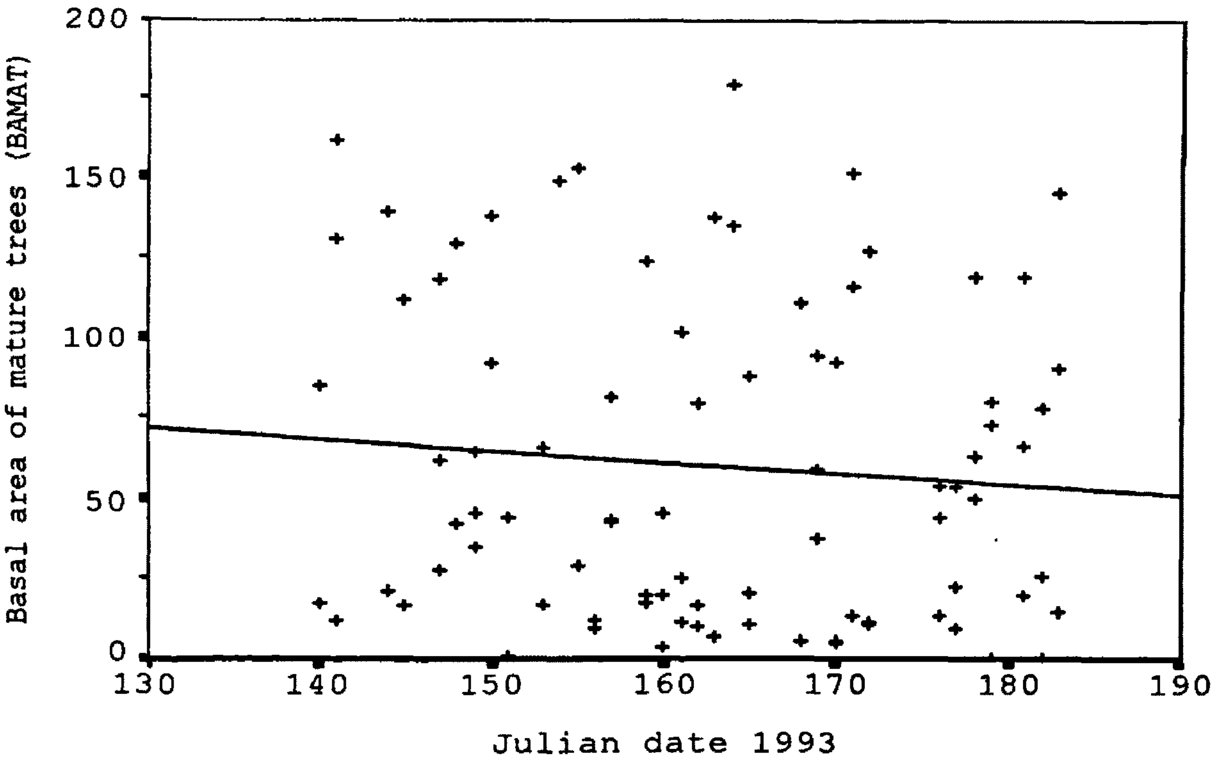


Figure 3. Frequency distribution of the basal area of mature trees (BAMAT) in sq ft per acre. Arrow indicates approximate point above which stands are natural, unlogged forests.

a.



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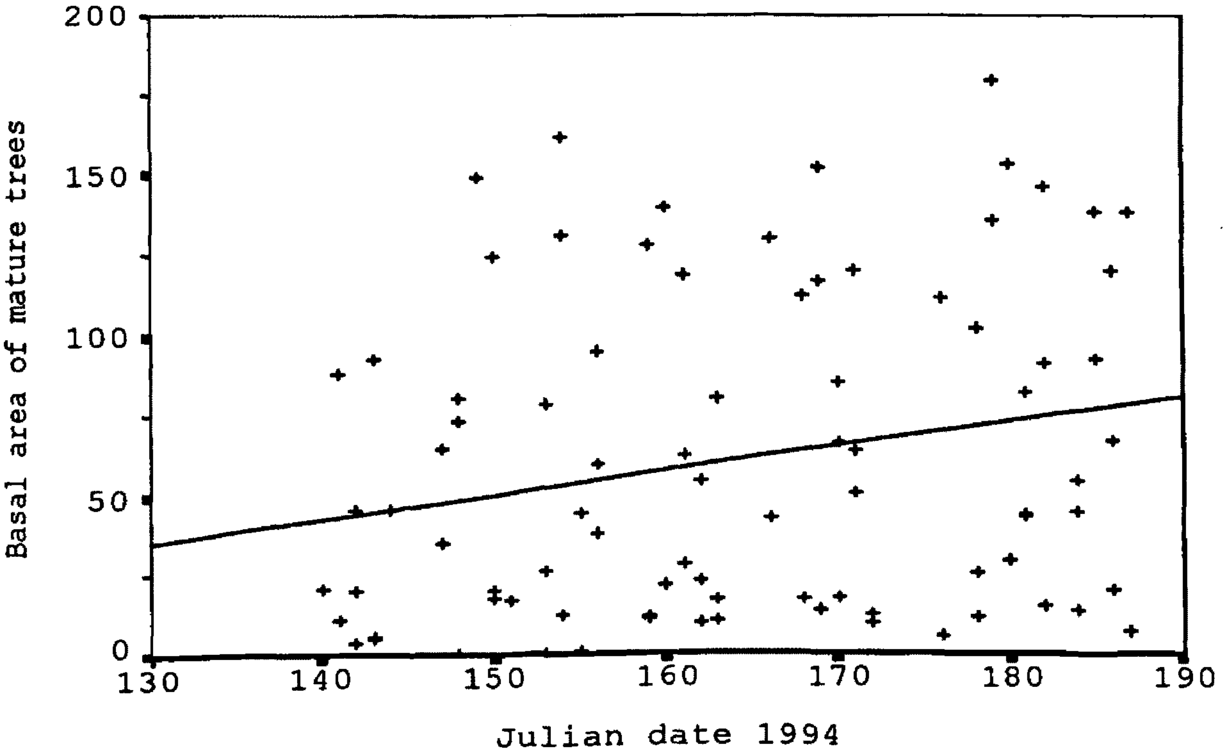


Figure 4. The temporal distribution of sites across the sampling period, with regard to the tree density gradient (1993: r= -.09,p= .43; 1994: r= .21; p= .05; Julian date 130 = May 10).

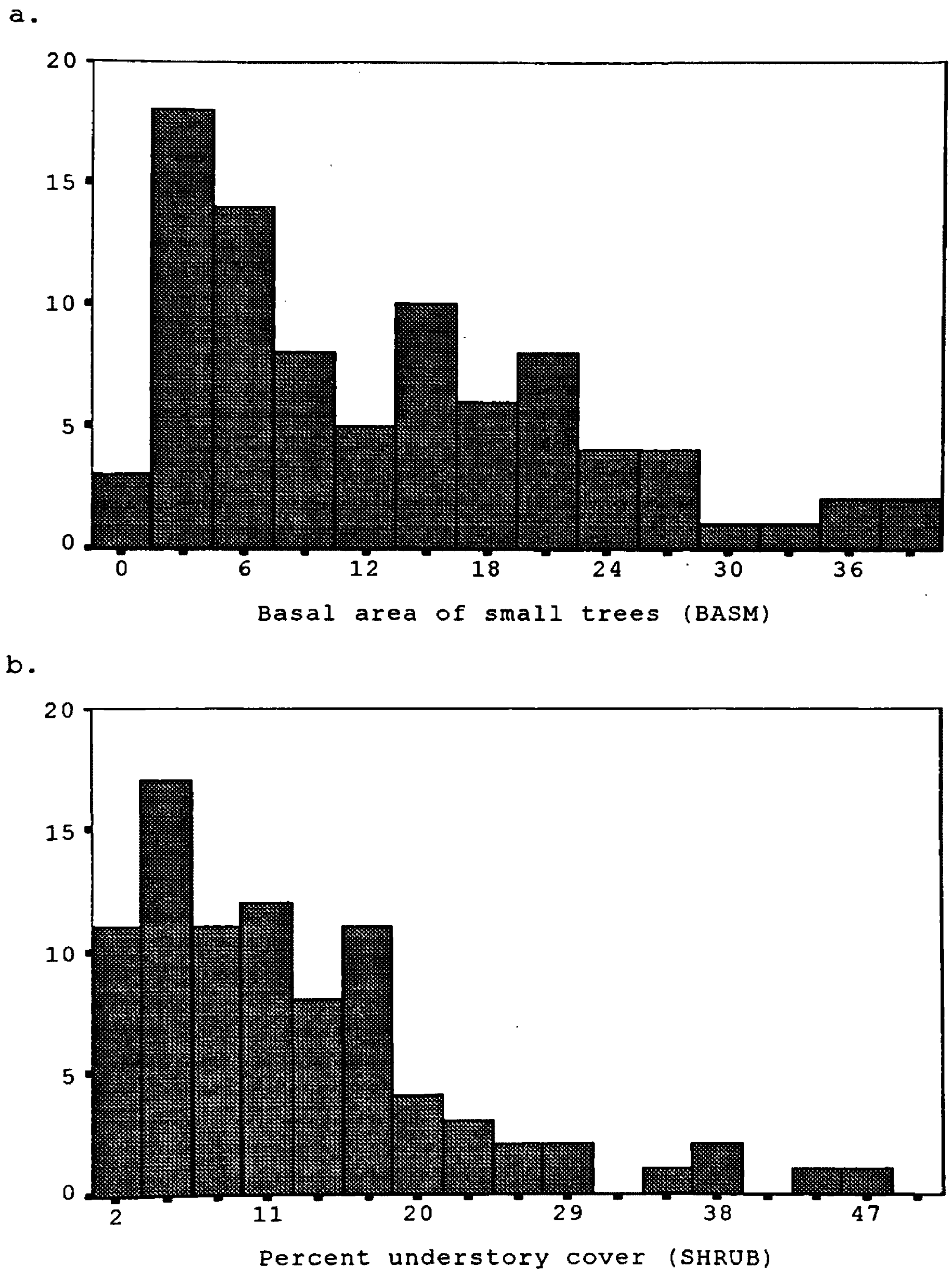
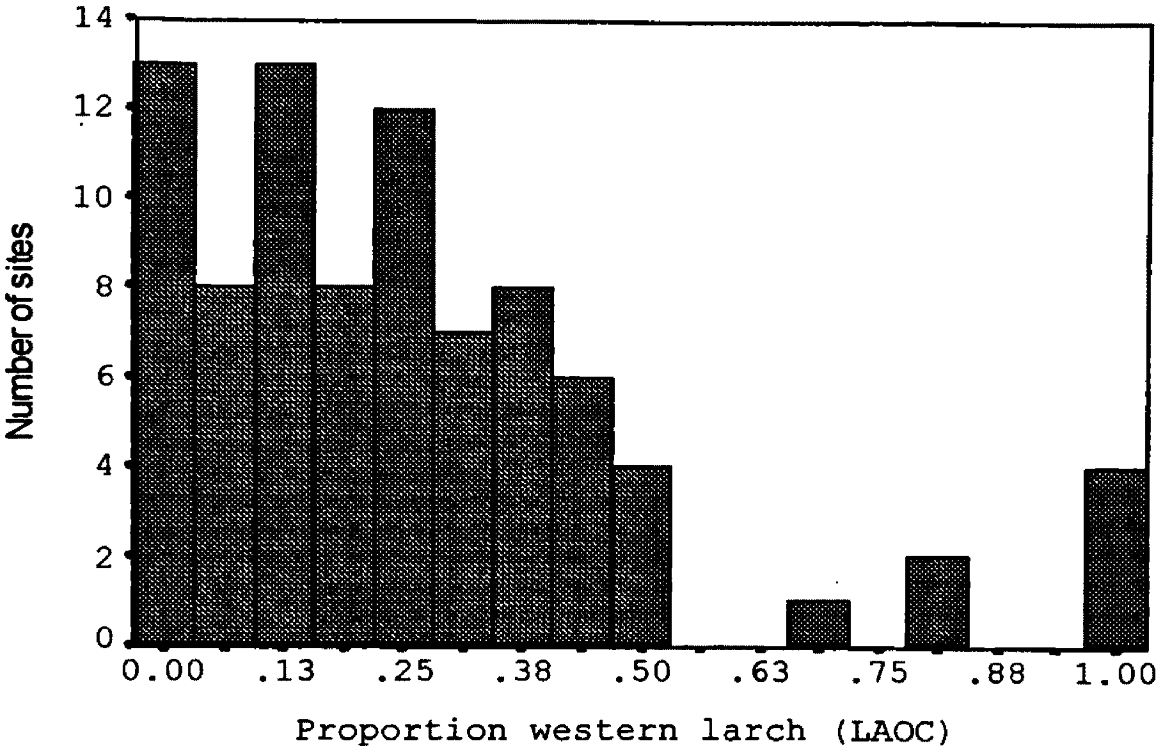


Figure 5. Frequency distributions of two measures of understory vegetation. a) basal area of small trees (BASM), dbh < 20 cm. b) percent cover of deciduous shrubs and conifer saplings (SHRUB).

a.



b.

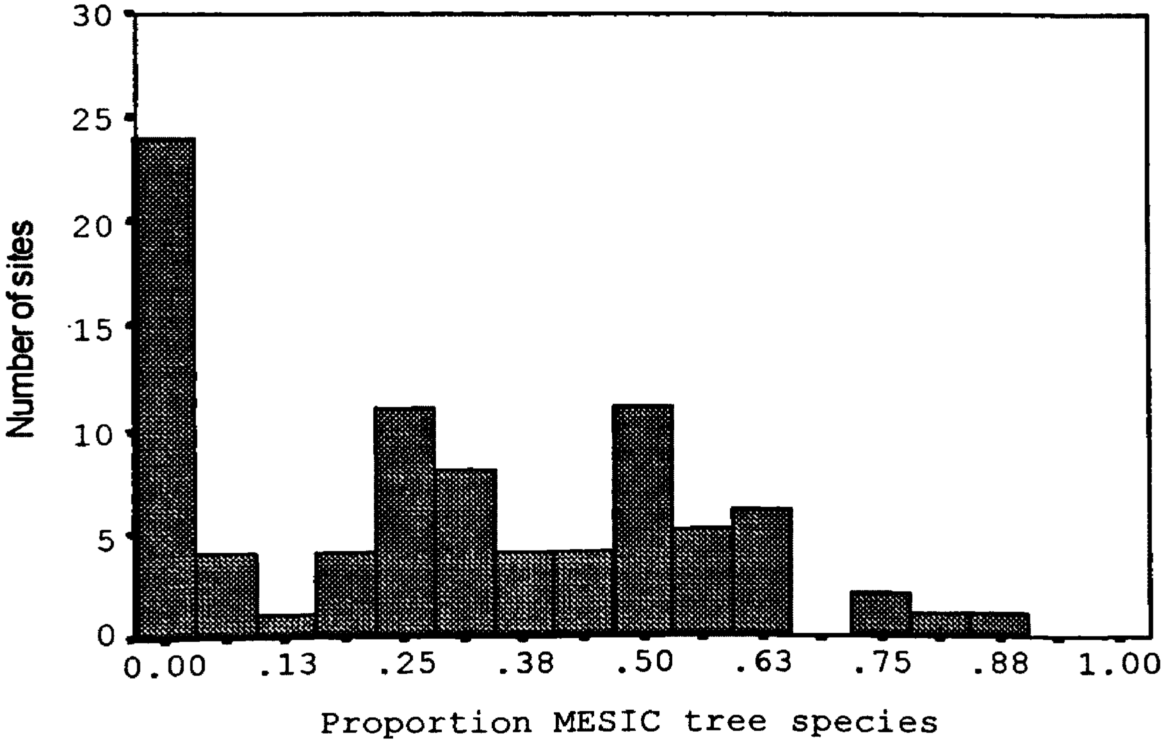


Figure 6. Frequency distributions of two measures of tree species composition: a) proportion of mature trees that were western larch (LAOC); b) proportion of mature trees that were mesic species (MESIC).

Table 2. Descriptive statistics for all continuous vegetation variables used in the analyses.

Variable*	Median	Mean	Std.Dev.	Coef.Var. (%)	Minimum	Maximum
BAMAT	45.54	60.73	49.69	82	1.0	180.0
BASM	13.19	13.19	9.91	75	.0	39.0
LARGE	.13	.20	.26	130	.0	1.3
AVGSIZE	32.26	32.91	6.24	19	25.0	55.0
CANHT	25.00	24.98	4.34	17	14.3	35.3
GROUND	48.83	49.01	17.82	36	11.2	88.0
BUSH	16.17	17.43	10.12	58	2.0	44.2
SHRUB	9.57	11.94	9.85	82	.3	47.5
SHRDEC	2.83	5.11	5.94	116	.0	28.7
SAP	5.83	7.51	6.85	91	.0	35.8
PSME	.24	.30	.26	87	.0	1.0
LAOC	.22	.26	.24	92	.0	1.0
PINE	.12	.15	.16	107	.0	.71
MESIC	.28	.29	.24	83	.0	.86
SPFIR	.22	.23	.21	91	.0	.80
SNAGBA	.28	.48	.60	125	.0	3.67

* Descriptions of variables in Table 1 (p. 12)

Table 3. Matrix of correlation coefficients, r, for habitat variables[a].

Variable[b]	BAMAT	LARGE	AVGSIZE	PSME	LAOC	PINE	MESIC	SPFIR
BAMAT	-	.68	.05	-.20	-.20	.17	.31	.27
LARGE	.68	-	.37	-.20	-.07	.04	.26	.19
AVGSIZE	.05	.37	-	-.31	.62	-.19	-.15	-.15
PSME	-.20	-.20	-.31	-	-.54	-.20	-.42	-.31
LAOC	-.20	-.07	.62	-.54	-	-.11	-.33	-.32
PINE	.17	.04	-.19	-.20	-.11	-	-.33	-.26
MESIC	.31	.26	-.15	-.42	-.33	-.33	-	.82
SPFIR	.27	.19	-.15	-.31	-.32	-.26	.82	-
CANHT	.37	.46	.62	-.38	.42	-.02	.01	-.01
SNAGBA	.64	.76	.14	-.14	-.22	-.02	.38	.30
BASM	.51	.27	-.31	.04	-.39	.15	.25	.29
SHRUB	.31	.41	.06	-.09	-.18	-.20	.41	.26
SHRDEC	.30	.31	.03	-.14	-.13	-.15	.38	.19
SAP	.22	.33	.04	-.03	-.16	-.15	.29	.25
BUSH	.13	.05	-.13	.24	-.19	.16	-.18	-.19
GROUND	-.19	-.29	-.03	.15	-.00	.33	-.38	-.16

	CANHT	SNAGBA	BASM	SHRUB	SHRDEC	SAP	BUSH	GROUND
BAMAT	.37	.64	.51	.31	.30	.22	.13	-.19
LARGE	.46	.76	.27	.41	.31	.33	.05	-.29
AVGSIZE	.62	.14	-.31	.06	.03	.04	-.13	-.03
PSME	-.38	-.14	.04	-.09	-.14	-.03	.24	.15
LAOC	.42	-.22	-.39	-.18	-.13	-.16	-.19	-.00
PINE	-.02	-.02	.15	-.20	-.15	-.15	.16	.33
MESIC	.01	.38	.25	.41	.38	.29	-.18	-.38
SPFIR	-.01	.30	.29	.26	.19	.25	-.19	-.16
CANHT	-	.19	-.20	.18	.20	.06	.07	-.11
SNAGBA	.19	-	.31	.43	.30	.38	-.04	-.37
BASM	-.20	.31	-	.21	-.00	.34	-.03	-.12
SHRUB	.18	.43	.21	-	.73	.79	.28	-.45
SHRDEC	.20	.30	-.00	.73	-	.18	.46	-.38
SAP	.06	.38	.34	.79	.18	-	.00	-.35
BUSH	.07	-.04	-.03	.28	.46	.00	-	-.06
GROUND	-.11	-.37	-.12	-.45	-.38	-.35	-.06	-

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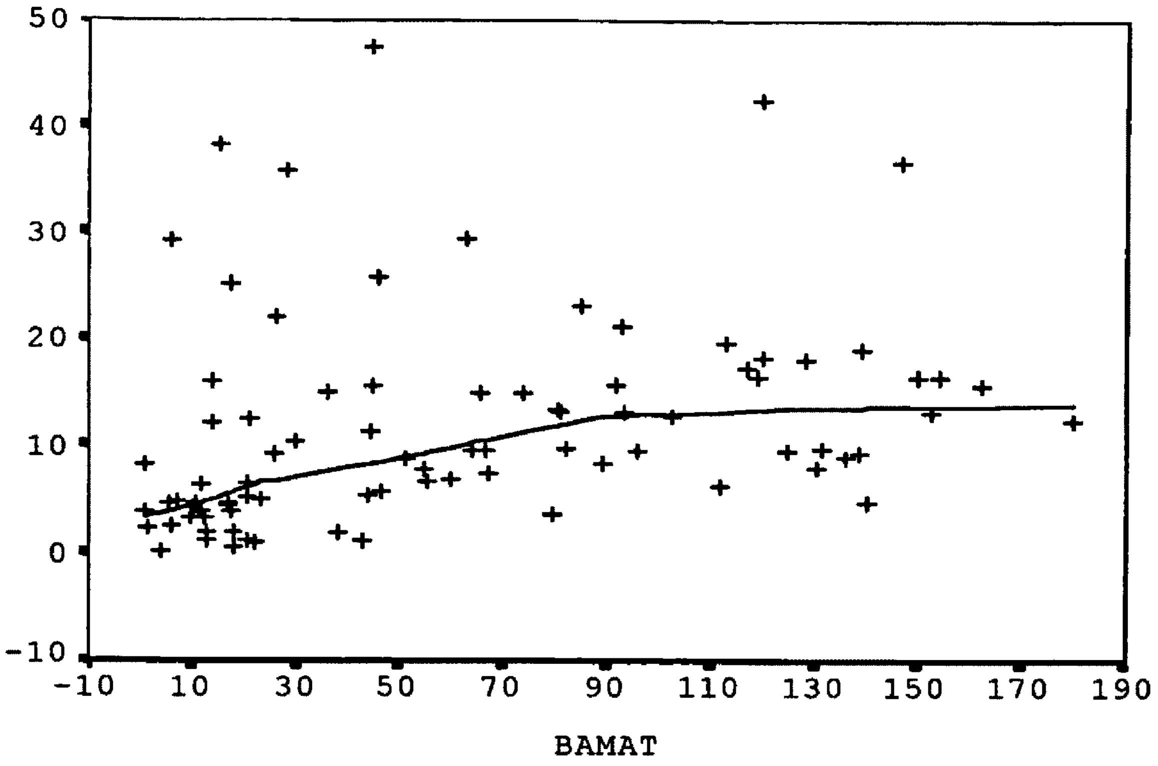
[a] $p = .05$ at about $r = 0.21$, $p = .01$ at about $r = 0.27$

[b] see Table 1 (p. 12) for descriptions of variables

a.



b.

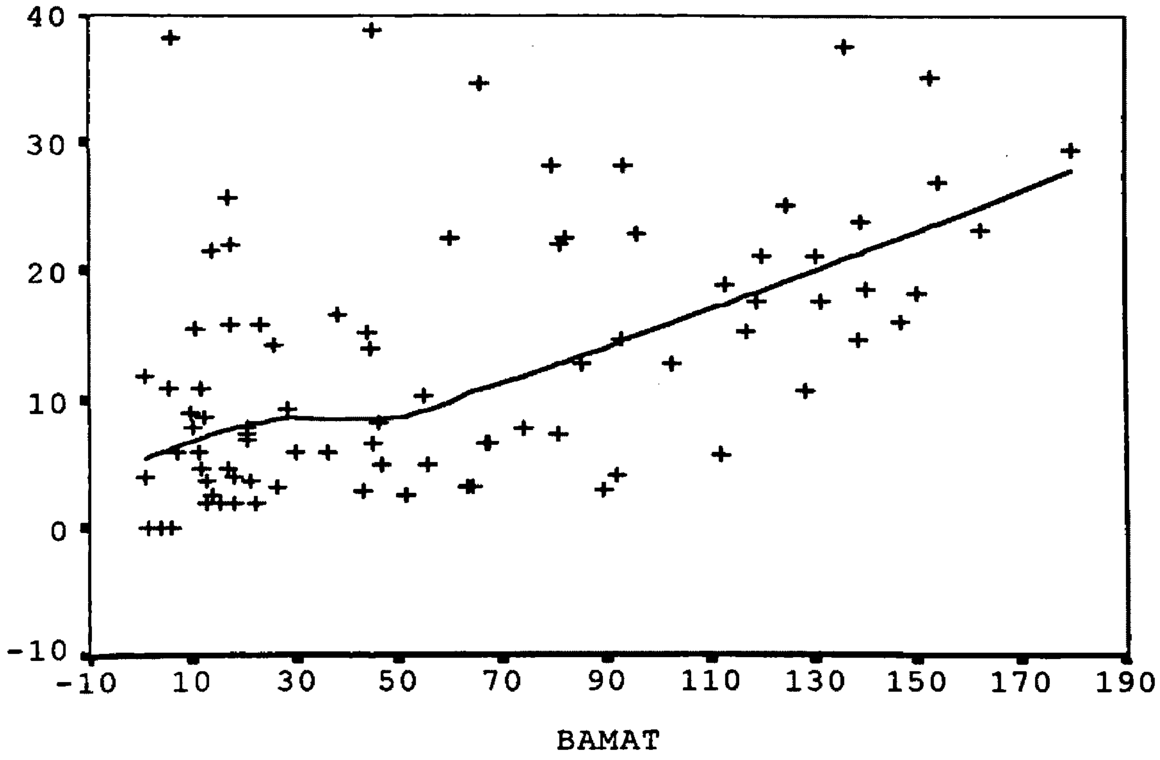
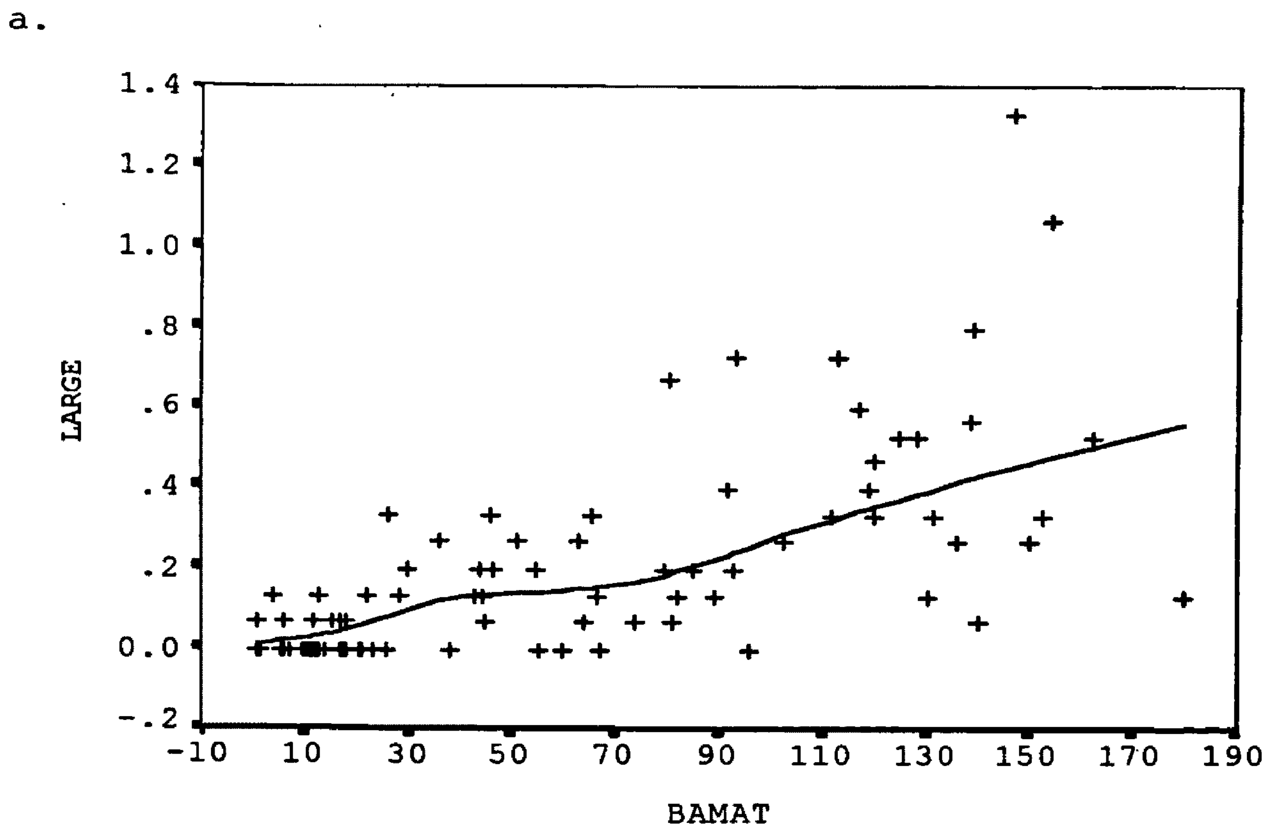


Figure 7. Bivariate scatterplots of the basal area of mature trees (BAMAT) with two other vegetation variables: a) percent tall understory cover (SHRUB), r^2=0.09. b) basal area of small trees (BASM), r^2=0.26. Curves were drawn by LOWESS smoothing.



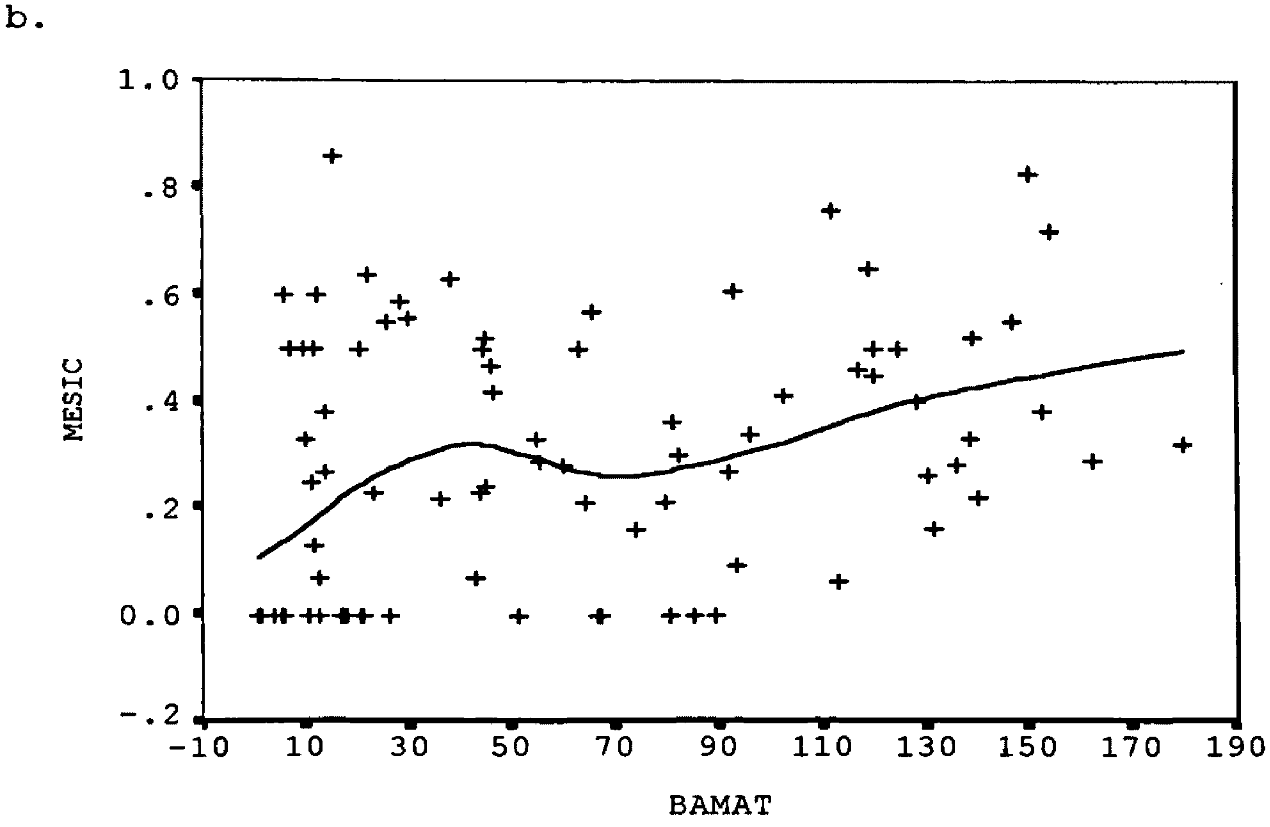


Figure 8. Bivariate scatterplots of the basal area of mature trees (BAMAT) with two other vegetation variables: a) density of large trees (LARGE), dbh > 50 cm; $r^2 = 0.46$. b) proportion of mature trees that were MESIC species; $r^2 = 0.09$. Curves were drawn by LOWESS smoothing.

A few of the densest sites had closed canopies and areas with no understory, but most had low bush, beargrass (Xenophylum tenax), or other ground cover, as well as gaps in the canopy allowing varied amounts of dense, tall shrubs and saplings. Two nearly old-growth stands were unusual in having dense thickets of "shrubby" Pacific yew, which resulted in very high values for understory cover (Figure 7a, upper right). Only the uncut sites had high numbers of large trees, as was expected, but some cut sites had a few large trees (Figure 8a). Uncut sites varied greatly in tree density (Figure 3; right of arrow), but most intermediate density sites (Figure 3; left of arrow) were thinned, usually with mature trees left, although some overstory removal sites were also fairly dense.

Most tree species were present on sites of all tree densities (e.g. Figure 8b), although the proportions of several species were correlated with BAMAT (Table 3). There was a tendency for denser sites to have more spruce and fir (sometimes with cedar mixed in), although many dense sites were mixtures of larch and lodgepole pine, with spruce and fir still in the understory. Broadleaf, deciduous trees were present on many sites, either as scattered birch or small stands of aspen or cottonwood (rare), usually near small potholes. Such clumps added to the high microhabitat heterogeneity within most stands.

We may be more likely to discover significant responses of bird species to variables that contain more variation within a sample. The variability of each variable in this study was compared by the coefficient of variation (Table 2), which expresses the standard deviation as a percentage of the mean. The highest coefficients of variation tended to be those variables with a large number of zeroes, which is not useful variation, and the lowest values were for variables measuring the size of trees (AVGSIZE and CANHT), which were constrained to mature trees in mature forests. This does not necessarily tell us what proportion of the variability actually present in the landscape was represented in the sample, which may be a more important index of how well the sample will show the true relationship of the species with that variable.

Bird species response curves

It was my original intention to report the species response curves for the 1993 data, and then to test whether these relationships were validated in 1994. It was apparent, however, that each bird species was detected on a substantially different set of sites in the two years of the study (Table 4). The repeatability of analyses based on one year of data is an important question (see last section of results); however, since I believe that many of the differences were due to species being present in both years but undetected in one or the other, I decided that the best predictive model should be based on both years combined. Therefore, I considered presence in either year to be sufficient to call the site occupied.

One reason a species may be undetected is due to within-season variation in singing activity, so the newly randomized order of visits to sites in the second year helped correct for this source of error. One of the sites was logged during the 1994 field season and was not censused in that year. Two additional sites had seed trees removed between years and became clearcuts. There were, therefore, only 86 sites that had not changed during the two-year study, so this was the set that was used for the pooled 2-year analyses. (Two sites had small areas -- less than 5% of the total area -- logged in one corner between years. Also, on 4-5, sites I could not find a census point and conducted the count perhaps 50-75 m from the previously used point, but well within the same stand. In all of these cases the bird detections

Table 4. Bird species detected on at least 20 of 86 sites during 1993 and 1994, with the number of sites on which the species was detected in each year, as well as the pooled presences used for model building. The last column is the proportion of sites which changed occupation status between years for that species (in descending order of abundance).

	Number of sites			Prop.
Bird Species	1993	1994	Either	change
Dark-eyed Junco (*Junco hyemalis*)	71	77	84	.23
Red-breasted Nuthatch (*Sitta canadensis*)	69	72	84	.31
Western Tanager (*Piranga ludoviciana*)	57	61	73	.33
Yellow-rumped Warbler (*Dendroica coronata*)	47	47	60	.30
Mountain Chickadee (*Parus gambeli*)	41	38	56	.38
Swainson's Thrush (*Catharus ustulatus*)	41	43	55	.30
Solitary Vireo (*Vireo solitarius*)	36	44	53	.30
Chipping Sparrow (*Spizella passerina*)	44	37	52	.27
MacGillivray's Warbler (*Oporornis tolmiei*)	34	39	51	.34
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	27	35	44	.30
Golden-crowned Kinglet (*Regulus satrapa*)	21	27	43	.30
American Robin (*Turdus migratorius*)	24	33	42	.31
Warbling Vireo (*Vireo gilvus*)	26	24	36	.26
Gray Jay (*Perisoreus canadensis*)	17	24	35	.34
Ruby-crowned Kinglet (*Regulus calendula*)	21	27	34	.23
Townsend's Warbler (*Dendroica townsendi*)	22	21	29	.17
Hairy Woodpecker (*Picoides villosus*)	15	14	27	.29
Pine Siskin (*Carduelis pinus*)	17	12	26	.27
Black-capped Chickadee (*Parus atricapillus*)	12	11	21	.22
Northern Flicker (*Colaptes auratus*)	11	14	20	.17

did not seem to be seriously affected, so these changes were not considered in the analyses.)

There were 67 species detected on the 86 sites considered during the combined-year study. Logistic regression models were produced for the 20 species that were detected on at least 20 of the 86 sites (Table 4), and each of these is discussed in the Appendix.

The most common two species (Dark-eyed Junco and Red-breasted Nuthatch) were detected on too many sites for analysis using the combined-year data set, so only the 1993 data were used in these two cases. These species are discussed in the appendix, but all subsequent discussion of logistic regression models, whether univariate or multivariate (Table 5), are for the combined-year analyses of the remaining 18 species.

Summaries of models

Most of the bird species analysed in this study responded to several habitat variables. The occurrence of each species showed significant univariate relationships with 2 to 11 variables, with most species responding to at least five. At least one of these relationships was quadratic for every species, and some species had as many as five quadratic relationships. In fact, of 144 significant univariate relationships, 67 (45%) included a quadratic term. In 41 (63%) of these cases (with significant quadratic relationships), the model with only the linear term was not significant (Table 6).

All of the habitat variables considered in this study had significant univariate relationships with the occurrence of more than one species (Table 6). All but two variables had at least one univariate quadratic relationship. At least one of the tall shrub cover variables (SHRUB and its components, SAP and SHRDEC) was a significant

Table 5. Multivariate logistic regression models for each bird species, chosen by stepwise backward elimination (except for HAWO and GRJA, see Appendix), based on presence in either year; expressed in terms of the logit, g(x).

Red-naped Sapsucker	$g(x) = -7.33\ \text{LARGE} + 6.86\ \text{LARGE}^2 - .120\ \text{SAP} + 8.10\ \text{PSME} - 10.3\ \text{PSME}^2 - 11.8\ \text{PINE} + 18.7\ \text{PINE}^2 + 1.74$
Hairy Woodpecker	$g(x) = -.042\ \text{BAMAT} - 1.20\ \text{SNAGBA} + .913\ \text{SNAGBA}^2 + 1.13$
Northern Flicker	$g(x) = -.223\ \text{BAMAT} + .173\ \text{AVGSIZE} - 1.68$
Gray Jay	$g(x) = .107\ \text{BASM} + 9.32\ \text{LAOC} - 9.46\ \text{LAOC}^2 - 3.16$
Black-capped Chickadee	$g(x) = .080\ \text{BASM} - .51\ \text{SAP} + .023\ \text{SAP}^2 - 5.01\ \text{PINE} + 3.98\ \text{SNAGBA} - 2.02\ \text{SNAGBA}^2 - 1.03$
Mountain Chickadee	$g(x) = .080\ \text{BAMAT} - .00063\ \text{BAMAT}^2 + 15.2\ \text{LARGE} - 9.72\ \text{LARGE}^2 - .162\ \text{SAP} + 3.78\ \text{PINE} - .244\ \text{CANHT} + 4.71$
Golden-crowned Kinglet	$g(x) = .083\ \text{BAMAT} - .00037\ \text{BAMAT}^2 + .077\ \text{BASM} + 3.75\ \text{SPFIR} - 4.73$
Ruby-crowned Kinglet	$g(x) = .072\ \text{BASM} + .058\ \text{GROUND} - .123\ \text{SHRUB} + 17.4\ \text{SPFIR} - 19.8\ \text{SPFIR}^2 - 5.32$
Swainson's Thrush	$g(x) = .059\ \text{BAMAT} - .0004\ \text{BAMAT}^2 + 3.87\ \text{BASM} - .0084\ \text{BASM}^2 + .083\ \text{BUSH} + .068\ \text{SHRUB} + 1.70\ \text{DECPRES} - 5.60$
American Robin	$g(x) = -.021\ \text{BAMAT} - .238\ \text{SHRUB} + .0054\ \text{SHRUB}^2 + 2.74$
Solitary Vireo	$g(x) = .315\ \text{SHRUB} - .0059\ \text{SHRUB}^2 - .204\ \text{AVGSIZE} - 5.05\ \text{MESIC} + 6.43$
Warbling Vireo	$g(x) = -.025\ \text{BAMAT} + 13.8\ \text{LAOC} - 21.1\ \text{LAOC}^2 - 0.242$
Yellow-rumped Warbler	$g(x) = .084\ \text{BAMAT} - .00037\ \text{BAMAT}^2 - 6.40\ \text{LARGE} + 11.9\ \text{LAOC} - 12.4\ \text{LAOC}^2 - 1.97$
Townsend's Warbler	$g(x) = .120\ \text{BAMAT} - .0005\ \text{BAMAT}^2 + .728\ \text{SHRUB} - .014\ \text{SHRUB}^2 - 5.34\ \text{LAOC} + 14.4\ \text{MESIC} - 17.0\ \text{MESIC}^2 - 13.4$
MacGillivray's Warbler	$g(x) = -.029\ \text{BAMAT} + .763\ \text{BUSH} - 8.03\ \text{PSME} + 13.5\ \text{PSME}^2 - 3.32\ \text{MESIC} + 16.7\ \text{MESIC}^2 + .255$
Western Tanager	$g(x) = .148\ \text{BAMAT} - .00071\ \text{BAMAT}^2 + .227\ \text{BUSH} + 18.5\ \text{MESIC} - 32.2\ \text{MESIC}^2 - 3.93$
Chipping Sparrow	$g(x) = -.033\ \text{BAMAT} + 2.52$
Pine Siskin	$g(x) = 2.25\ \text{MESIC} + 2.01\ \text{CANHT} - .04\ \text{CANHT}^2 - 25.9$

Table 6. The occurrence of vegetation variables in habitat-relationships models (2-year) across the assemblage of 18 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"). The last row is for the only categorical variable.

	Univariate relationships			Multivariate relationships			
	Only	Linear +	Only	Linear		Quadratic	
Variable	Linear	Quadratic	Quadratic	Pos	Neg	Pos	Neg
BAMAT	9	3	2	0	5	0	6
BASM	10	2	0	4	0	0	1
LARGE	9	1	2	0	1	1	1
AVGSIZE	1	2	7	1	1	0	0
GROUND	3	0	0	1	0	0	0
BUSH	5	0	0	3	0	0	0
SHRUB	4	5	3	1	1	2	2
SAP	5	1	5	0	2	1	0
SHRDEC	3	3	3	0	0	0	0
PSME	3	0	2	0	0	1	1
LAOC	1	3	4	0	1	0	3
PINE	2	2	3	1	1	1	0
MESIC	4	3	4	1	1	1	2
SPFIR	5	1	1	1	0	0	1
SNAGBA	9	0	2	0	0	0	1
CANHT	4	0	3	0	1	0	1
Totals:	77	26	41	13	14	7	19
DECPRES	3			1	0		

univariate predictor for 15 of the 18 species. Two of the species without significant responses to tall shrubs were canopy-associated species (Yellow-rumped Warbler and Solitary Vireo), but one was the MacGillivray's Warbler, which is surprising (see appendix). At least one of the tree species composition variables was a significant univariate predictor for 16 of the 18 species.

Some of these univariate relationships clearly reflected important biological relationships, but many represented redundant or misleading information, due to the intercorrelations between many variables (Table 3). For example, ten species, both open-cup and cavity nesters, showed strong univariate relationships involving the basal area of snags (SNAGBA). Most of these relationships seemed to be nonsensical until I realized that SNAGBA was strongly correlated with BAMAT ($r=0.64$, $p < .001$), and the relationships were almost certainly due to the high significance of the latter confounding variable. These problems are partially averted by examining all variables simultaneously in multiple regression models.

The multivariate analyses reduced the number of variables (not all univariate relationships were retained), so that each species was associated with 1-5 variables (Table 7; column 2). All except two of the species had at least one quadratic relationship retained in its multivariate model (Table 5).

Deciduous shrub cover was the only variable that was not retained in any multivariate model, although it may still have had an influence on some species as an element of overall SHRUB cover. At least one tree species composition variable was retained in the models for 13 of the 18 species. Twelve of the sixteen habitat variables had at least one quadratic relationship retained in a multivariate model (Table 6). Besides the six quadratic relationships with BAMAT, there were ten

Table 7. Comparison of multivariate habitat-relationships models obtained by considering linear terms only with those that allowed quadratic terms (reported in Table 5). Included are the number of variables in the chosen model, the p-value for the Hosmer-Lemeshow Goodness-of-fit test (d.f.= 8), and the percent of observed presences and absences that were correctly predicted by the models. Bird species are in the same order (phylogenetic) as in Table 5.

	No. Vars. in model		Goodness-of-fit (p)		% correctly predicted			
Species	Linear terms only	Quadratic terms allowed	Linear terms only	Quadratic terms allowed	Linear only		Quadratic allowed	
					pres.	abs.	pres.	abs
RNSA	2	4	.79	.80	70	64	75	71
HAWO	2	2[a]	.37	.89	67	83	74	80
NOFL	2	2	.08	.08	85	92	85	92
GRJA	1	2[a]	.71	.26	43	80	60	80
BCCH	2	4	.72	.56	10	100	29	95
MOCH	1	5	.64	.74	75	47	88	57
GCKI	2	3	.12	.59	79	84	86	86
RCKI	4	4	.09	.90	53	81	79	83
SWTH	3	5	.27	.72	87	68	89	68
AMRO	2	2	.60	.03	79	73	74	75
SOVI	3	3	.77	.20	79	52	87	61
WAVI	2	3	.92	.35	56	72	73	82
YRWA	1	3	.07	.17	76	19	97	54
TOWA	5	4	.78	.73	79	90	83	91
MGWA	2	4	.75	.21	78	63	78	74
WETA	3	3	.56	.12	97	38	100	77
CHSP	1	1	.05	.05	88	74	88	74
PISI	1	2	.52	.35	0	100	19	90

[a] Not as chosen by backward elimination (see Appendix)

involving tree species composition, six involving a measure of understory structure, and three involving a measure of tree size (CANHT or LARGE). Overall, there were about the same number of quadratic relationships retained in the multivariate models as linear ones (26 and 27, respectively). Even though the linear relationships were evenly divided between positive and negative coefficients (Table 6), most of the quadratic relationships (19 of 26) had negative coefficients for the quadratic term (and were thus "unimodal", or concave down).

The high incidence of quadratic relationships resulted in multivariate models that were very different from those that would result from traditional linear approaches. To demonstrate this, I redid the analyses with the same model-building protocol, except that I ignored all quadratic relationships. For 10 of the 18 species, there were fewer variables retained in these alternative multivariate models (with linear terms only) than in the models that allowed quadratic relationships (Table 7). The traditional linear approach missed many potentially important relationships; but were the models actually inferior? In 8 of the 18 cases the Hosmer-Lemeshow goodness-of-fit statistic suggested that the fit was better for the models with only linear terms (in 6 cases it was worse, and in 4 cases it was about the same). However, the classification success of the these alternative models was clearly inferior in most cases to the models that allowed quadratic terms. A better criterion may be the likelihood ratio test comparing these alternative models. This was the same test used for model building (deciding whether a model is improved by the addition of a term), which was essentially the same question. By this criterion, all but four of the models with only linear terms were clearly inferior to those with quadratic terms. Two of these four (Northern Flicker and Chipping Sparrow) did not include quadratic terms even when they were allowed, so the model did not change. In conclusion, the multivariate models for 14 of the 18 species were significantly improved by the consideration of quadratic relationships. However, a true test of their relative performances would require validation with new data.

Predictive ability

The prediction of new data is the key step in validation of any model. I did not validate the models in this study with independent data, but I attempted to predict occurrence on the sites in 1994 based on the 1993 data. I did this in two ways. First, I developed multivariate logistic regression models based on the 1993 data (using the same methods as for the 2-year models reported here) and used these to predict 1994 occurrences. Second, I also predicted 1994 occurrence based on the simple premise that species would be present on the same sites as in 1993. The success of these predictions was not very good in either case (Table 8).

Detectability

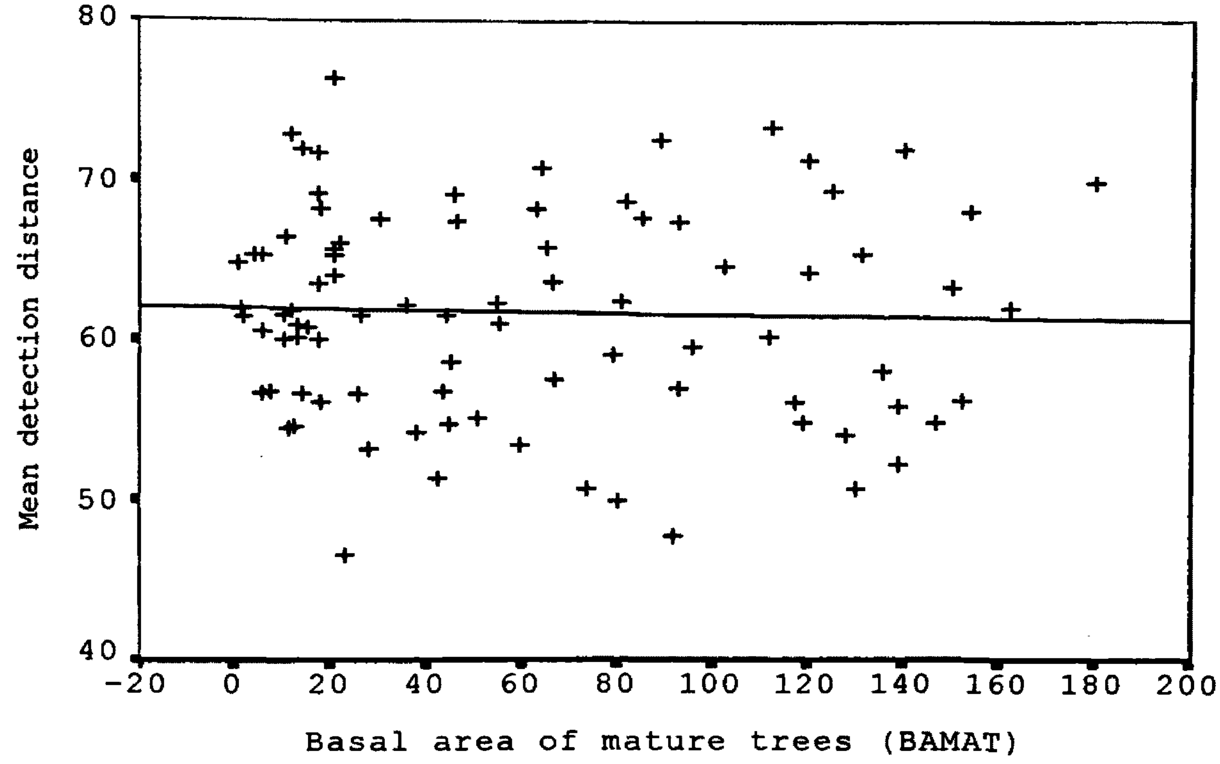
To compare the detectability of birds among sites in relation to vegetation density, I examined two indices that should be related to the detectability of birds on each site. First, for each site I calculated the average estimated distance to all individuals of common bird species detected within 100 m (because these were the data used in all analyses). This mean detection distance was not related to the density of vegetation on the sites, as estimated by basal area of either mature (Figure 9a) or small trees, or by shrub cover (Figure 9b). In fact, the mean detection distance was not significantly correlated with any measured habitat variable except low bush cover ($r=.34$, $p=.002$), which there was no biological reason to expect.

Second, I examined the proportion of the common bird species

Table 8. Success of predicting 1994 bird occurrences based on 1993 data. At left is the percent of observed presences and absences that were correctly predicted by multivariate models constructed from 1993 data. At right is the success of simply predicting that birds will be on the same sites in 1994 as in 1993.

	Based on 1993 model		Based on 1993 occurrence	
	% correctly predicted		% correctly predicted	
Species	Absences	Presences	Absences	Presences
Dark-eyed Junco	11	93	22	83
Red-breasted Nuthatch	21	97	14	79
Western Tanager	48	82	52	74
Yellow-rumped Warbler	56	70	67	72
Mountain Chickadee	69	63	63	61
Swainson's Thrush	67	70	72	67
Solitary Vireo	17	100	79	61
Chipping Sparrow	67	89	69	78
MacGillivray's Warbler	89	51	74	56
Red-naped Sapsucker	84	26	82	51
Golden-crowned Kinglet	100	0	96	41
American Robin	100	27	83	45
Warbling Vireo	81	50	81	58
Ruby-crowned Kinglet	88	30	88	52
Townsend's Warbler	86	62	88	67

a.



b.

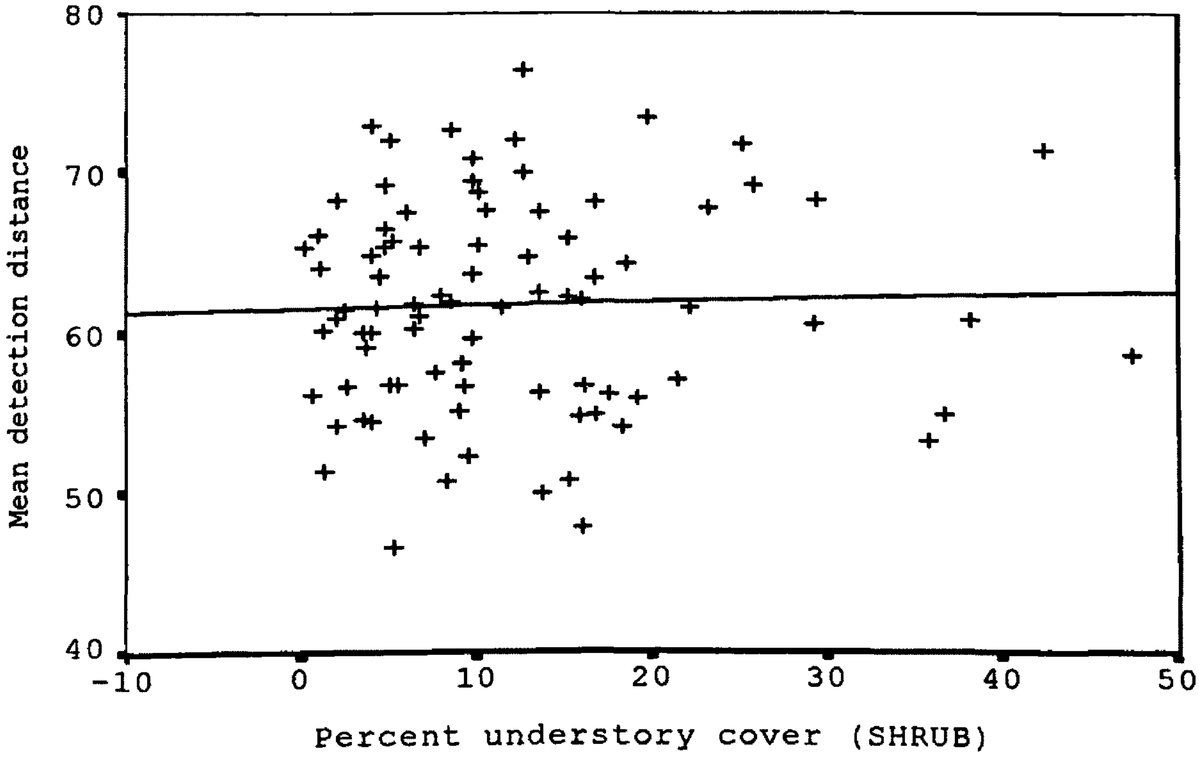


Figure 9. The mean detection distance to all individuals (within 100 m) detected on a site (mean = 61.8 m, s.d.= 6.6 m), as a function of two measures of vegetation density: a) basal area of mature trees (BAMAT; r=-.03,p=.81); b) percent cover of tall understory (SHRUB; r=.03,p=.78).

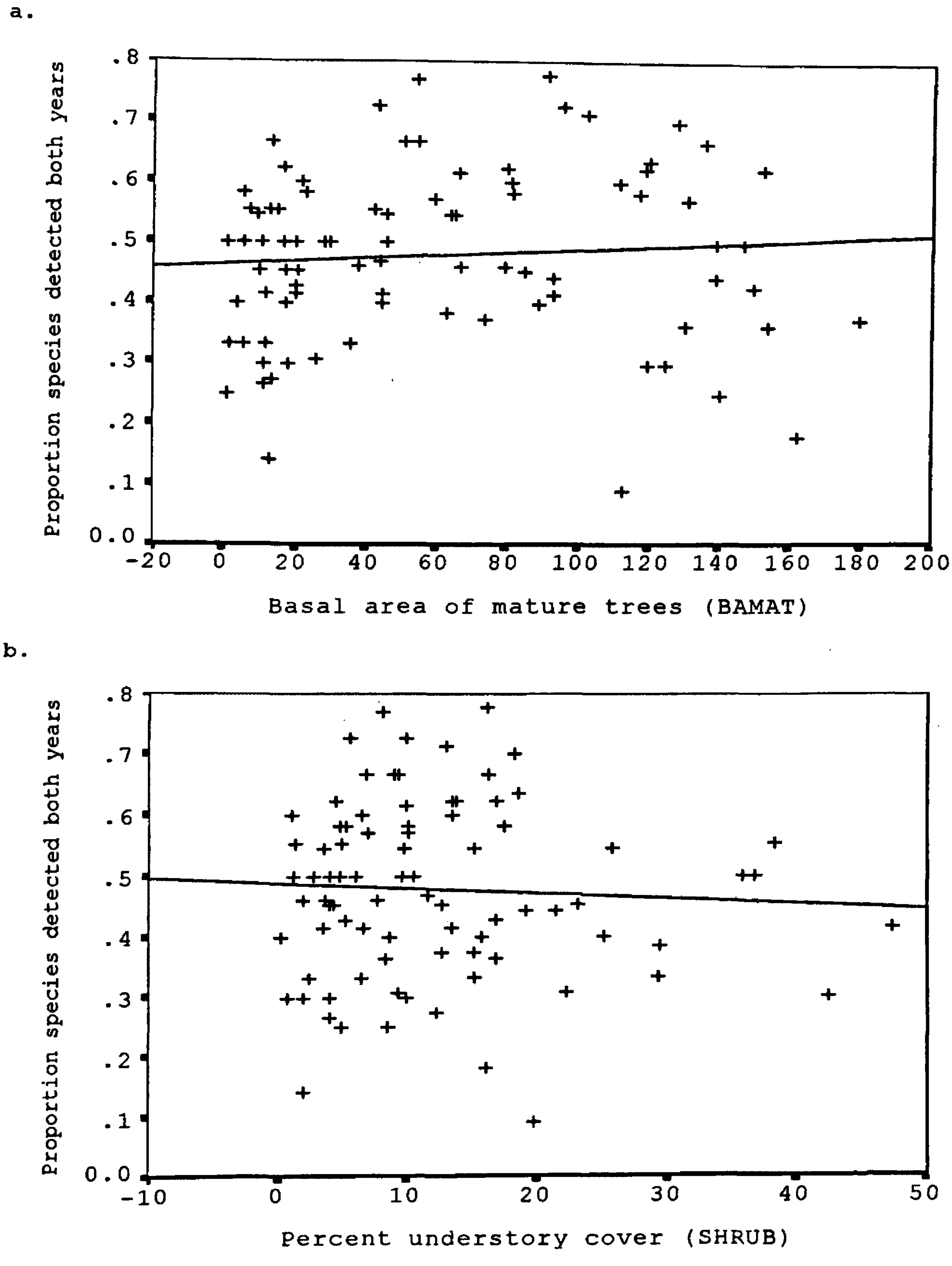


Figure 10. The proportion of species detected on a site that was detected in both years (mean=.45, s.d.=.14), as a function of two measures of vegetation density: a) basal area of mature trees (BAMAT; r=.09,p=.42); b) percent cover of tall understory (SHRUB; r=-.06,p=.60).

detected on a site that was detected in both years (within 100 m). This is a measure of census repeatability. If denser vegetation decreases the detectability of birds such that some species go undetected in one year or the other, then this index should be positively related to such measures of vegetation density as the basal area of mature trees (BAMAT) or tall understory cover (SHRUB). However, it was not correlated with these (Figure 10) or any other measured habitat variables. Also, this proportion was negatively correlated with the mean detection distance ($r = -.33$, $p = .002$).

DISCUSSION

Model structure

The development of empirical models that describe bird-habitat relationships involves the discovery of habitat variables that appear to be associated with the distribution or abundance of the bird species in question. The application of our basic biological knowledge is required throughout this process, not only in choosing the variables to measure, but also in several aspects of model development. First, the view of niches as n-dimensional hypervolumes (Hutchinson 1957) leads to the explicit prediction that many variables will be important in modeling the distribution of species. In fact, the multivariate models produced in this study indicated that several vegetation variables were important for describing the habitat distribution of most bird species. Second, many vegetation variables are partially intercorrelated (Green 1971, Shugart 1981, Morrison et al. 1992), so that it is necessary to study their effects simultaneously, thus controlling for some while testing the importance of others. This is well illustrated in the present study by the large number of apparent univariate relationships that were not retained in the multivariate models. This supports the well-established idea that multivariate analyses are necessary in the study of wildlife-habitat relationships (e.g. Capen 1981).

Third, niche theory predicts that the responses of species to many important environmental gradients will be unimodal. Although all biologists are aware of this, it is not taken into account very often during the modeling process. In this study, I found many nonlinear responses of bird species to tree density and other important habitat variables. In fact, about 45% of the significant univariate relationships in my study included a quadratic term. Most importantly, of those relationships that were significant with a quadratic term in the model, 63% were not significant when only the linear term was included; these variables would not have been considered important using traditional methods that only examined linear relationships, so potentially important biological information would have been overlooked. Multivariate logistic regression models also included quadratic terms for about half of the component variables. Models for 14 of the 18 species showed significant improvement when quadratic terms were included, relative to the models that included only linear terms.

Nonlinear relationships have usually been found in the few studies that have looked for them. In a study of songbird responses to hedgerow characteristics in England, Green et al. (1994) found that the Gaussian response model gave a significantly better fit than a linear model in 17 of 50 (34%) univariate relationships. Meents et al. (1983) found significant quadratic terms in 36% of univariate relationships, and in about half of these cases (19% overall) the linear relationship was not significant.

In spite of these findings, nonlinear relationships are rarely considered in published studies of habitat relationships. For example, of 93 recently published studies of wildlife-habitat relationships in 3 journals (Journal of Wildlife Management, Journal of Applied Ecology, and Condor; 1991-1995), 34 used regression approaches (linear regression, logistic regression, or correlation) to model the effects of continuous variables on habitat use. Only 4 (12%) of these considered nonlinear relationships. In addition, two papers used detrended or canonical correspondence analyses -- statistical techniques used more often in plant studies (Ter Braak 1986) -- which assume unimodal species-response curves.

Unimodal responses of birds to habitat gradients also complicate the use of any analysis method that compares the means or medians of continuous variables between used and unused sites (such as t-tests, ANOVAs, and discriminant analyses). If used sites are clustered in the middle of the gradient, with unused sites at both extremes of the gradient, then the mean of the two groups may be similar even when the variable explains some of the variation in bird occurrence. None of the 30 recent papers that used these types of methods considered this problem.

Because of the simplicity of working with linear relationships, mathematically as well as in interpretation, linearity can be (and usually is) considered as a first hypothesis (Morrison et al. 1992). However, there is a priori theory as well as empirical evidence for the existence of unimodal relationships. Therefore, all relationships should be screened for nonlinearities. This could simply involve the examination of bivariate plots or residual plots, which should routinely be done when conducting regression analyses of any type. If this were done in the published studies I surveyed, it was not reported. If visual inspection gives any hint of nonlinearity, it would seem wise to quantify the results of such inspection by screening quadratic terms in regression models.

The prevalence of quadratic relationships in my study further suggests that bird-habitat relationships are often nonlinear. The fact that most of these quadratic relationships were unimodal (negative quadratic terms) may provide further evidence that this method is revealing biologically meaningful relationships, because unimodal relationships are expected from niche theory.

There are, however, alternative explanations for the occurrence of unimodal relationships. First, the models produced in any study are a product of the statistical methods used and the structure of the particular data set. It is always possible for a relationship to be statistically significant even when there is not a true biological relationship. Beyond the ubiquitous concerns of sample size and Type I error, there can be unique patterns of multicollinearity in any data set that may cause a particular technique to incorrectly indicate a relationship. At the least this will lower the predictive power for situations in which the data structure is different (Morrison et al. 1992, p. 307).

Second, the frequency distribution of the independent variables can also influence a statistical relationship (Best and Stauffer 1986, Hosmer and Lemeshow 1989). The true relationship between two variables can best be found with a uniform sampling effort across all values of the independent variable. In my data set, sampling effort for most variables tended to be highly non-uniform (Figures 5-6); most variables had many low (or zero) values, and few very high values. This means that the few sites with highest tree density (or shrub cover, etc.), may have had a disproportionate effect on the shape of the modeled curve in that region of the data. If a particular bird species was undetected at one or two of these extremely dense sites, then the curve may be pulled downward and a quadratic term may become significant in the model. For example, this may be the case for the relationships between BAMAT and the Western Tanager (Figure 12a), Golden-crowned Kinglet (Figure 19a), and Townsend's Warbler (Figure 24a). There may not be sufficient data to know if this were the true nature of the relationship in this region of the data (for the latter two species it was probably not). However, very dense sites did have lower overall bird abundance, and perhaps even the species that occurred in these habitats were present in lower densities. It is noteworthy that all of the relationships with BAMAT that were retained in the models were either negative linear or unimodal. It makes sense that there would be no models with positive quadratic terms (U-shaped relationships) with this variable. It is implausible that a species would prefer seed tree cuts and dense forests, and avoid anything in between. We might, however, expect to see positive linear relationships, but every response curve that started out positive, in more open forests, eventually curved downward. This may be real, showing the unimodal relationships expected from wide gradients, but it may also be due to the above-mentioned sampling problems, or to a decline in the detectability of birds in dense forests.

Third, a species may have a positive, monotonic relationship with a measure of habitat structure, such as tree density or shrub cover, but individuals in very dense habitats may be less easily detected. This may result in apparent absences for sites on which the species was actually present, and it may cause the response curve to bend downward at higher habitat densities, causing a nonlinear, unimodal relationship to be suggested by the erroneous data. Since most detections of birds are made by sound alone, the detectability of birds is strongly affected by the ability of their songs to carry through the vegetation in any habitat. Because the density of vegetation is one of the main factors controlling the attenuation of bird song (Morton 1975), and because I was comparing bird abundance along gradients representing large changes in vegetation density, this potential bias should be addressed (Verner 1985). Most of the bird species in this study have songs or calls that can be heard from well over 100 m away. However, many songs are undoubtedly missed within 100 m, and this may be more likely when they have been attenuated by vegetation in the denser forests. However, I found that the mean detection distance, for all individuals of all species, was uncorrelated with tree or shrub density. The proportion of species observed on a site that were seen in both years was also uncorrelated with vegetation density, suggesting that differences in detectability did not affect the overall repeatability of surveys. There could still be lower detectability in the few very dense sites that so strongly influence many of the relationships, especially for a species like the Golden-crowned Kinglet, which has a soft, high-pitched song that is more likely to be attenuated by vegetation (Morton 1975) and to go unnoticed.

For all of the above reasons, it is possible that many of the quadratic relationships reported in this study are not true biological relationships that will hold up under model validation. However, many are statistically clear and provide plausible biological hypotheses for investigation. Nonlinear relationships seem to be neither rare nor unimportant, and should be routinely considered in studies of bird-habitat relationships.

Biological interpretation

A biological relationship can be best understood when the full range of possible variation is studied. Any response of a species to a variable is more likely to be significant with greater variation in the variable, and the nature of any nonlinear relationship is more likely to be revealed. In this study, more species responded to the basal area of mature trees than to any other variable (Table 6). Although this was expected to be an important variable, this could in part be due to the study design, which attempted to maximize the tree density gradient while allowing the other variables to vary more randomly. Other variables may have shown fewer significant relationships (or more linear than nonlinear relationships) simply because the entire range of variation was not represented as well as it was for BAMAT.

Most species responded in some way to the removal of trees by logging operations. Researchers have found such responses in many other studies, but most have only compared uncut sites to some single type of logging, usually with very small numbers of sites. Hejl et al. (1995) reviewed 19 such studies in conifer forests of the Rocky Mountains. It was not surprising that many studies revealed a difference in bird abundances between clearcuts and uncut forests, but there were also 13 studies comparing some form of partial cut to uncut forests. With respect to the 20 common species I analyzed in this study, the Hejl et al. (1995) synthesis showed that 8 of them generally responded negatively to partial cutting, 4 responded positively, and 8 had mixed responses. Many of these responses were consistent with my findings. Species such as American Robin and Chipping Sparrow responded positively to most forms of cutting in this study and others, although the robin had mixed responses to partial cuts in many studies. Species such as Townsend's Warbler and Golden-crowned Kinglet responded negatively to all forms of cutting in most studies, including the present one. The Red-naped Sapsucker and Pine Siskin were species that had no strong response to logging in either this or other studies, suggesting that tree density may not be the most important variable for them. This may also have been true for the Warbling Vireo and MacGillivray's Warbler. These two species showed a generally positive response to logging in the present study, but showed mixed results in other studies, with the vireo increasing more often than the warbler in partial cuts. The response of both of these species to clearcuts depended strongly on the presence of tall shrubs (Hejl et al. 1995), suggesting that this is what the birds were actually responding to.

Comparisons among studies of bird responses to logging are difficult when each study includes only a few sites with only 2 or 3 categories of tree density. Results depend on the unique vegetation structure of each particular cut, and its relative location along the response curve of each bird species. For example, the Western Tanager usually shows a strong negative response to clearcutting, but no clear trend to partial cuts (Hejl et al. 1995). A similar pattern could be seen in the present study. The probability of occurrence was very high for all tree densities except very low values (Figure 12a). Most partial cuts would be above this threshold. Although the Yellow-rumped

Warbler shows a similar pattern to the Western Tanager in my study, in other studies (Hejl et al. 1995) this species responded negatively to partial cuts almost as strongly as to clearcuts. There may be many reasons why responses varied among studies, but one important factor is the type of partial cut and the resulting tree density. The pattern of response is clearer when a continuous gradient is available. This is especially true for species that show unimodal responses. The Mountain Chickadee and Swainson's Thrush had unimodal responses to BAMAT in my study, suggesting that intermediate tree density (partial cuts) may be best for them. However, they both respond negatively to partial cuts in other studies, although not as consistently as with clearcuts (Hejl et al. 1995). On closer inspection, it can be seen that the highest probability of occurrence in my response curves are at the level of tree density corresponding to the sparsest uncut sites, so even partial cutting does lower the probability of occurrence. Such patterns can only be revealed by a continuous gradient.

Many researchers have used tree density as a continuous variable in studies of habitat ordinations, and have found that many species respond to it (e.g. Anderson and Shugart 1974, James 1971). But these studies involved natural ranges of tree densities in unlogged forests, and were generally conducted on a smaller habitat scale. Few studies have included many sites across a continuous range of tree densities, including logged and unlogged sites. Hansen et al. (1995) combined sites from several studies to form a tree density gradient, and found responses that were similar to those in this study. They considered several polynomial and nonlinear models, which made interpretation difficult, but it was apparent that most species respond-ed to tree density, and that these responses were generally nonlinear.

All but one of the common species responded to other habitat variables besides tree density. The multivariate models included 18 relationships with some measure of understory structure, 16 relationships involving tree species composition, and 7 relationships involving the size or height of canopy trees (see appendix for discussions of specific relationships). There are clearly many aspects of habitat structure and species composition that are important to the bird community. This also implies that mitigating the effects of silvicultural practices will be more complex than leaving a certain number of trees per acre.

There were several cases in which vegetation elements known to be important to certain species were not included in the models. For example, I found no association between the occurrence of Red-naped Sapsuckers and the presence of deciduous trees, even though these trees provide important nesting sites for this species (Li and Martin 1992, Tobalske 1992). Failure to detect such relationships may be due to the scale of vegetation sampling. Specific habitat elements that need to be present in only limited quantities may be missed in sample plots distributed randomly around the local habitat. This is more likely to be the case for nesting sites than for foraging sites. Nest sites may be relatively uncommon on a site and still be sufficient for maximum population density if there are suitable sites within each territory. Foraging substrates would have to be more abundant. For example, Red-naped Sapsuckers prefer to nest in deciduous trees, but they often forage in conifers. Thus they only need one or a few deciduous trees within a larger number of conifers for suitable habitat. In addition, there is likely to be stronger selection on nest site choice than on foraging site choices, because of the greater likelihood of failure and the higher fitness consequences (Martin and Roper 1988). Therefore, nest sites may be more specialized, so that appropriate sites are rare within a habitat. Not only are such sites less likely to be sampled because of their rarity, but their specialized characteristics may not even be measured by general habitat sampling (e.g. specific substrate species, size, concealment, or surrounding patch characteristics). Nest-centered micro-habitat sampling may be more likely to reveal such associations. If potential nest sites are thought to be poorly sampled in studies at the habitat scale, then perhaps nest-centered plots should be sampled as a supplement to traditional methods. If found to be important, any uncommon elements may need supplemental searches to help predict the suitability of a site (Steele 1993).

It is less clear why tall shrub cover was not included in the models for either the MacGillivray's Warbler or Warbling Vireo, species with known shrub associations. These species use shrubs for both foraging and nesting, and would thus require a reasonable amount of shrub cover. However, if the distribution of shrubs is highly clumped, it is possible that sufficient shrubs may be present without being detected by traditional vegetation sampling designs. This would be the case for any habitat feature exhibiting high spatial heterogeneity, and such variables will require higher sample sizes. Nonetheless, I believe I had sufficient vegetation plots to reasonably characterize the overall gradient in shrub cover. I think it is more likely that most sites had sufficient shrub cover for occupancy by these species, so that variation in occurrence was due to other factors. This is a case where the abundance of each species on the sites may reveal more than presence/absence data. When bird abundance was considered using Poisson regression, MacGillivray's Warbler abundance was found to be positively associated with shrub cover, apparently because of higher numbers on the four sites with extremely dense shrub cover.

Predictive ability

I obtained a model with adequate fit for all but one of the twenty most frequently detected species (Table 7), and this one (AMRO) was fit well by the alternative multivariate model with only linear terms. That is to say, the models explained the data significantly better than random predictions. However, a large amount of variation in the distribution of the bird species was still unexplained. The p-values for the fit of the various models varied greatly. Some models fit the data much better than others, but how good is good enough? The question is not really relevant to measures of fit, which is a mathematical problem. A more useful question is how well a model can predict the occurrence of birds on new sites in the future.

There was a large amount of unexplained variation in the distribution of all bird species, so the models did not always correctly predict the occurrence data on which the model was based. The sites where each species was present were correctly predicted, for most species, between 70 and 100% of the time (Table 6), although some of the higher values were at the expense of accuracy in predicting absences, since classification always favors the larger group. Besides this sensitivity to the relative sizes of the two groups, classification tables turn continuous residuals into binary predicted outcomes. These disadvantages make such tables inappropriate for assessment of fit for a model, but they are more appropriate for predicting occurrence, since this is a classification problem (Hosmer and Lemeshow 1989).

The prediction of new data is the key step in validation of any model. The only opportunity to do so in this study was to predict occurrence on the sites in 1994 based on the 1993 data (a "same place, different time" validation; Morrison et al. 1987). In general, the predictive ability was not strong (Table 8). Although low predictive ability is common in habitat-relationships models (e.g. Rotenberry 1986), part of the problem in the present study may have been due to detection failures.

Detectability

In the second year of the study each species was detected on a different set of sites than in the first year. These differences could have been due to changes in habitat occupancy of the birds or to failure to detect birds on some visits when they were actually present. If the distribution of birds changes greatly between years, then predictability of habitat occupancy will be very difficult, although if these changes occur within a species-specific parameter space of habitat suitability, then pooling of data over two or more years may reveal this general selection function. If detection of a species in only one year is the result of missed detections in the other year, then the habitat distribution will be more consistent and may be revealed by pooling the data. Both explanations were probably true in this (or any other) study. However, I have reason to believe that detection failures played a large role in this study.

It would be quite reasonable to expect that a species may have been present on a site without being detected. Each site was visited only once per year, and the total observation time for data collection on each site was 30 minutes. Many breeding male songbirds will sing repeatedly during this time period. However, it is very unlikely that all species present on a site were detected from three stationary positions during one short visit. I did, in fact, observe species on some sites, during incidental activities, that were not detected during the point counts.

If many birds were missed that were actually present on a site, then the proportion of the species on a site that were detected in both years may be low. There was high variation in this proportion among my study sites, but it was not related to vegetation density, nor was it positively related to the mean detection distance. This suggests that the variation in this proportion was not due to detectability differences. However, detectability is affected by more than the attenuation of sound by distance or vegetation. If a bird does not sing or call during the ten-minute observation period, it will not be detected regardless of distance, unless it is close and active enough to be seen. Song rates and activity may vary with species, weather (Robbins 1981), or season (Best 1981). In the present study, each site had a different assemblage of species, and two visits may not have been enough to correct for weather and season, even though their timing was independently randomized. There may also be characteristics of particular sites that affect the frequency of singing. For example, a site that is marginal for a species may have a greater proportion of unmated males, which may sing more throughout the season.

Meaning of response curves

Observed species response curves across environmental gradients describe the density (or in the case of point coints, an abundance index or probability of occurrence) of the species as a function of measured environmental variables (Whittaker 1967). Whether linear or unimodal, a significant response curve implies that the variable is a proximate cue used by the species for habitat selection. The first step in confirming this hypothesis would be to validate the models with independent data, and examine the proposed relationships with further research.

A strong, repeatable correlation between an environmental variable and a species' distribution implies that there is a causal factor involved. A complete understanding of the phenomenon of habitat selection would require the identification of these causal factors through confirmatory studies. However, the causal mechanisms do not necessarily need to be known in order to develop a predictive model which, if validated, would be useful for management decisions as well as for generating ecological hypotheses.

If we wish to suggest that a demonstrated species response curve reflects the ecological needs of a bird population, another assumption we must make is that density reflects "habitat quality," or the total fitness of animals in a habitat (Van Horne 1983). There are many circumstances that may result in birds using habitats in which their fitness is low or even zero, but it is unclear if any of these circumstances are likely to completely reverse the expected positive relationship between density and habitat quality (sensu Van Horne 1983).

All individuals do not settle in the best possible habitat for several reasons. One is that animals make mistakes, either because they have not found the best habitat or have not assessed it correctly. Secondly, all individuals cannot be supported by the best habitat, so some will settle in less productive habitats (Fretwell and Lucas 1970). Whether this is a "free" choice, or forced by "despotic" territoriality, the Fretwell and Lucas model still predicts a positive correlation between density and habitat quality. For this relationship to be reversed for a territorial species, the individuals in the poor habitats must be less capable of maintaining territories against intruders (Van Horne 1983); but the intruder pressure should be lower in poor habitats, and the owners would be expected to maintain larger territories if fewer resources were available. Therefore, I think it is likely that, in the majority of cases, density will still reflect habitat quality.

There are at least two important factors that may lead to a breakdown of the relationship between density and habitat quality, and each involves an animal's response to habitat alteration. The first of these is site tenacity. Many birds will return to breed at a site where they were previously successful, even when the habitat has been disturbed and is no longer suitable (Van Horne 1983, Wiens 1989). This will slow the free movement of individuals between habitats, an assumption of the Fretwell-Lucas model, and will result in many individuals being observed in unsuitable habitats. It would be unlikely to reverse the density-quality relationship in a widespread study, however, because the error should be short-term and localized. It would be useful to examine the time since disturbance as a variable in the model.

Secondly, human-caused habitat alteration may produce habitat configurations that differ from the evolutionary experience of a species. If the proximate cues they use to settle in habitats are no longer correlated with their subsequent fitness in those habitats, they may be caught in an "ecological trap" (Gates and Gysel 1978). Although this may destroy the relationship between density and habitat quality, the birds may still exhibit a quantifiable response to the same proximate cues they have always used. Even if density is no longer correlated with fitness, we can still assume that density is correlated with proximate assessment cues, or with the perception by the animal that the habitat is appropriate for settling. We still expect significant habitat associations, because the animals should agree on which habitats <u>seem</u> appropriate, based on past adaptation, regardless of the current fitness consequences. Observed habitat relationships should still indicate important proximate cues, and a demonstration of predictive power through validation would help confirm them. The next step would then be to determine the fitness consequences of these choices.

Whether or not the models accurately reflect the fitness of species in habitats, if occurrence is related to the proximate cues used by the species, then we may expect that the models will at least be useful in predicting occurrence on new sites. The models I have developed here still require such validation. It may be that this modeling approach is best suited to discovering the habitat variables that are important to each species, rather than predicting occurrence with exact equations. Any one local study may have confounding problems from population variability, site fidelity, and Type I error, and even with a good equation prediction is only a probabilistic process. However, a widespread study or combination of studies should help reach a consensus on the important variables for each species. The modeling approach used in this study, with multivariate methods and consideration of unimodal response curves, should aid in this process.

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APPENDIX

This appendix contains discussions of the multivariate models for each individual bird species, in phylogenetic order. The main model discussed for each species is that chosen by backward elimination (Table 5), unless otherwise stated (see Hairy Woodpecker and Gray Jay). In addition, I discuss the two most common species (Red-breasted Nuthatch and Dark-eyed Junco), which were too common to analyse with logistic regression and are not discussed elsewhere in this paper. All figures in the appendix (Figures 11-28) show univariate relationships, with the presence/absence data (coded 1 or 0, respectively) depicted by plus signs (some plus signs may represent multiple sites). A smoothed curve is drawn for easier visualization, using LOWESS smoothing.

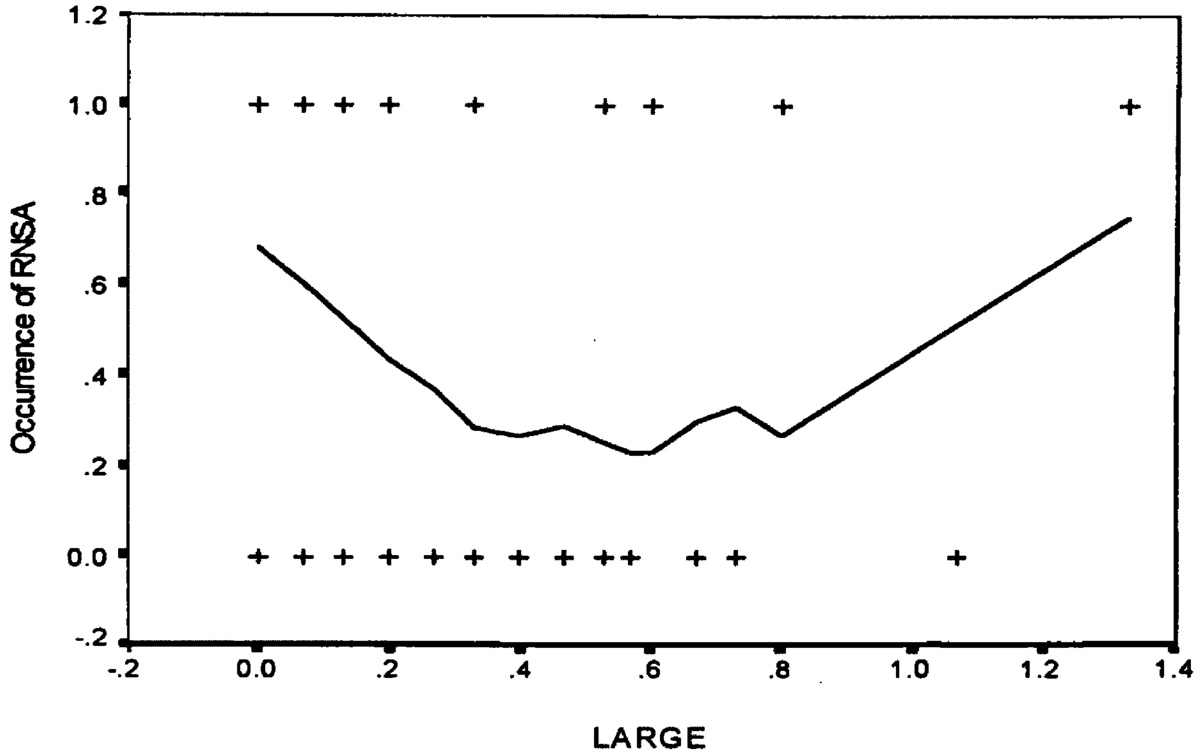
SPECIES Page

Red-naped Sapsucker

The model produced by backward elimination for the Red-naped Sapsucker (Table 5), was one of the few that did not have basal area of mature trees (BAMAT) included in the multivariate model, although there was a significant negative relationship with BAMAT in the univariate test. The relationship with density of LARGE trees was also mostly negative (Figure 11a); the positive quadratic term was due to sapsucker presences on only 3 sites at the high extreme of this variable. LARGE and BAMAT were negatively correlated ($r = 0.68$), and the univariate relationships of sapsuckers with both variables were about equally strong ($p < .01$), so whichever variable is entered into the model first will likely preclude the other. Both the forward selection and all-possible-subsets procedures also produced the same model, and the result showed a high fit to the data ($p=0.80$; Table 6). However, the model was not readily interpretable from a biological perspective.

It is unclear why there should be a negative relationship with either large tree density or sapling cover, although these variables were correlated with each other. The tree species composition relationships also seemed ambiguous. In fact, their univariate relationships were very weak, and their inclusion in the multivariate model was marginal. The univariate relationship with PINE was negative over the region with most of the data (Figure 11b), so sapsuckers may be less likely to occur on sites with a lot of pine (especially ponderosa pine, as suggested by examination of individual sites). This may be a reflection of a preference for more mesic sites. The widespread occurrence of Red-naped Sapsuckers with respect to tree density was corroborated by the regional monitoring study (Hutto, in press), which found this species to be more abundant in cut than uncut forests. Apparently, even seed-tree cuts provided sufficient trees for the occurrence of this species, as long as other variables were at

a.



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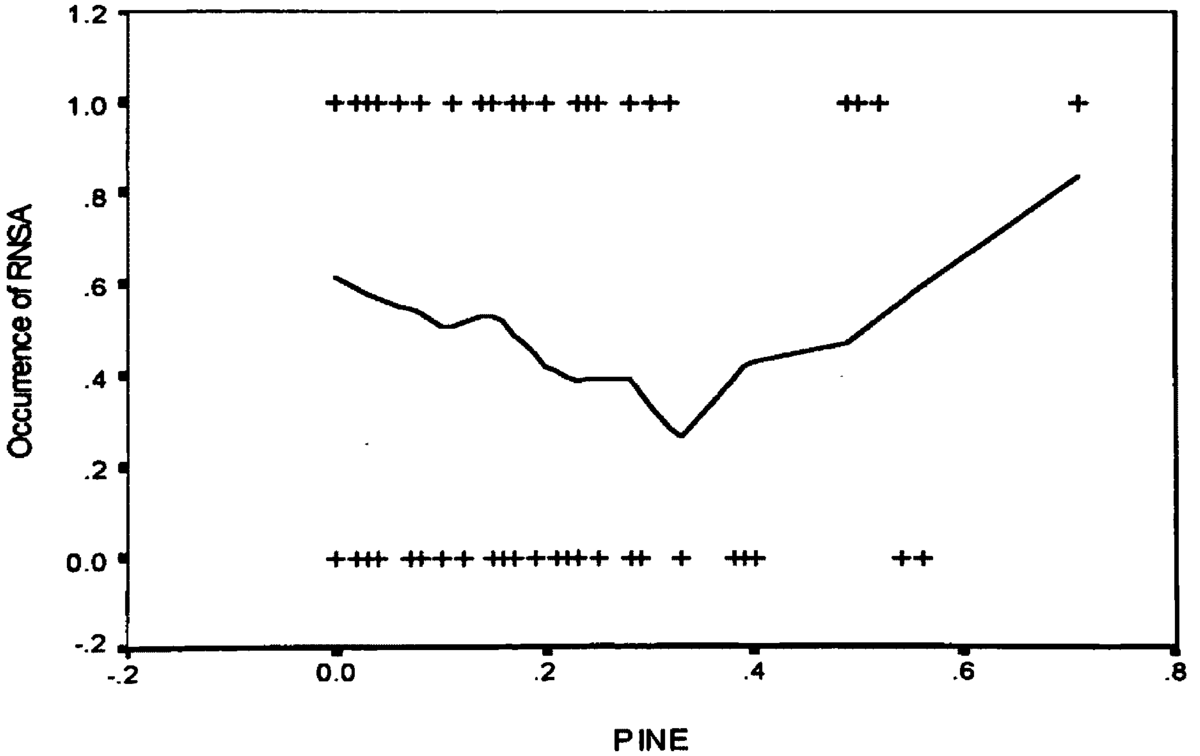


Figure 11. Univariate relationships of the Red-naped Sapsucker with two habitat variables: a) density (per plot) of large trees (dbh > 50 cm; LARGE); b) proportion of mature trees that were pine (PINE).
The curves in this and all other figures in the Appendix were generated by LOWESS smoothing. Some plus signs may represent multiple sites.

appropriate levels. Tobalske (1992) found that there was also no difference in fledging success between uncut forest and clearcuts with snags and live paper birch retained, although his sample size was small (23 nests).

Because sapsuckers are known to have a close association with aspen, it is surprising to see it occur so commonly in mixed-conifer stands, and even more surprising that this occurrence is not associated with the presence of deciduous trees on these stands (p=0.89). Most of the deciduous trees were paper birch (Betula papyrifera). Red-naped Sapsuckers readily nest in paper birch trees within mixed-conifer stands in western Montana (Tobalske 1992). I detected aspen in my vegetation samples on only three sites, and Red-naped Sapsuckers occurred on all three of these. Other sites had pockets of aspen within or next to them that were not sampled. I recall such pockets near most sites with sapsuckers. In fact, there were very few areas in the Swan Valley that did not have small waterholes near them, and this was probably why Red-naped Sapsuckers were so widespread. However, a model with a good fit was achieved using vegetation variables sampled within the sites, although only 75% of the occurrences were correctly classified. Better predictions might be achieved by including larger-scale variables (such as proximity to riparian areas).

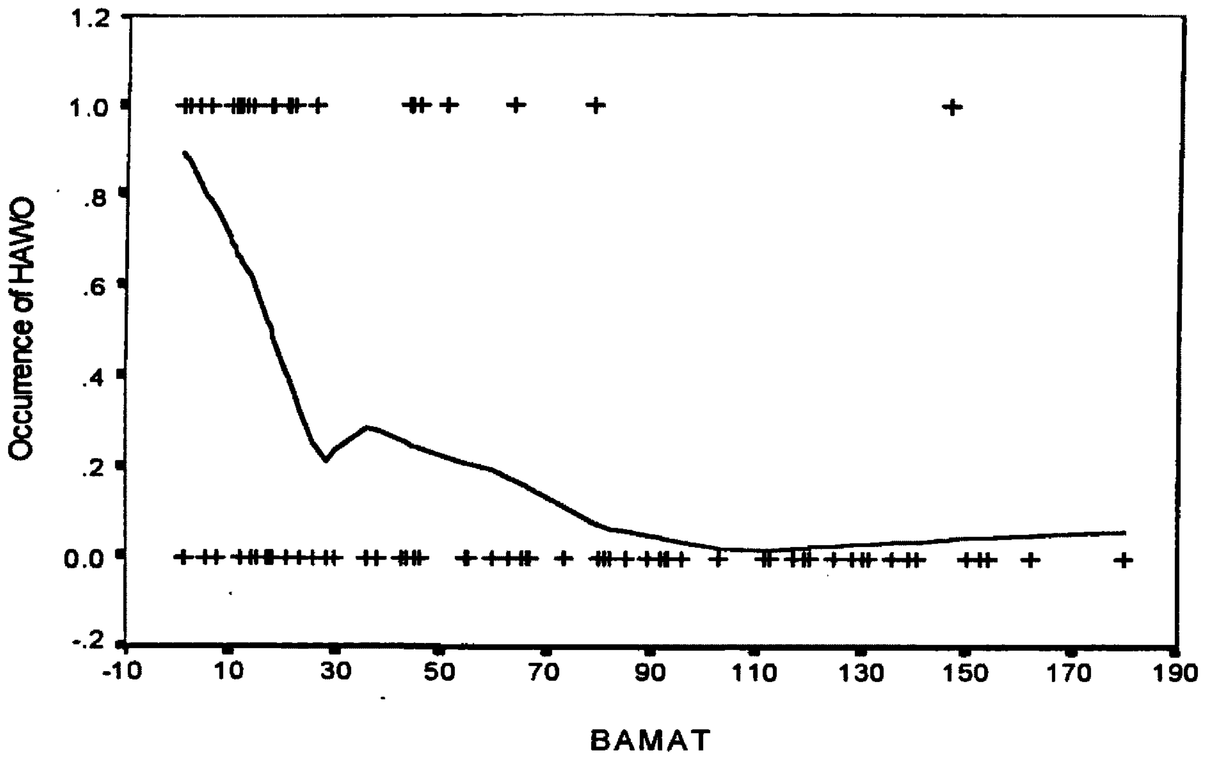
Hairy Woodpecker

The Hairy Woodpecker had significant (or nearly significant) associations with every habitat variable considered in the univariate tests. Only those with clearly significant relationships ($p < .05$) were considered as candidates for the multivariate model, and stepwise backward elimination did not eliminate any of these variables (only a couple of quadratic terms). Even when the variable with the highest p-value was forced out of the model, no other variable was close to elimination. The model thus chosen included 8 variables (BAMAT, BASM, LARGE, AVGSIZE, SHRUB, PINE, MESIC, AND SNAGBA) and 4 quadratic terms. This model did have a very good fit (p=.93), and it is possible that all of these variables are important to the species, but it is not a very parsimonious model. It is also possible that the structure of the data set, perhaps due to intercorrelations, somehow prevented irrelevant variables from being removed in the stepwise procedure. This possibility was supported by the all-possible-subsets procedure, which indicated that the best model was a much simpler one involving BAMAT and SNAGBA, and I chose to report that alternative model here (Table 5). This is one of only two species (see also Gray Jay) for which I rejected the model chosen by backward elimination and reported an alternative model in Table 5.

The negative relationship with the basal area of mature trees (BAMAT) was very strong in the univariate case ($p < .0001$; Figure 12a). This species occurred most often in open forests created by logging, as Hutto (in press) also found in a regional monitoring study. In the northern Rockies this species is particularly abundant in post-fire habitats (Hutto 1995). It is possible that it occurred in logged forests because of their superficial resemblance to burned habitats (Hutto, in press). It is unknown whether these logged habitats provide the necessary requirements for the reproductive success of this species.

The univariate relationship of this species with the basal area of snags (SNAGBA) was largely negative, although only a positive quadratic term made it significant, and this was included in the multivariate model (Table 5). The quadratic term was apparently included only because of the presence of this species on the one site with the highest snag basal area (Figure 12b). The overall negative relationship was undoubtedly due in large part to the positive correlation of SNAGBA with BAMAT (r=0.64), although both variables included in the multivariate

a.



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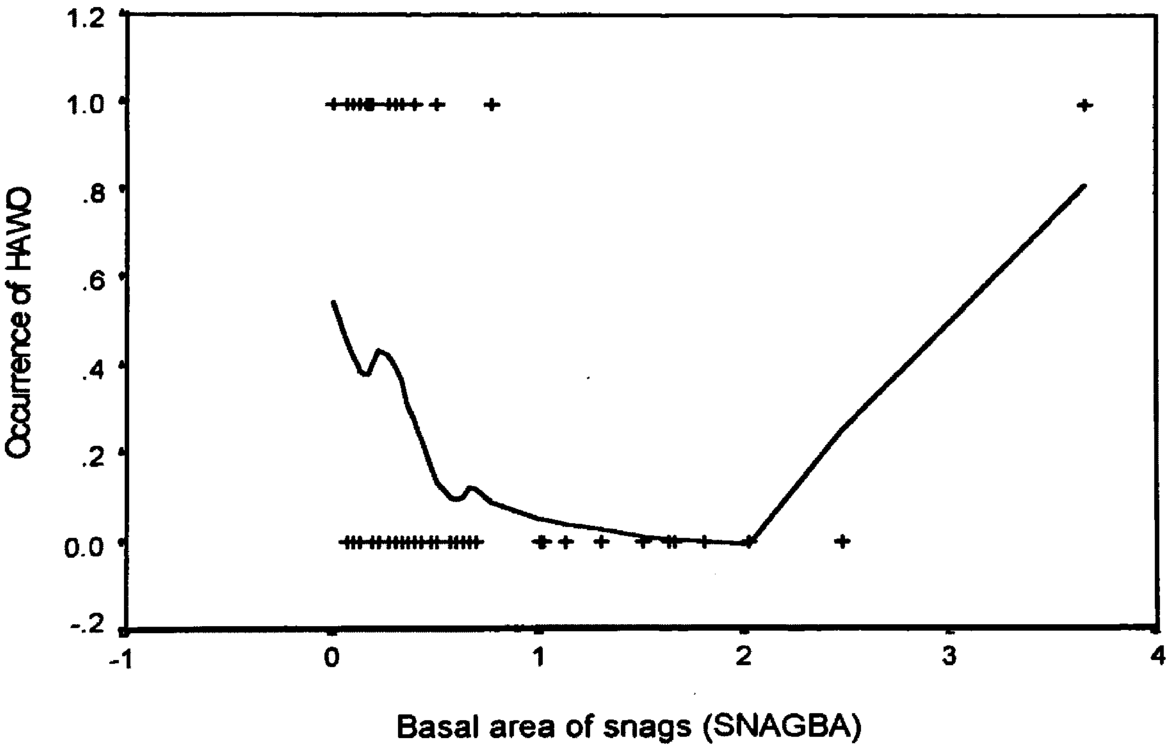


Figure 12. Univariate relationships of the Hairy Woodpecker with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) basal area of snags with dbh > 20 cm (SNAGBA).

model. During the forward selection procedure, only a positive linear term for SNAGBA was included, after BAMAT was entered. Therefore, the abundance of snags may still explain additional variation for this species after tree density is considered. The true relationship may be revealed only with more rigorous sampling of snags.

Northern Flicker

The negative relationship of the Northern Flicker with the basal area of mature trees (BAMAT) was the strongest univariate relationship of any species with any variable. This was also one of the clearest logistic relationships (Figure 13a), with the species being entirely absent from any stand denser than a very open shelterwood or overstory-removal cut. It is not surprising that this species was also positively related to the average size of mature trees (Table 5), since only larger trees can produce the snags necessary for nesting. It is unclear, however, why the overall fit of the model was so low ($p=0.08$; Table 7).

The preference of this species for open forests, and the lack of any relationship with tree-species composition, is consistent with many other studies (Moore 1995, and references therein). The regional monitoring program also found flickers much more often in logged forests, although they still occurred in some uncut forests (Hutto, in press). The preference for open sites may be due to the need for open ground for foraging. No understory variables were retained in the multivariate model, although there was some evidence for the avoidance of shrub cover. The univariate relationship with tall understory cover (SHRUB) had a positive quadratic term (U-shaped; Figure 13b) and was very significant ($p < 0.01$). However, flickers were detected on only 4 sites with SHRUB over 8.5%, and otherwise the relationship looked strongly negative. There were probably not enough sites with flickers to be able

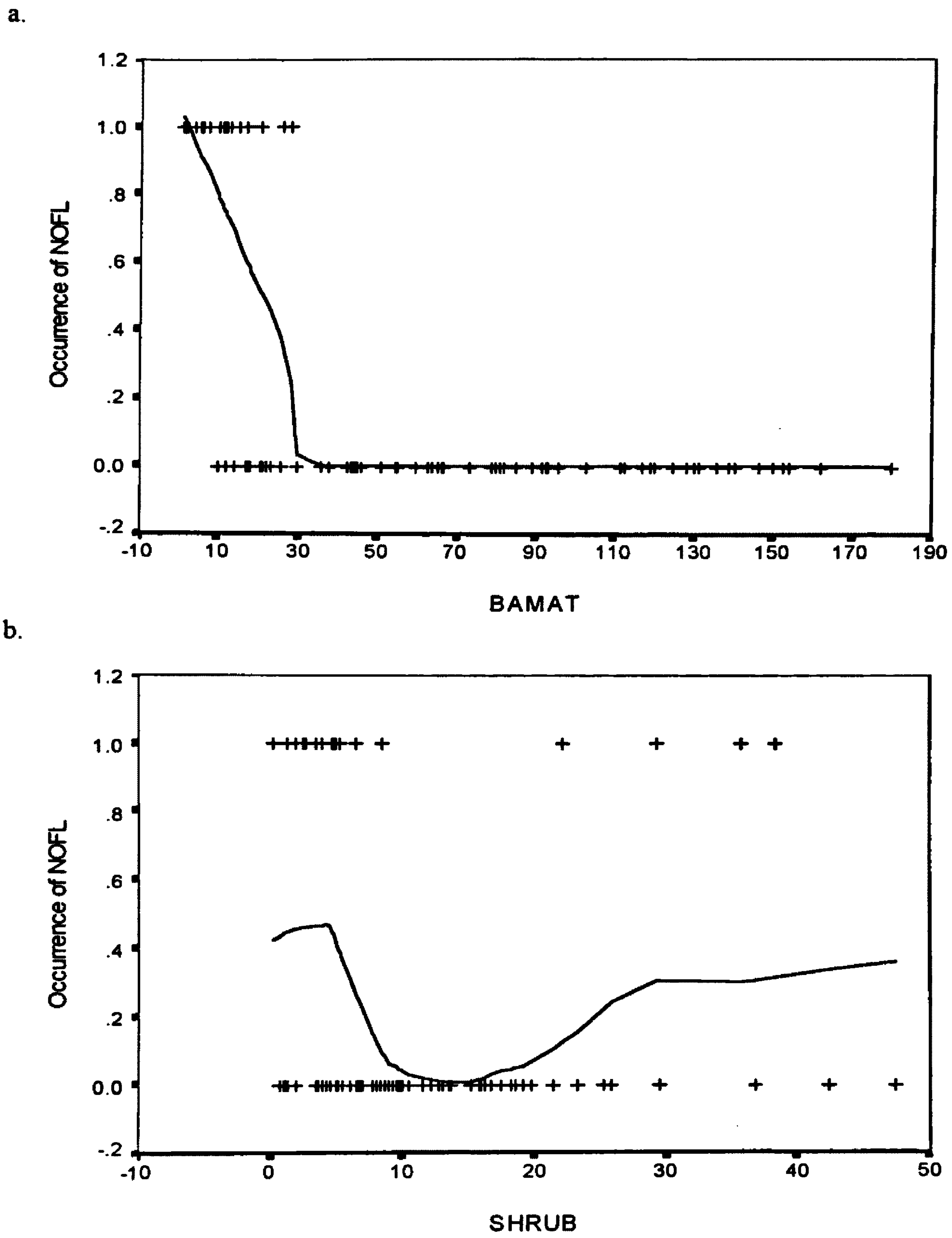


Figure 13. Univariate relationships of the Northern Flicker with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) percent cover of understory vegetation (SHRUB)

to examine the residual effect of SHRUB when the correlated variable BAMAT was included in the multivariate model.

Gray Jay

The model chosen by stepwise backward elimination for the Gray Jay contained 5 different variables, but the Hosmer-Lemeshow goodness-of-fit test rejected it (p=0.01). Stepwise forward selection produced the alternative model reported in Table 5, and the all-possible-subsets procedure agreed that this was a much better model. It also had a much better fit (p=0.26). This is one of only two species (see also Hairy Woodpecker) for which I rejected the model chosen by backward elimination and reported an alternative model in Table 5.

This species had positive linear associations with basal area of both mature (BAMAT; Figure 14a) and small trees (BASM; Figure 14b). Because BASM and BAMAT were strongly correlated (p=0.51), it is not surprising that the multivariate model included only one of them. BASM was considered more important by most modeling procedures (it had the stronger univariate relationship; Figure 14), but the backward elimination model retained BAMAT instead. If both variables were combined into one measure of basal area it might provide a more powerful predictive tool, but it is not clear if all sizes of trees are important. It appears that this species is less common on open, logged sites, as found by Hutto (in press).

Gray Jays are usually considered to be associated with spruce (Strickland and Ouellet 1993), although this may be on a landscape or regional scale. Hutto (in press) found this species most commonly in spruce/fir forests, although it was common in all conifer habitats. There was a nonsignificant positive correlation with spruce/fir in my study. This species has very large territories (means from several

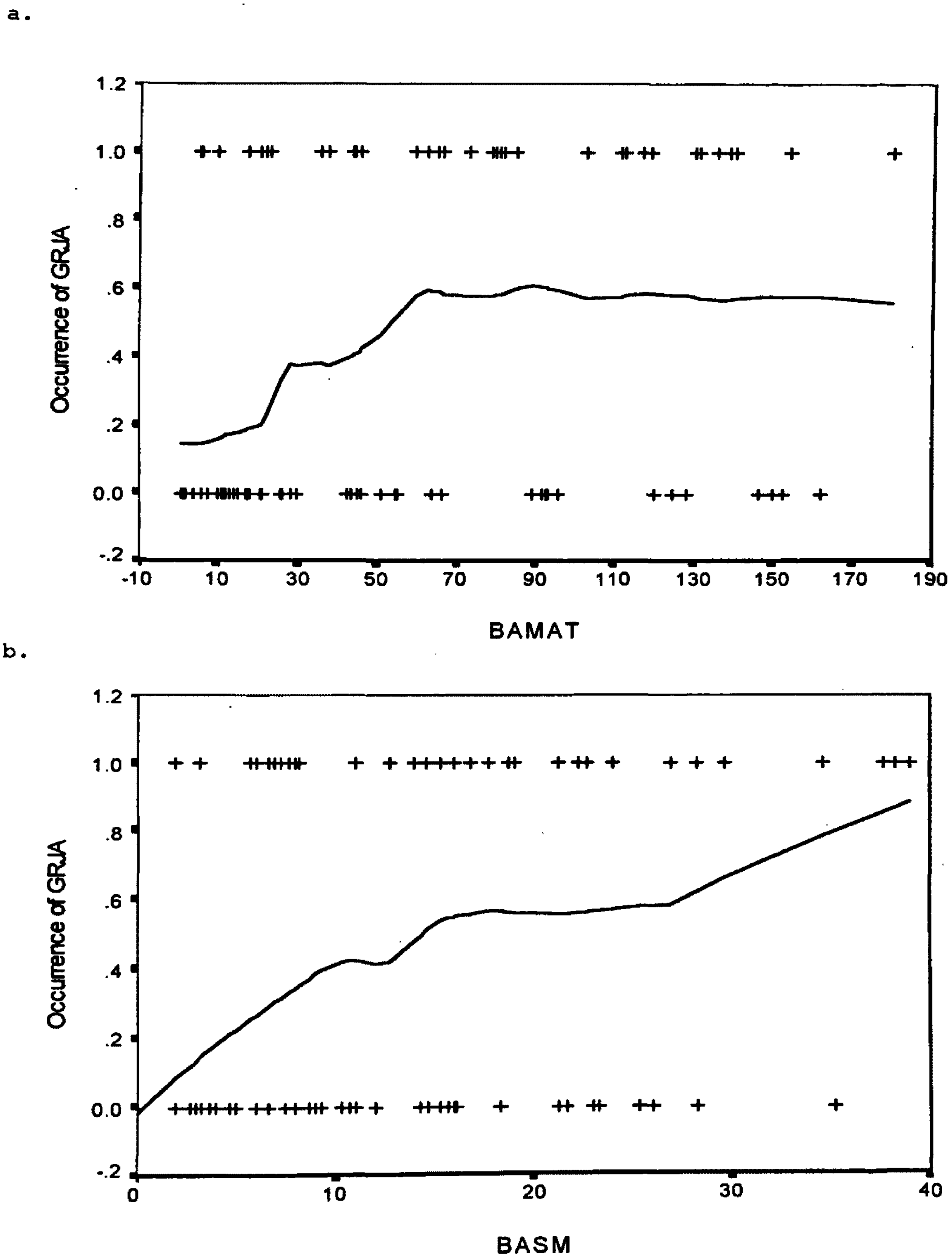


Figure 14. Univariate relationships of the Gray Jay with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) basal area of small trees (< 20 cm dbh; BASM)

studies range from 41 to 146 ha; Stickland and Ouellet 1993), so even if it occurred in some stands without spruce, there may have been enough spruce elsewhere in the territory. During the course of the summer I saw this species on most sites, from dense forest to seed-tree cuts. It may range through most habitats in a landscape, which would make it difficult to determine the elements it needs for reproductive success.

Black-capped Chickadee

The occurrence of Black-capped Chickadees associated with very few variable. The only significant univariate relationship was a U-shaped, quadratic relationship with sapling cover, which has no apparent biological interpretation. An association with the occurrence of deciduous trees (DECPRES, a binary variable) was nearly significant (p=.051), however, and this association was expected from the biological knowledge of the species (see below). However, when the stepwise model was built by backward elimination, DECPRES was not included (Table 5), but several other variables were. I have reported this model, even though I do not think it is the best possible model. Forward stepwise selection produced a model containing only DECPRES and the quadratic relationship with sapling cover, and the all-possible-subsets procedure indicated it was a better model. The Black-capped and Mountain Chickadees are two species for which a case might be made for rejecting the backward elimination model, as I did for the Hairy Woodpecker and Gray Jay, because it seemed to include too many irrelevant variables. However, without consistent criteria for making such a decision, I report the backward elimination model in Table 5, as I did for other species.

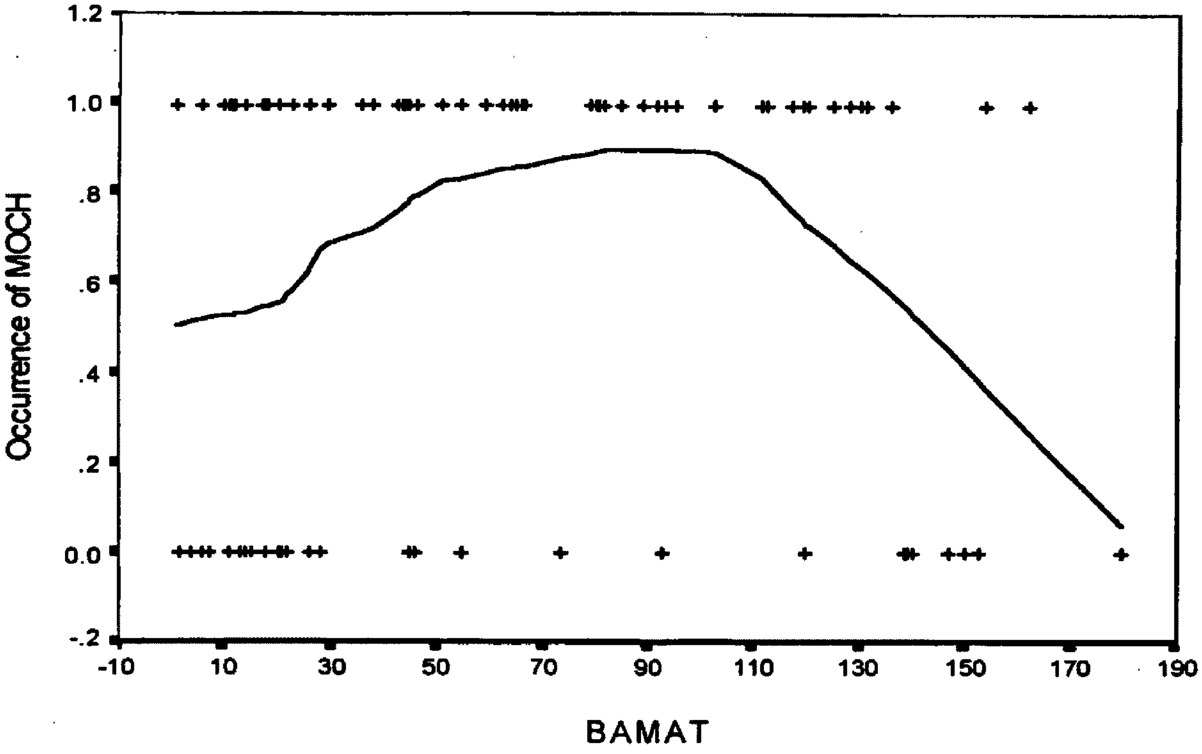
The Black-capped Chickadee is not usually considered a coniferous-forest species. It is generally associated with broadleaf tree species (Sturman 1968, Smith 1993), although it is flexible in its usage of conifer trees in habitat mosaics (Sturman 1968, Hill and Lien 1988). In Montana, it is generally associated with riparian habitat (Hutto, in press). In the Swan Valley, there may be an unusual situation with numerous pockets of aspen interspersed throughout the mixed-conifer forest. As in the case of the Red-naped Sapsucker, an association between Black-capped Chickadees and deciduous trees may be difficult to detect, because these trees may be just outside of a site or uncommon enough to be missed during vegetation sampling. The negative relationship with PINE (Table 5) may be indicative of a preference for moister sites.

The habitat relationship of the Black-capped Chickadee was not clearly defined in this study, but there was an indication of an association with deciduous trees, and of the possible importance of understory [Sturman (1968) found understory volume as well as canopy to be important]. There may have been other factors influencing the distribution of chickadees, such as nearby forest edge (Smith 1993), elevation (Sturman 1968, Smith 1993), or perhaps distance to the Swan River riparian zone.

Mountain Chickadee

The multivariate model for the Mountain Chickadee (Table 5) was complex, containing five different variables and two unimodal relationships. The model had a strong unimodal relationship with the basal area of mature trees (BAMAT; Figure 15a). BAMAT was always retained in the model, whatever the variable-selection method. All-possible-subsets and forward selection procedures both indicated that the quadratic term for the density of large trees (LARGE) and the negative relationship with canopy height (CANHT) were unnecessary. Apparently, the structure of the data set somehow locked these two terms into place during backward elimination, because when either was dropped from the model, the other became highly non-significant. Even the negative relationship with

a.



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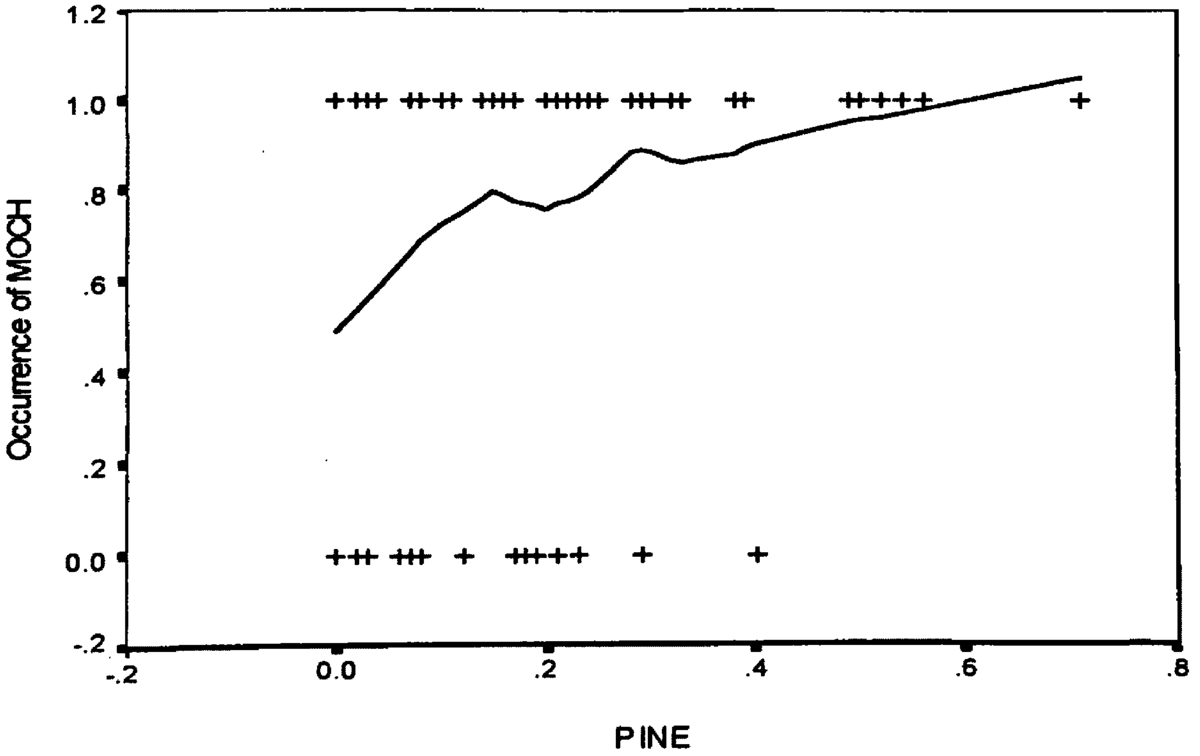


Figure 15. Univariate relationships of the Mountain Chickadee with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) proportion of mature trees that were pine (PINE).

sapling cover appeared marginal in some methods, and since part of this relationship was due to chickadee absences on two sites where the dense "sapling" cover was pacific yew, the generality of this relationship might be low, although sapling cover was important in each year analyzed separately. This is another species for which a case might be made for rejecting the backward elimination model, as I did for the Hairy Woodpecker and Gray Jay, because it seemed to include too many irrelevant variables. However, without consistent criteria for making such a decision, I report the backward elimination model in Table 5.

All model-building methods indicated a strong positive response of this species to the proportion of pine in the stand (Figure 15b). This variable included both ponderosa and lodgepole pines, and examination of the data suggested that both tree species contributed to the positive relation-ship with the occurrence of Mountain Chickadees. In mixed-conifer forests of the Sierra Nevada, Morrison et al. (1987) found this species to be more abundant in plots with more sugar pine foliage, and in the same forest it preferred to forage in white fir and pine, especially ponderosa pine (Airola and Barrett 1985). On a larger scale, Mountain Chickadees were most frequently detected in lodgepole pine forests throughout Montana and northern Idaho (Hutto 1995), although they were also widespread in all other conifer habitats except cedar-hemlock. Although there may be a tendency toward the use of drier forest types, especially pine, this should still be considered a generalist conifer species.

Red-breasted Nuthatch

The Red-breasted Nuthatch was present in one year or the other on all but 2 of the 86 study sites in the combined-year data set. Therefore, there was no power to perform any analyses with these data. Instead, I will briefly discuss a model based on the 1993 data only, when this species was detected on 70 of the 89 sites visited that year. This model is not reported in Table 5. With only 16 unoccupied sites from which to draw conclusions, this model may not be generalizable.

The model indicated a unimodal, quadratic relationship with the basal area of both small and large trees. However, in both cases the quadratic term seemed to be due to 1 or 2 very dense sites that were unoccupied (Figure 16). There was a positive relationship with the density of large trees and a negative one with the proportion of western larch (LAOC). However, the fit of this model was very poor (p=0.01). The relationship with larch was probably due to the species' absence on four larch seed tree cuts, which may have been due more to the low tree density than the tree species per se. When LAOC was removed, a much simpler model resulted, including only the quadratic relationship with BAMAT, and the fit actually improved (p=0.14). Generally, this species seems ubiquitous on most forested sites, above a very low threshold (Figure 16). It was less likely to occur on the most open sites such as seed tree cuts, but it was present on some of these.

Golden-crowned Kinglet

The Golden-crowned Kinglet had positive univariate relationships with the density or cover of almost every measure of vegetation structure. The linear relationship with the basal area of small trees (BASM) was the strongest of any species with that variable (Figure 17b), and the linear term with the basal area of mature trees (BAMAT) was also one of the most significant of any species. The quadratic term for BAMAT was retained in the multivariate model (p=.024), although there were only 2 sites above BAMAT = 80 that did not have kinglets (Figure 17a). The term was not quite significant in the univariate case, and its retention in the model was probably not meaningful.

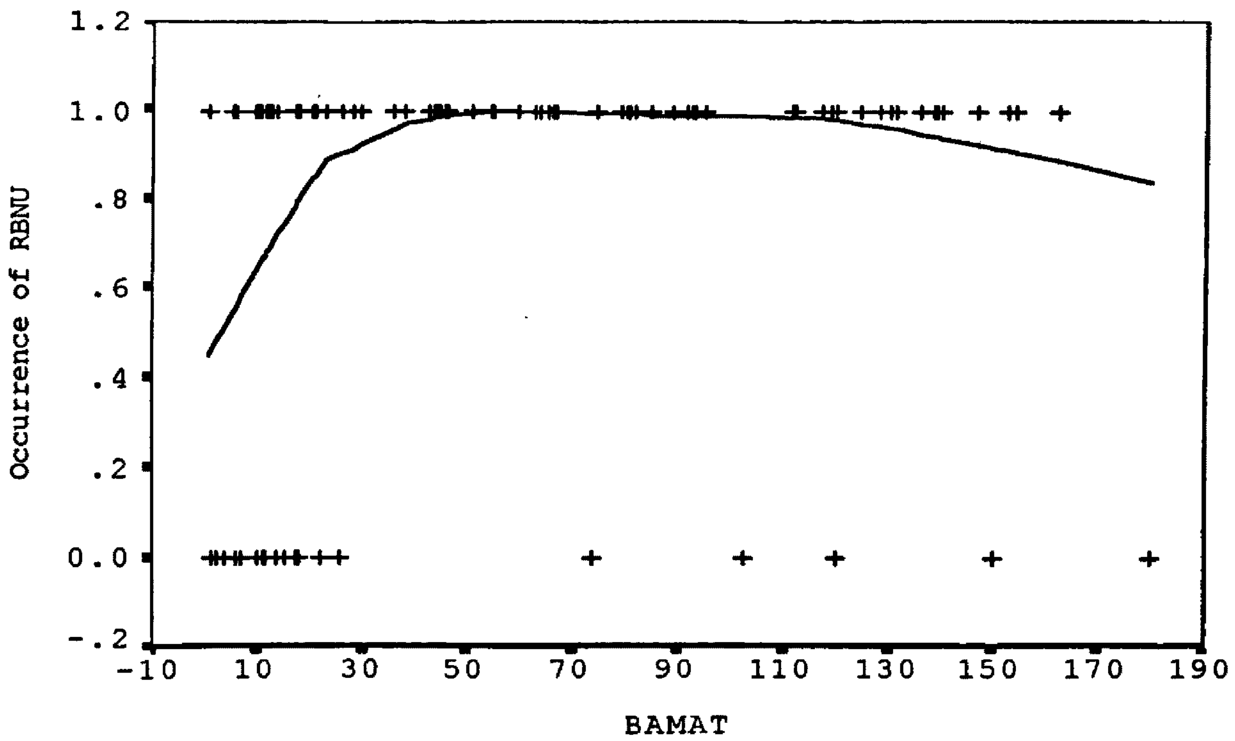


Figure 16. Univariate relationship of the Red-breasted Nuthatch (RBNU) with the basal area of mature trees (sq ft/acre; BAMAT), using 1993 data.

a.

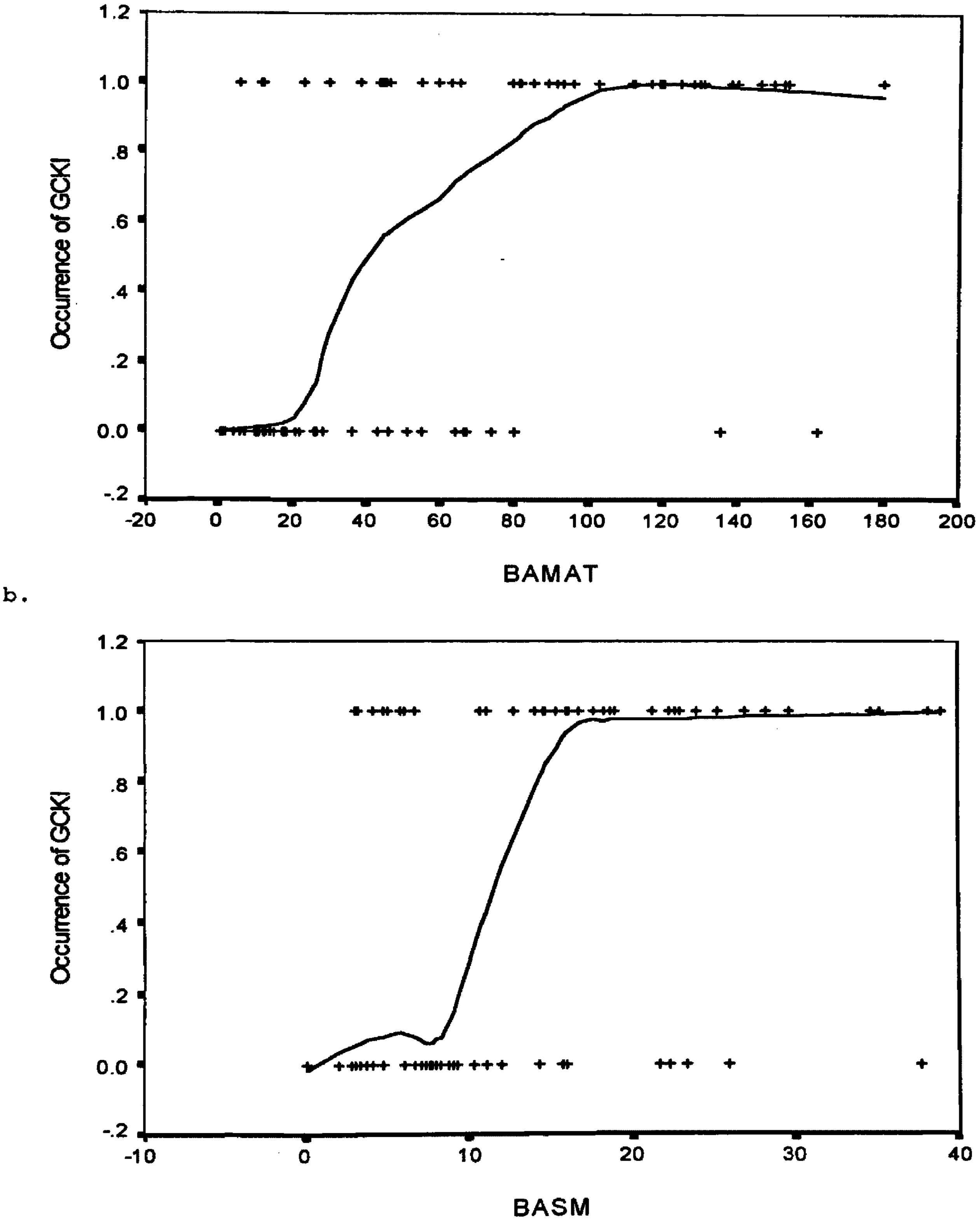


Figure 17. Univariate relationships of the Golden-crowned Kinglet with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) basal area of small trees (< 20 cm dbh; BASM)

There was a strong positive relationship with the proportion of mesic species in the overstory, especially spruce-fir. This is consistent with several other studies that show an association of this species with spruce-fir and cedar-hemlock forests, especially in the northern Rockies (Hutto 1995, in press). On the scale of individual trees, both species of kinglets seem to prefer spruce and fir trees for foraging, and to avoid pines (Franzreb 1984). Golden-crowned Kinglets seem to be even more specialized with regard to tree species than are Ruby-crowned Kinglets (Franzreb 1984, Keast and Saunders 1991, Ingold and Wallace 1994). Golden-crowned Kinglets may have specialized morphological adaptations for hanging on to the tips of conifer branches (Keast and Saunders 1991).

Hansen and Hounihan (1995) found this species to be positively associated with conifer density in the High Cascades of Oregon, and Hansen et al. (1995) combined several studies in Oregon to show a positive logistic relationship of kinglets with mature tree density (>10 cm dbh). The positive relationship I found with the basal area of smaller trees (BASM), is also consistent with this latter finding, since most of these trees were 10-20 cm dbh. Also, Mannan and Meslow (1984) found greater stem density around Golden-crowned Kinglet nests than at random sites in old-growth forests of northeastern Oregon, especially in the smaller size classes (2.5-10 and 10-30 cm dbh). I also found a positive univariate relationship with conifer sapling cover in this study, although it was not retained in the multivariate model.

Ruby-crowned Kinglet

The Ruby-crowned Kinglet was positively associated with the basal area of small trees (BASM), which might be expected by a species that nests in conifers, often at fairly low heights (Ehrlich et al. 1988). The plotted curve (Figure 18a) suggests that there may be a threshold

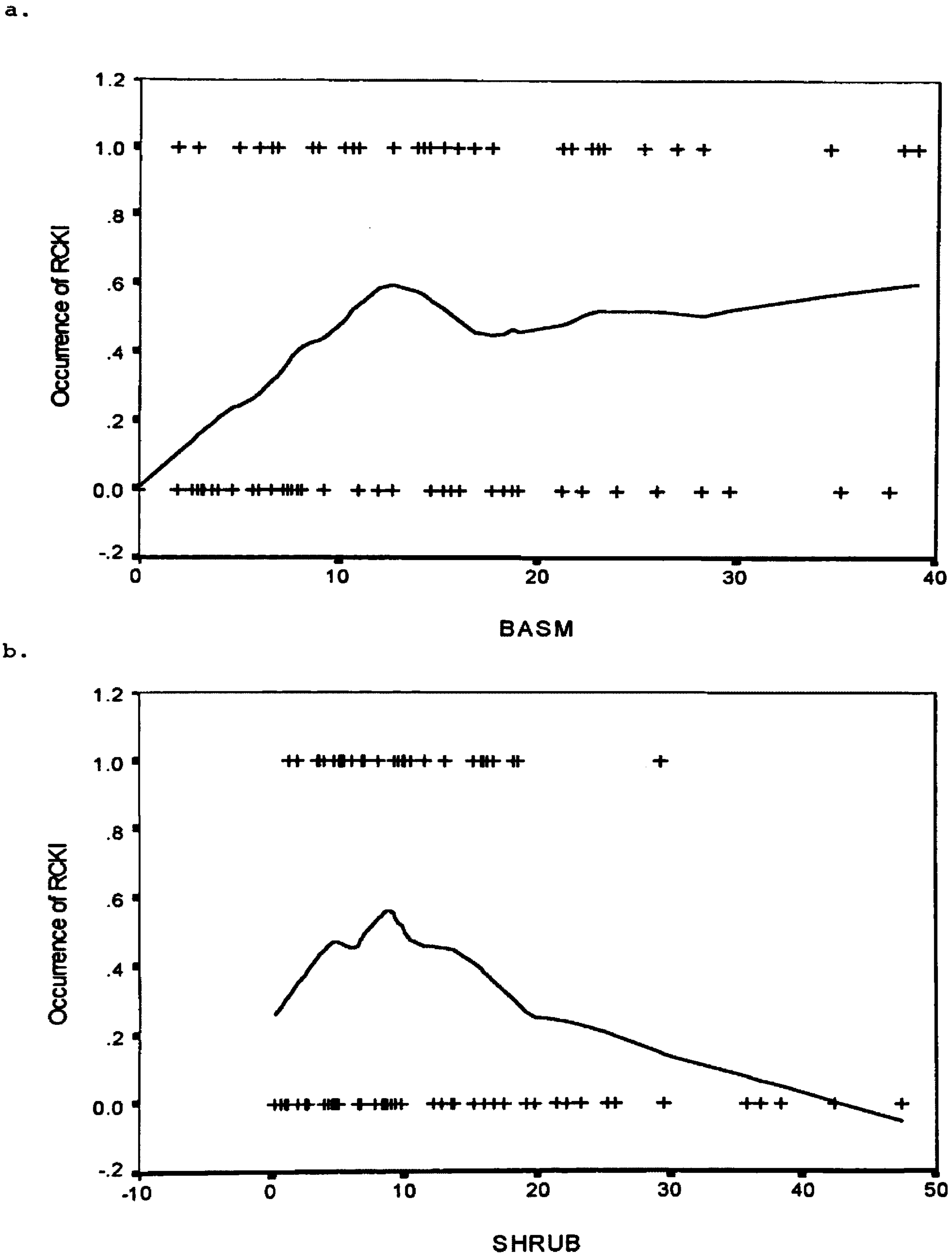


Figure 18. Univariate relationships of the Ruby-crowned Kinglet with two habitat variables: a) basal area of small trees (< 20 cm dbh; BASM); b) percent cover of understory vegetation (SHRUB)

above which BASM no longer influences the probability of occurrence. Interestingly, the curve for the basal area of mature trees (BAMAT), although not significant overall, showed a similar threshold. It may well be the case that this species declines with increased removal of trees, as found by Hutto (in press), but this may be one species for which some thinning is not a serious problem, as long as there is sufficient nesting and foraging substrate. However, the effect on population levels and reproductive success is unknown.

The negative relationship with tall understory cover (SHRUB) seemed to be due mostly to deciduous shrubs (there was no significant relationship with conifer sapling cover alone). The strong negative relationship was due mostly to absences on sites with very high shrub cover, however, and over most of the data the relationship looks unimodal (Figure 18b). This may be related to the finding of Hutto (in press) that the species was less likely to occur where riparian vegetation was nearby.

The multivariate model for this species included the proportion of mature trees that were spruce or fir (SPFIR), although the relationship was quadratic. On a microhabitat scale, kinglets strongly prefer to forage in spruce and fir trees over more open canopy species such as pine (Franzreb 1984), although they occur in all conifer habitats.

Swainson's Thrush

The Swainson's Thrush showed strong univariate relationships with many variables, generally indicating a greater use of stands with high or intermediate levels of both understory and canopy elements. The model chosen by backward elimination (Table 5) included quadratic relationships with both the basal areas of mature (> 20 cm dbh; Figure 19a) and small trees (< 20 cm, and mostly > 10 cm dbh). There was also a strong positive relationship with the cover of both low (BUSH) and

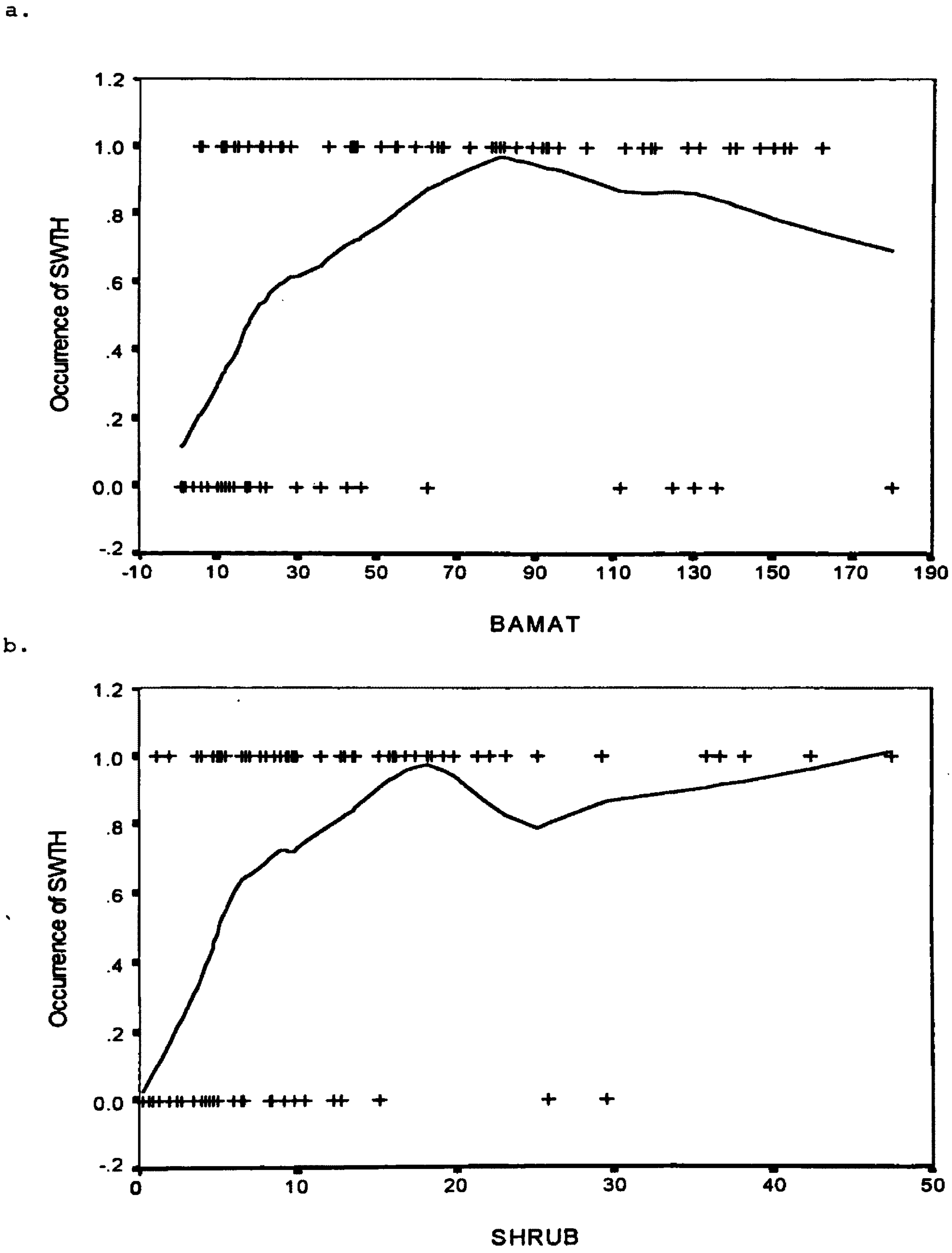


Figure 19. Univariate relationships of the Swainson's Thrush with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) percent cover of understory vegetation (SHRUB)

tall (SHRUB) understory layers (Figure 19b). This is to be expected for a species that is strongly associated with the understory shrub layer. Interestingly, however, when the SHRUB variable was separated into its components, the cover of conifer saplings had the stronger linear relationship, whereas that of deciduous shrubs was more quadratic.

This species did not seem to be affected by the tree species composition of the conifer stands, although it was more common on sites which included deciduous trees. This could be because such sites also tended to have a greater deciduous understory ($t = 4.08$; $p < .001$).

American Robin

The American Robin had a strong negative relationship with the basal area of mature trees (BAMAT; only Chipping Sparrow and Northern Flicker had stronger associations), although it was present on several uncut sites (Figure 20a). A quadratic (U-shaped) relationship with shrub cover was also retained in the multivariate model (Table 5). This relationship was negative over most of the range covered by the data set (Figure 20b), as expected for a species that often forages on the ground. However, there were a few sites with very high shrub cover that had robins, which resulted in the significance of the quadratic term. Most of these sites probably had areas without shrubs (the highest average shrub cover was only 47.5%). It is not clear if this represented the true shape of the relationship in this region, or if the shape could be extrapolated beyond 50% shrub cover. It may be that a larger sample of sites with dense shrubs, or the use of bird abundance or reproductive success data, would reveal a more consistent negative association with shrubs. A quadratic relationship with PINE (U-shaped), seen in the univariate case, was nearly retained in the multivariate model ($p=.09$), but overall this species seemed largely unconcerned with tree species composition.

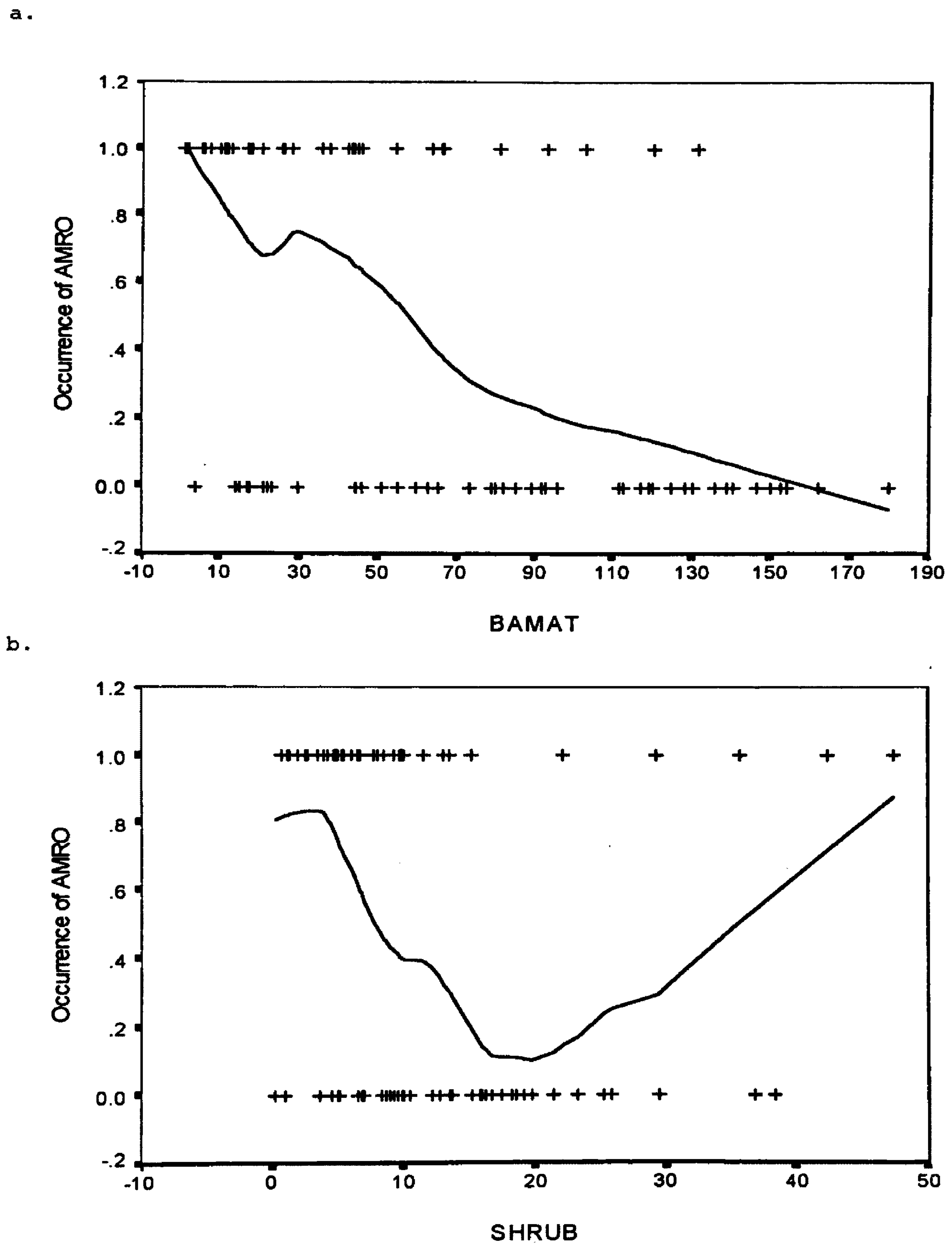


Figure 20. Univariate relationships of the American Robin with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) percent cover of understory vegetation (SHRUB)

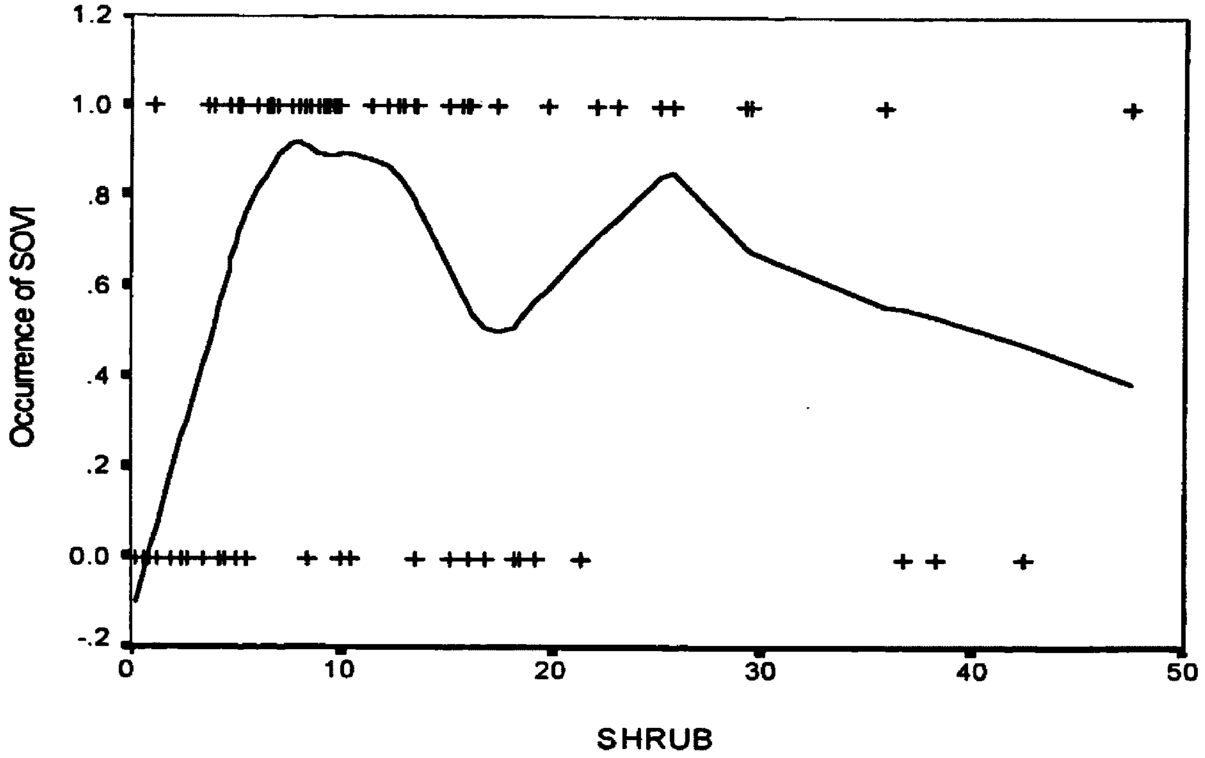
The American Robin can be found in a very wide diversity of habitats in the northern Rockies (Hutto 1995). Although it is often found in uncut forest, it has previously been found to be negatively associated with tree density (Hansen et al. 1995), and to be relatively more common in logged and burned cover types (Hutto, in press).

Solitary Vireo

The Solitary Vireo was one of the few species whose occurrence was not significantly related to the basal area of mature trees (Table 5). There was a dip in frequency at the most open sites, which helped give a trend toward a quadratic relationship ($p = 0.12$), but there was no reason to include this in the model. The quadratic relationship with total shrub cover seemed to be driven mostly by the absence of this species on sites with less than a very low threshold (it was not detected on 12 of 13 sites below 3.7% SHRUB cover; Figure 21a). Otherwise, there were no indications of any relationships with tall understory elements. There was, however, a very strong positive relationship with low bush cover (<1 m tall) in the univariate test, but this was not retained in the multivariate model.

The model included a negative linear relationship with the proportion of MESIC tree species (Figure 21b). This fits the general view that this species prefers somewhat drier sites. Hutto (1995) found it to be very infrequent in spruce-fir sites, and less likely to occur on points with riparian cover nearby. The negative association with the average size of mature trees (AVGSIZE) was unexpected, but potentially interesting. Hejl et al. (pers. comm.) found more Solitary Vireos in mature second-growth conifer stands than in old-growth stands. These second-growth stands had more medium-sized trees and fewer large trees, but they also contained more ponderosa pine.

a.



b.

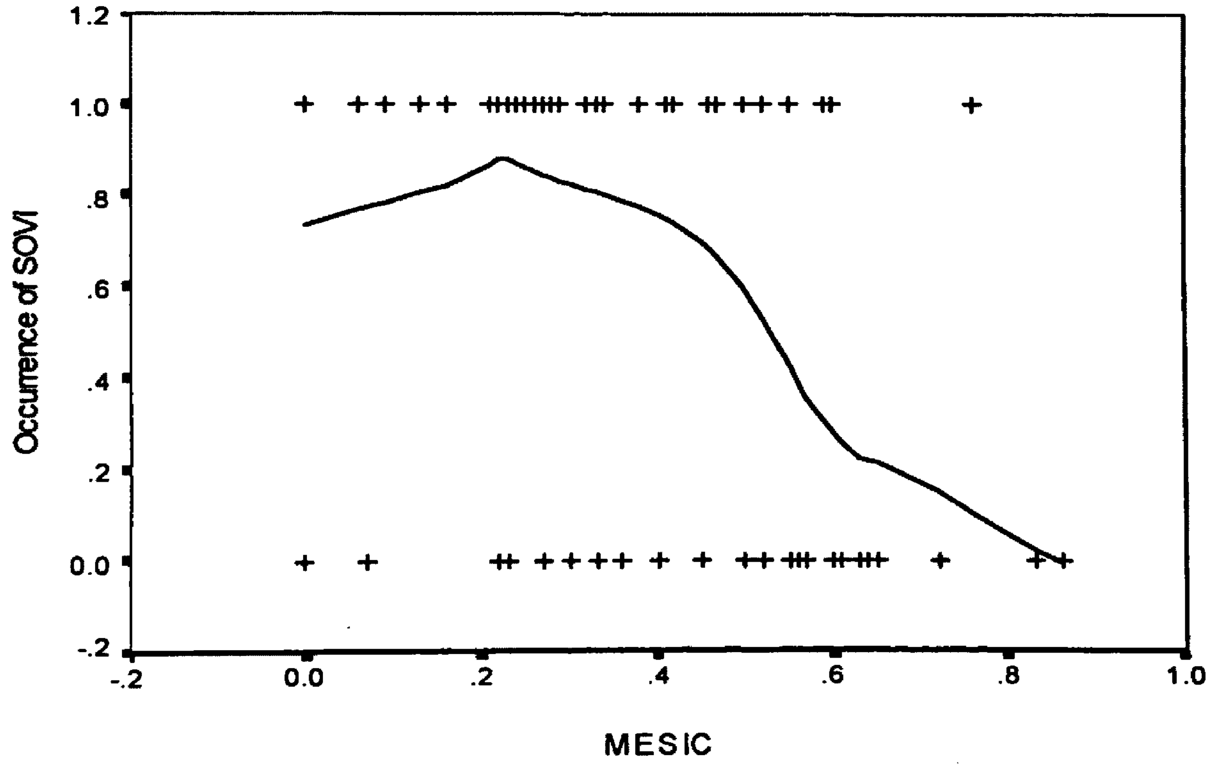


Figure 21. Univariate relationships of the Solitary Vireo with two habitat variables: a) percent cover of understory vegetation (SHRUB); b) proportion of mature trees that were mesic species (MESIC)

Warbling Vireo

The Warbling Vireo was negatively associated with the basal area of mature trees (BAMAT), although it occurred less often on the extremely low density sites (Figure 22a). The quadratic term was not retained in the multivariate model (although marginally significant in the univariate case), but perhaps a different polynomial or nonlinear model may show a better fit. The quadratic relationship with the proportion of larch (LAOC) was influenced by the absence of this species on the four larch seed tree cuts, which were 100% larch and were probably too recent to have sufficient shrubs. Many other sites with low tree density had probably also been logged too recently. Studies reviewed in Hejl et al. (1995) showed that this vireo often increased in partial cuts relative to uncut forest, and that the response of this species to clearcuts depended strongly on the presence of tall shrubs.

The well known association of the Warbling Vireo with shrubs was not observed in this study. The tall understory cover (SHRUB) variable was not retained in the model, although it was nearly significant (p=0.09). It should probably be retained for improved predictive ability, although the nature of the relationship was not clear from the data. The form that was almost retained in the model had a positive quadratic term, and the U shape can be seen in the univariate plot (Figure 22b). However, the form on the left side of the figure, where most of the data were represented, looked unimodal. There may be a low threshold of shrubs required by this species, and a high probability of occurrence where there are very dense shrubs, but what happens in between may be dependent on other factors. When I tried an alternative multivariate model with deciduous shrubs only (SHRDEC instead of SHRUB), a positive linear term was retained in the model. However, this was entirely due to the few occurrences at high shrub density. The curve

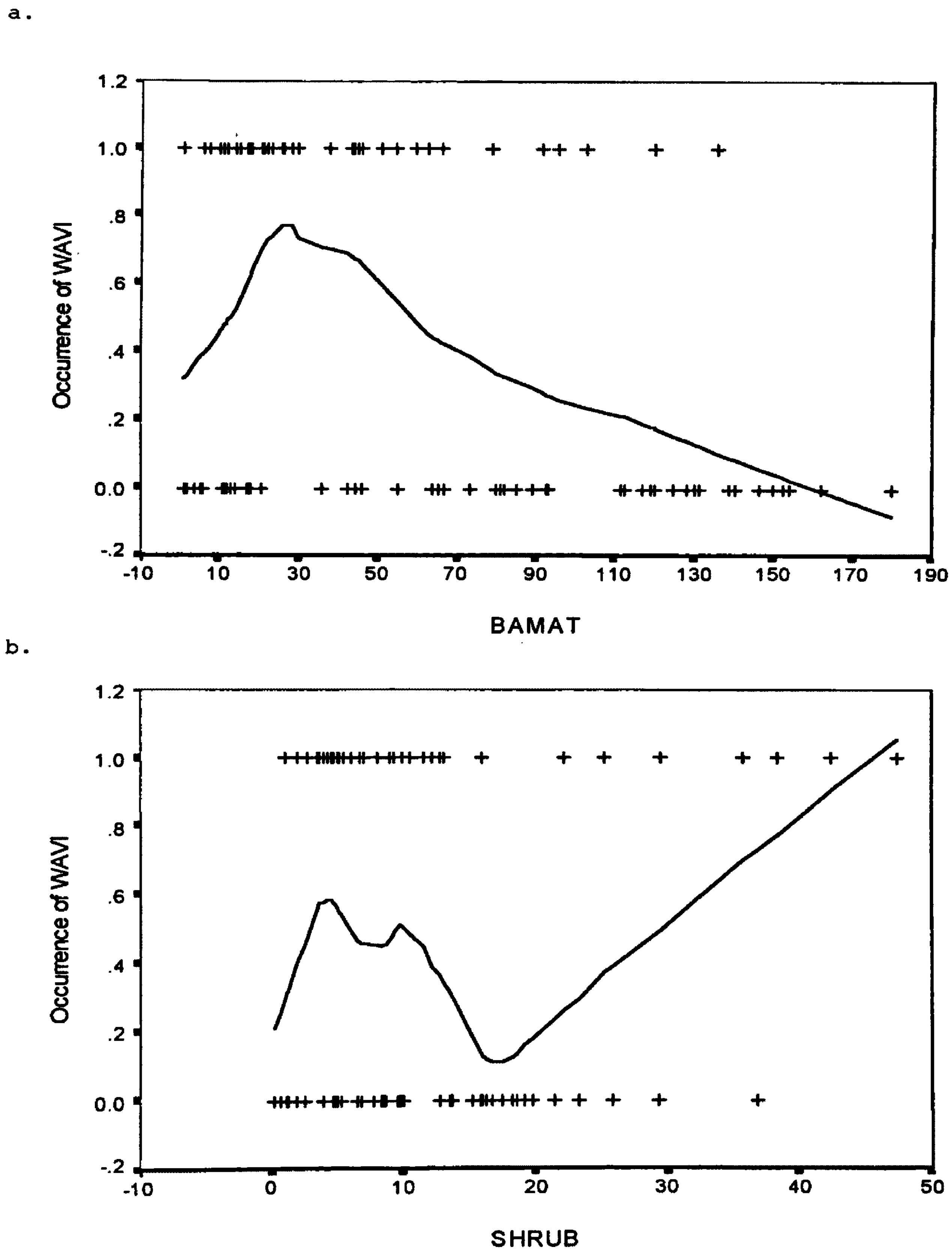


Figure 22. Univariate relationships of the Warbling Vireo with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) percent cover of understory vegetation (SHRUB)

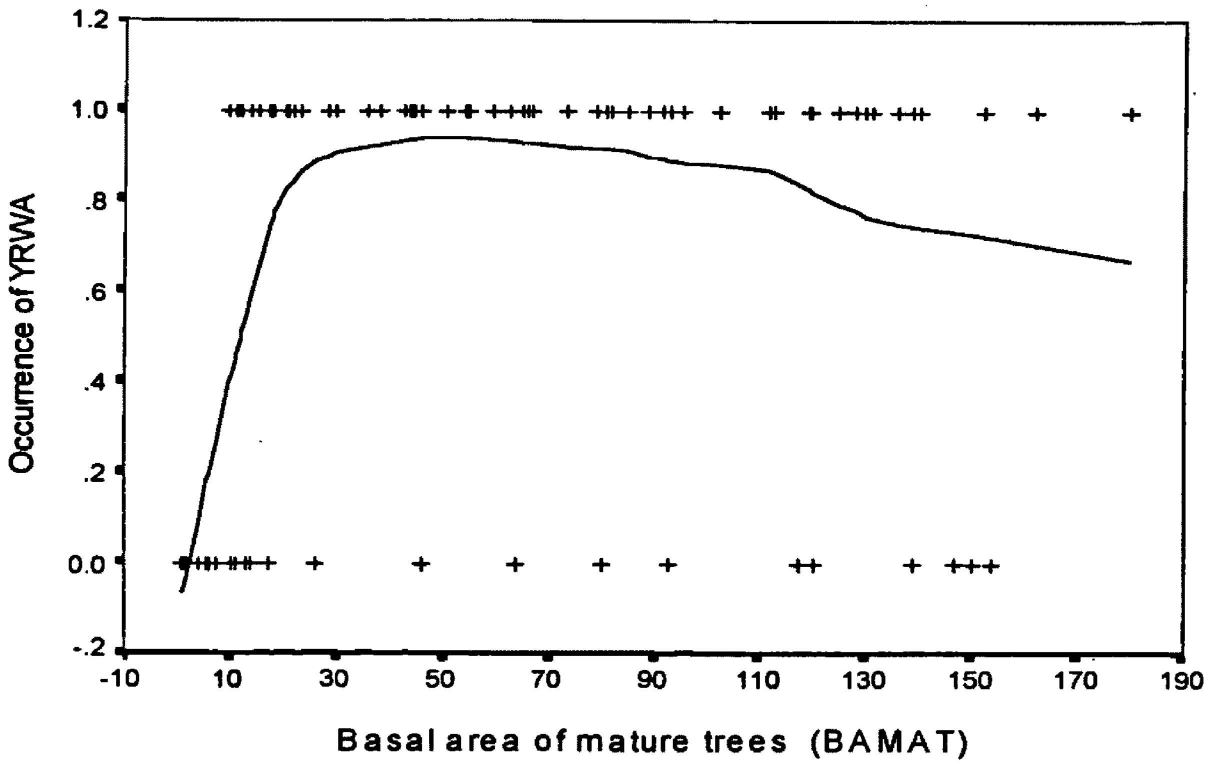
throughout most of the data was essentially flat. The few sites with very dense deciduous shrubs had numerous Warbling Vireos, so a consideration of abundance data using Poisson regression may indicate a stronger relationship.

Yellow-rumped Warbler

The univariate screening for the Yellow-rumped Warbler suggested that both the size and density of mature trees were important variables. This is to be expected for a species that nests and forages in the coniferous canopy (Ehrlich et al. 1988). The multivariate model chosen by stepwise backward elimination (Table 5) included the basal area of mature trees (BAMAT), as a unimodal relationship, and the density of large trees. A unimodal relationship with the proportion of trees that were larch (LAOC) was also included in the model, although an all-possible-subsets procedure indicated that the model without the quadratic term would be equally good. I included the quadratic term because it was highly significant in the univariate relationship (Figure 23b); however, a model without this term would be more parsimonious, and the quadratic relationship was apparently due to the absence of this species in the four larch seed-tree sites.

If canopy volume is important to this species, it may seem strange that they were most likely to be found at intermediate levels of BAMAT. However, the decline in probability of occurrence at high BAMAT was not strong (Figure 23a), and this plot suggests that the species was generally ubiquitous above a minimal threshold (it was absent on all of the 8 sites below BAMAT = 10). If low tree density was the reason this species was not present on the larch seed tree sites, then the quadratic term should not be included for LAOC, because without these sites the relationship was positive linear.

a.



b.

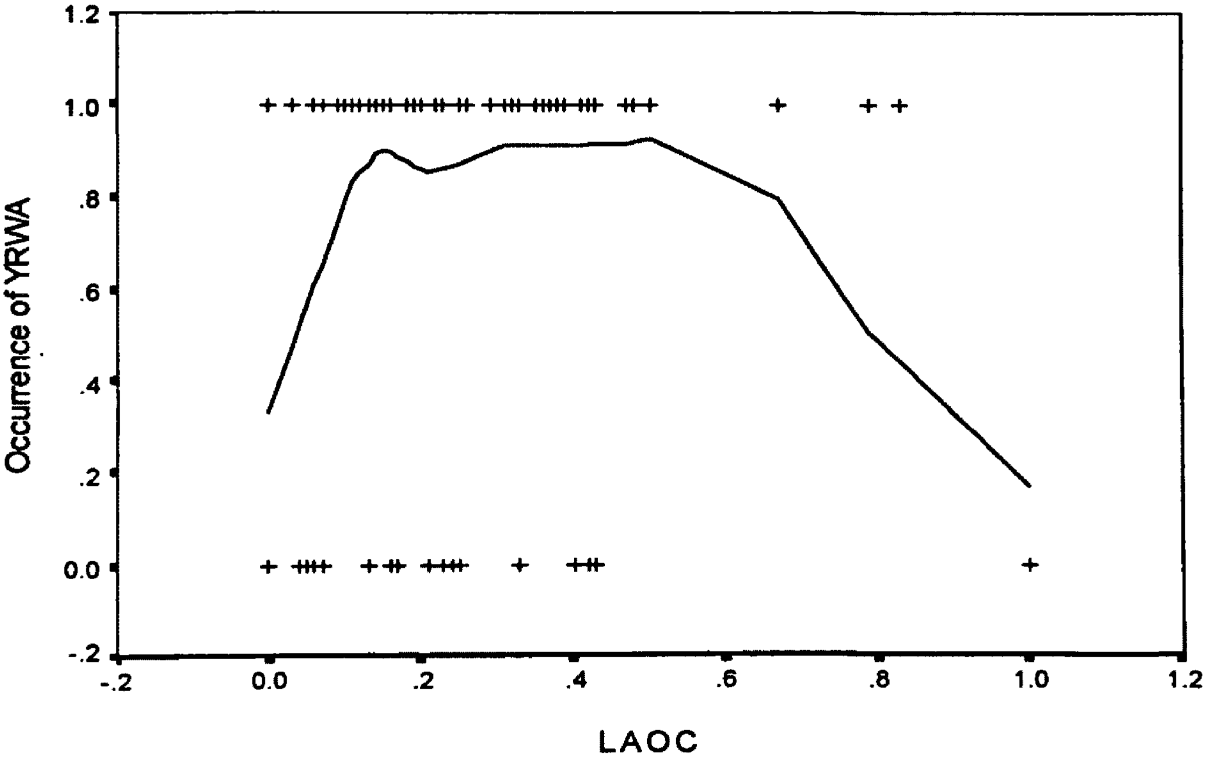


Figure 23. Univariate relationships of the Yellow-rumped Warbler with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) proportion of mature trees that were western larch (LAOC)

Townsend's Warbler

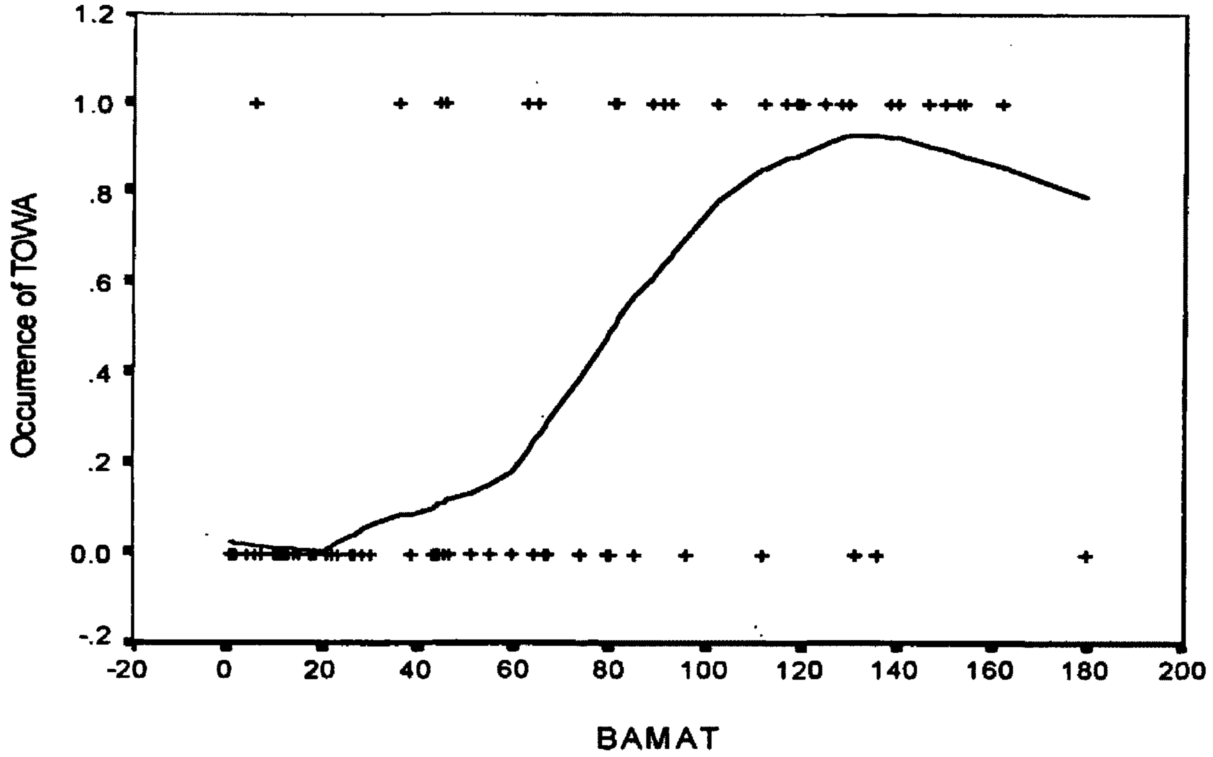
Like the Golden-crowned Kinglet, the Townsend's Warbler showed strong positive univariate relationships with every structural variable in the canopy and understory. The linear relationship with the basal area of mature trees (BAMAT) was the strongest positive relationship of any species with that variable (Figure 24a). Again, there was a quadratic term retained in the multivariate model for this species (Table 5), even though it was not significant in the univariate case ($p=0.08$), and it seemed due mostly to the absence of this species on the one densest site.

The negative relationship with LAOC was not strong in the univariate case ($p=0.052$), although it was retained in the multivariate model. It may have been in part a result of the positive association with mesic species (Figure 24b), and in part due to the several larch seed-tree sites, which were 100% LAOC and never had Townsend's Warblers, probably because of the open canopy. It is unlikely that a multivariate analysis can fully control for these intercorrelations.

Townsend's Warblers are usually found to be associated with more mesic forest types, especially cedar-hemlock and spruce-fir forests (Hutto 1995, in press). Within mixed-conifer forests, Mannan and Meslow (1984) found greater canopy volume of grand fir around TOWA nests than at random sites.

This species has also been found to be progressively less common in more open forests created by logging (Hutto, in press). Hansen et al. (1995) found this species to be positively related to tree density, and considered it to be a closed-canopy species, but unlike many other species it was common in structurally simple plantations as well as complex, old-growth forests. Others have also found the species in younger closed-canopy forests as well as older stages (Gilbert and

a.



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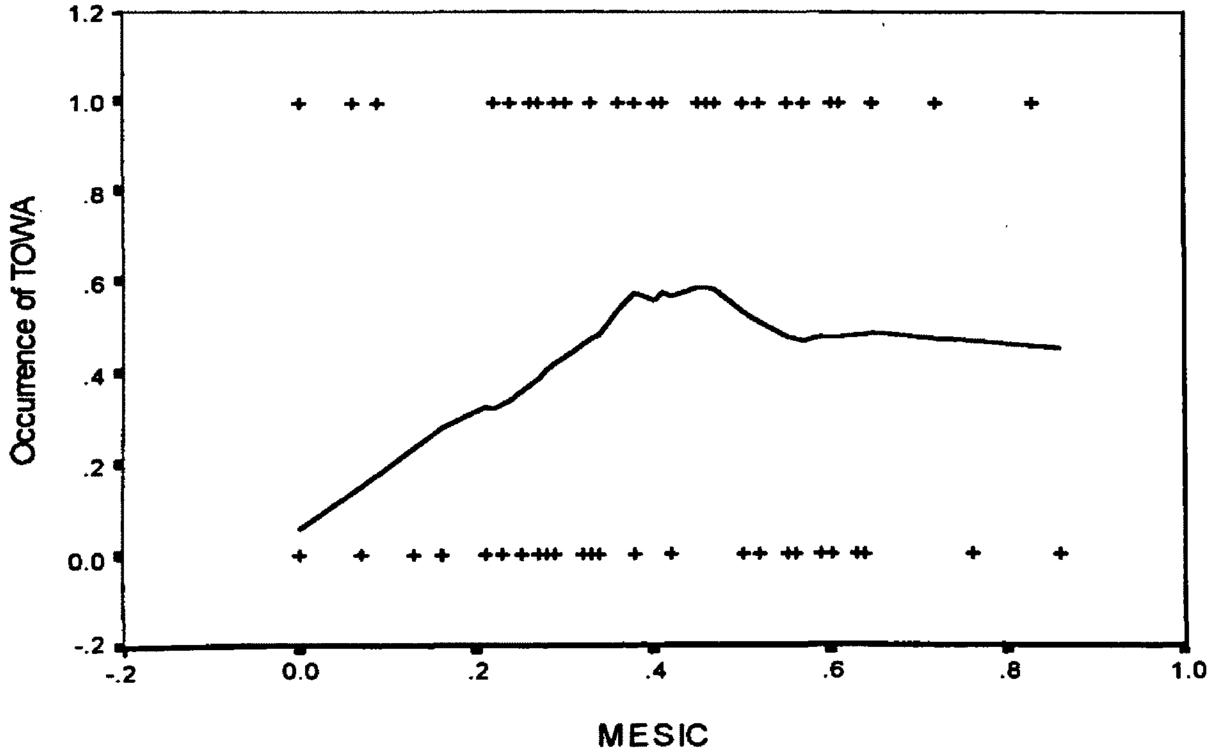


Figure 24. Univariate relationships of the Townsend's Warbler with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) proportion of mature trees that were mesic species (MESIC)

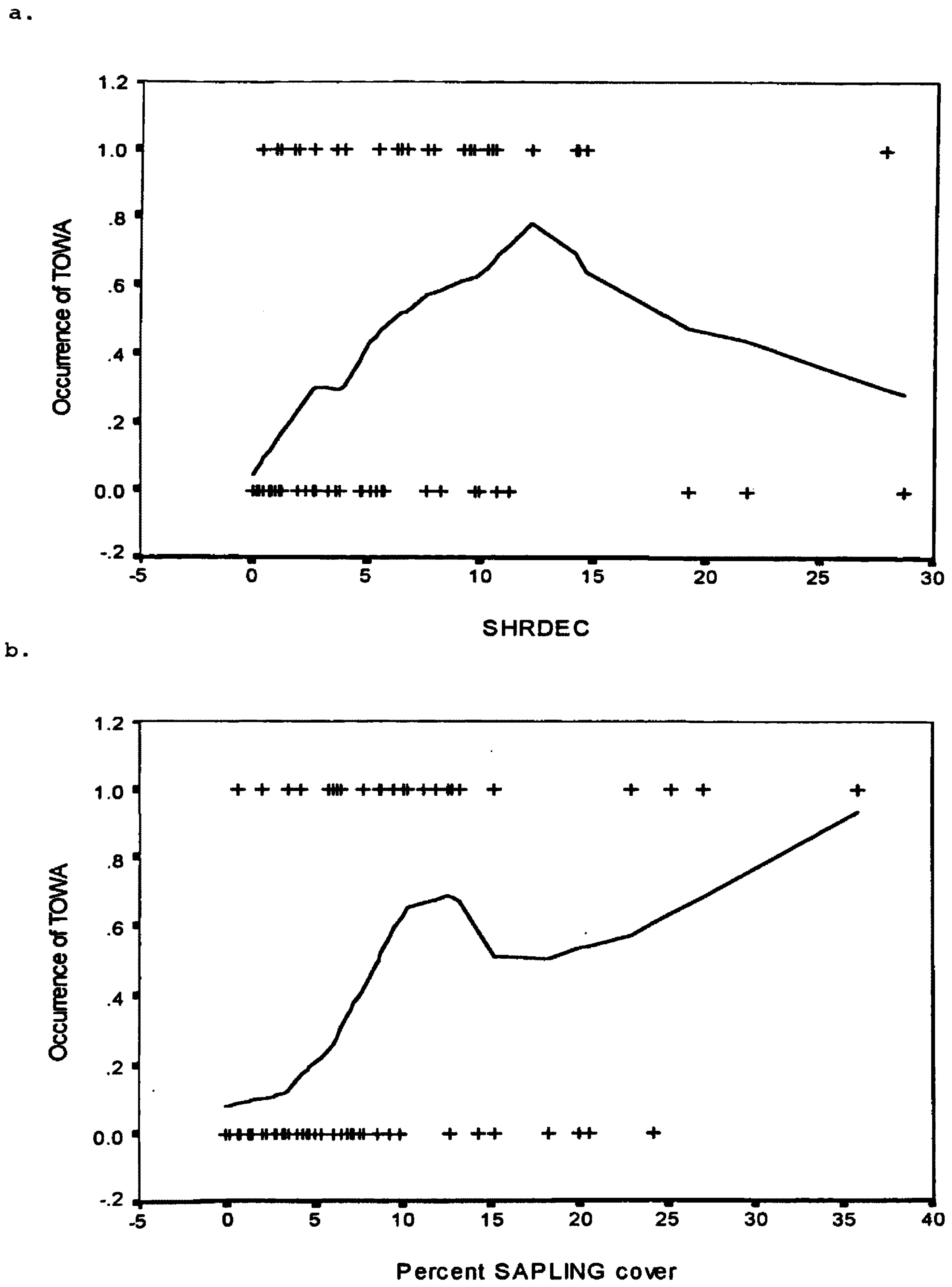


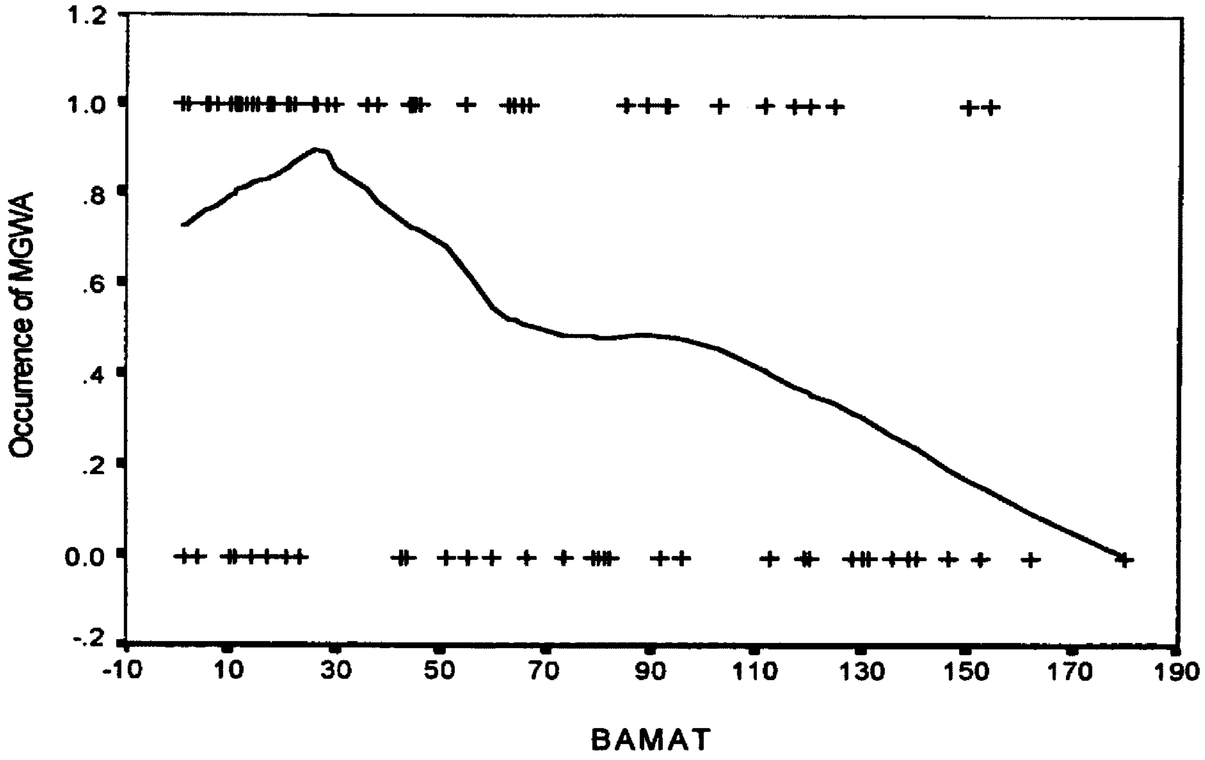
Figure 25. Univariate relationships of the Townsend's Warbler with two habitat variables: a) percent cover of deciduous shrubs (SHRDEC); b) percent cover of conifer saplings (SAP)

Allwine 1991), and Peterson (1982) found them most abundant in tall shrubs mixed with conifers and in sapling conifers. Although all of these studies were in more mesic Cascadian forests of the Pacific Northwest, it seems from my results that both deciduous shrubs and conifer saplings may be important habitat elements for this species (Figure 25).

MacGillivray's Warbler

The MacGillivray's Warbler generally favors open forests or clearcuts (Hutto, in press). This was reflected in this study by a strong negative relationship with the basal area of mature trees (BAMAT; Figure 26a). It is usually assumed that the association with more open areas is due to a requirement for a dense understory of deciduous shrubs (Pitoccheli 1995). However, in this study there was no significant relationship with the tall shrub layer, either in the univariate or multivariate cases. However, the cover of low bushes (BUSH) was included in the model (Table 5), although this was not significant in the univariate case. This species usually nests very low in shrubs or on the ground (Ehrlich et al. 1988), and it forages in this zone as well (Pitoccheli 1995). Most of the foraging observations in two separate studies were within 1 m of the ground (Hutto 1981, Morrison 1981). Since this is the zone represented by the variable BUSH in my study, this may be an important vegetation element. An examination of the data (Figure 26b) showed that this species was present on many sites with little or no tall shrub cover sampled. I recall that most of these sites had riparian elements nearby, or sometimes actually on the site. Other sites probably had small patches of shrubs that were not sampled. It may not take very many shrubs for a site to be occupied by at least one MacGillivray's Warbler. An analysis of abundance data may indicate

a.



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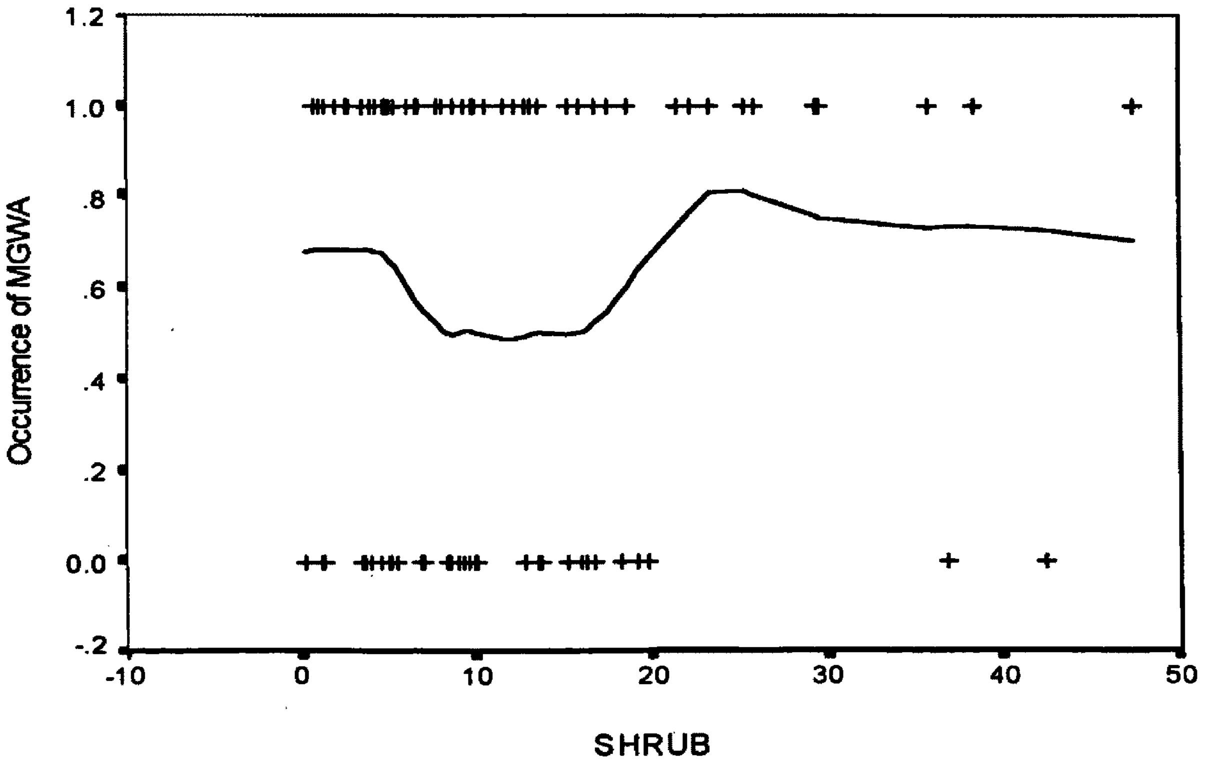
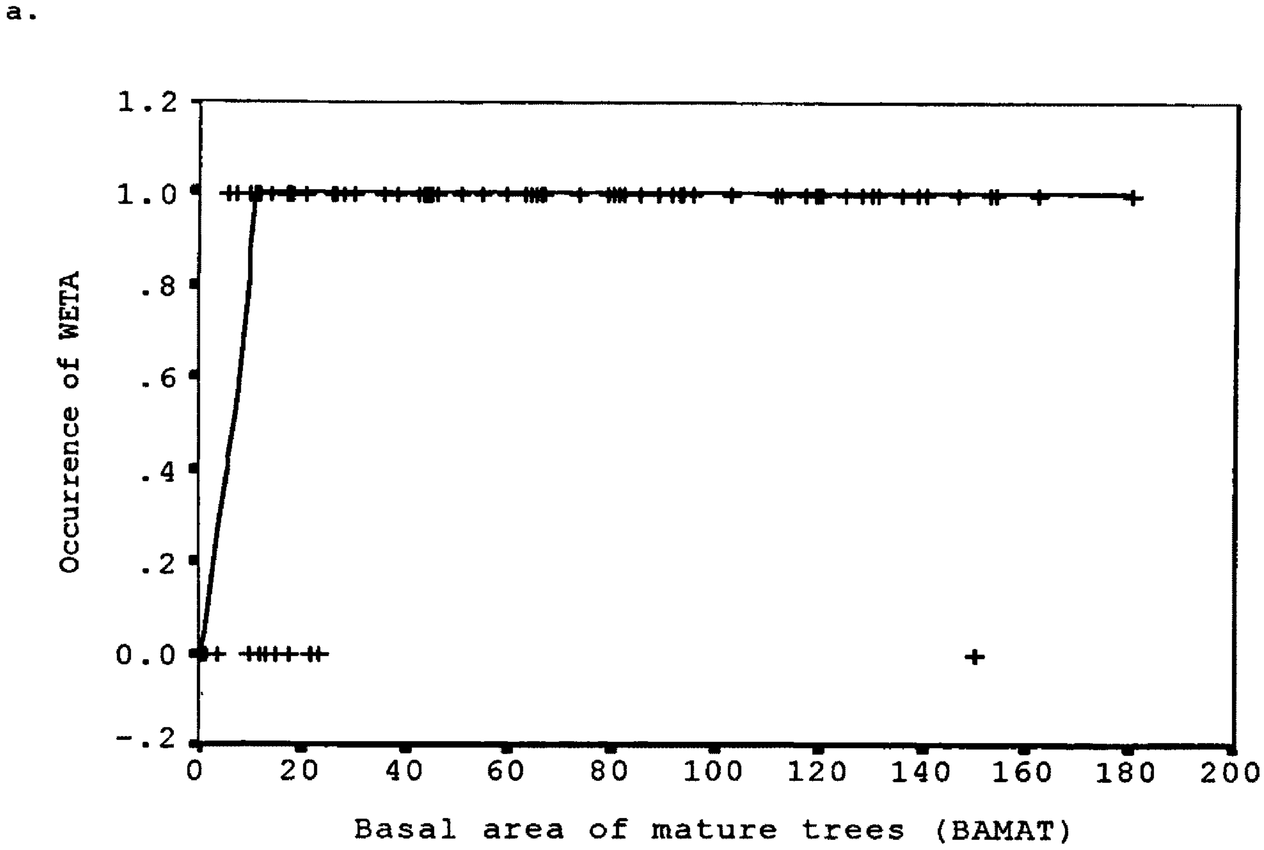


Figure 26. Univariate relationships of the MacGillivray's Warbler with two habitat variables: a) basal area of mature trees (sq ft/acre; BAMAT); b) percent cover of understory vegetation (SHRUB)

a stronger advantage of increasing shrub cover for populations of this warbler, and of course the relative reproductive success on these sites is not known. In fact, a preliminary analysis using Poisson regression has shown that the abundance of this species was positively related to SHRUB cover.

Western Tanager

The Western Tanager was present in one year or the other on 73 of the 86 study sites. With only 13 unoccupied sites to work with, the logistic regression models may be suspect. However, the occurrence of the Western Tanager was associated with most of the habitat variables in the univariate tests, generally indicating a preference for denser vegetation of all types. Stepwise backward elimination and forward selection produced the same multivariate model (Table 5). The positive relationship with the basal area of mature trees (BAMAT) was very clear (Figure 27a). Tanagers were nearly absent on sites with the lowest tree densities, and were nearly ubiquitous at higher densities. There was only one site with BAMAT > 25 sq. ft/acre where this species was absent (Figure 27a). It is, therefore, unclear why the quadratic term for BAMAT was included; perhaps this one site had a strong effect because there were so few total absences. Tanagers also seemed to respond to elements of the understory. The positive relationship with low bush cover (BUSH) was highly significant (p = .001). Tall understory cover (SHRUB), which had a significant quadratic relationship in the univariate case, was not retained in the multivariate model. However, when I tried the separate components of tall understory cover (SHRDEC and SAP), a linear relation-ship with SAP (conifer sapling cover) was retained in an alternative multivariate model, under both backward and forward selection. I do not know if the understory layer has a direct



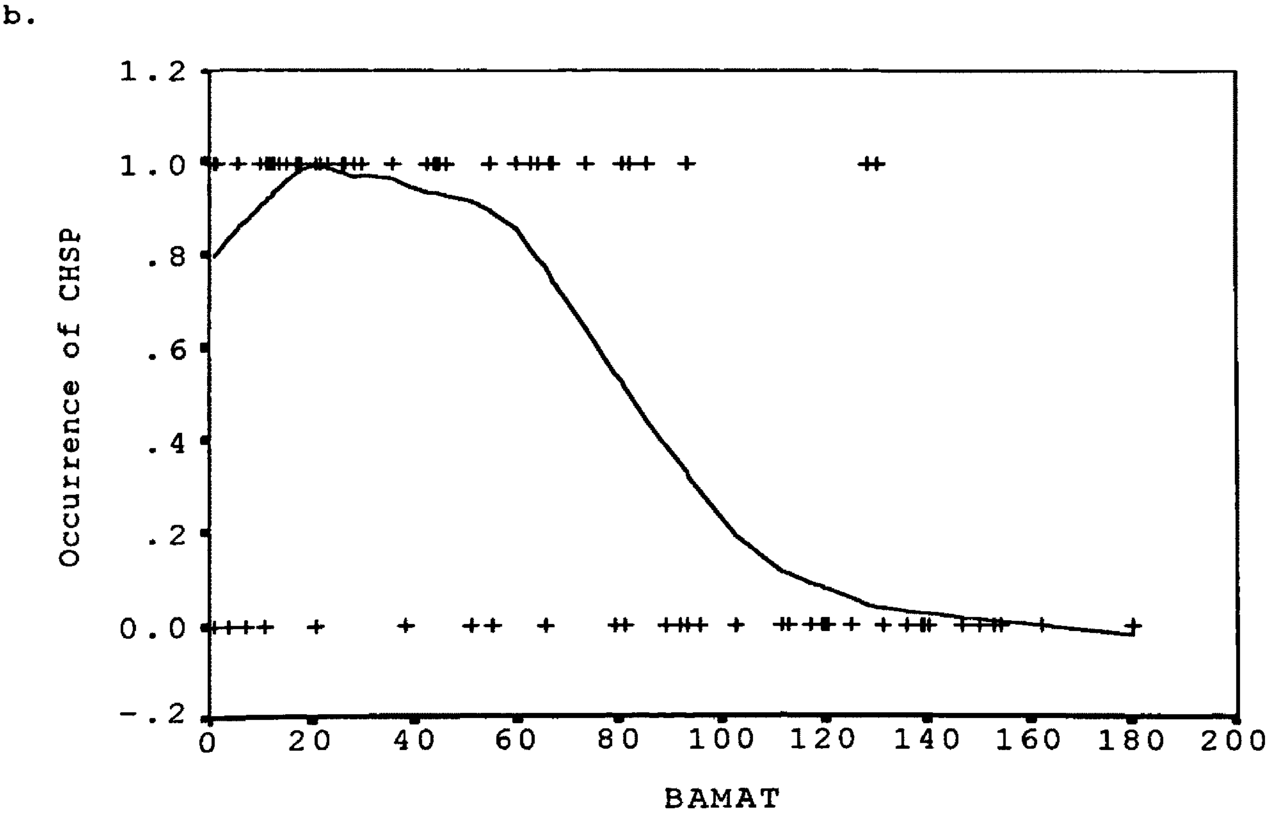


Figure 27. Univariate relationships of two species with the basal area of mature trees (sq ft/acre; BAMAT): a) Western Tanager (WETA); b) Chipping Sparrow (CHSP).

biological relevance to this species, although I have observed tanagers foraging in low bushes on several occasions.

There was some indication of a response of this species to tree species composition. A unimodal relationship with the proportion of mature trees that were MESIC was included in the multivariate model, and a positive relationship with Douglas-fir (PSME) was nearly retained (p=.07); it may be argued that the latter should be included in the model if the goal is to provide the best predictive ability. Tanagers are often considered to be more associated with drier forest types, especially ponderosa pine (Hutto, in press). In this study, this species was positively associated with PINE in 1993 only. This relationship is of potential interest, although the species is certainly common in all conifer types.

Chipping Sparrow

In the univariate tests, the Chipping Sparrow showed strong negative associations with all sizes of trees and with mesic species. The negative association with the basal area of mature trees (BAMAT) was one of the strongest for any species (only the Northern Flicker had a stronger univariate relationship with this variable). When this was entered into the model, no other variable was still significant (Table 5). This species was absent on only four low-density sites (Figure 27b), but this was enough to make the quadratic term for BAMAT nearly significant (p = .09). Basically, this species was more likely to occur where there were fewer trees.

The Chipping Sparrow responded positively to most forms of cutting in many other studies in the Rocky Mountains (Hejl et al. 1995). In the Forest Service monitoring program (Hutto, in press), the species was most common on partially-logged stands and uncut, ponderosa pine stands. It was much less likely to occur in uncut, mesic forests, with intermediate frequency in clearcuts and mixed-conifer stands. All of this is in agreement with the common perception that this is a bird of open, pine forests. It also suggests that the possible negative relationship with SPFIR in this study may have been real. The failure to find an association with PINE was apparently due to the merging of lodgepole and ponderosa pine into this category. Although I did not usually screen a variable for ponderosa pine by itself (because of the large number of zeroes), it does appear to be a significant predicter of Chipping Sparrow occurrence (with or without BAMAT in the model).

Dark-eyed Junco

The Dark-eyed Junco was the most abundant and widely distributed species, not only in both years of this study, but also in a widespread monitoring program in the region (Hutto, in press). They were present in one year or the other on all but 2 of the 86 study sites in my combined-year data set. Therefore, there was no power to perform any analyses with these data. Instead, I will briefly discuss a model based on the 1993 data only, when this species was detected on 72 of 88 sites visited that year. This model is not reported in Table 5. With only 16 unoccupied sites from which to draw conclusions, this model may not be generalizable.

Juncos are generally more likely to occur on open sites, and there was a negative relationship with the basal area of mature trees (BAMAT) in this study. However, the species was also present on the 5 sites with highest BAMAT, so a positive quadratic term was significant. Juncos were not very abundant on the dense sites, however; when abundance, rather than occurrence, was plotted against BAMAT, it showed a monotonic negative relationship. The univariate relationships for Juncos indicated a positive response to ground cover, as expected for this ground-nesting species, and a negative response to shrub cover.

However, since ground and shrub cover were negatively correlated ($r = -0.45$), only shrub cover was retained in the multivariate model. The species seems more likely to occur on open sites with lower understory cover and higher ground cover. However, without more extensive sampling or measures of reproductive success, it may be difficult to better illuminate the habitat relationships for this widespread species.

Pine Siskin

The Pine Siskin had the fewest significant univariate relationships of any species. The model reported in Table 5 was produced by both backward and forward selection, although there was a problem with the modeling of canopy height, such that the program was unable to calculate a standard error. The unimodal relationship with canopy height was strong ($p < .005$; Figure 28). The model may be appropriate for this data set, although it is unclear what it says about the species. There is no apparent biological reason for a preference for intermediate canopy heights, and an association with mesic forests would be unexpected for this species. In fact, it appeared to be more common in drier forest habitats throughout Montana (Hutto, in press), although it was generally widespread throughout all forest habitats. Because this is a wide-ranging, opportunistic species, local habitat variables may not be sufficient to understand its distribution, and the model presented here is probably not very useful for future predictions. Local abundances may be determined more by seed crops (Bent 1968) and insect outbreaks (Hunt 1989).

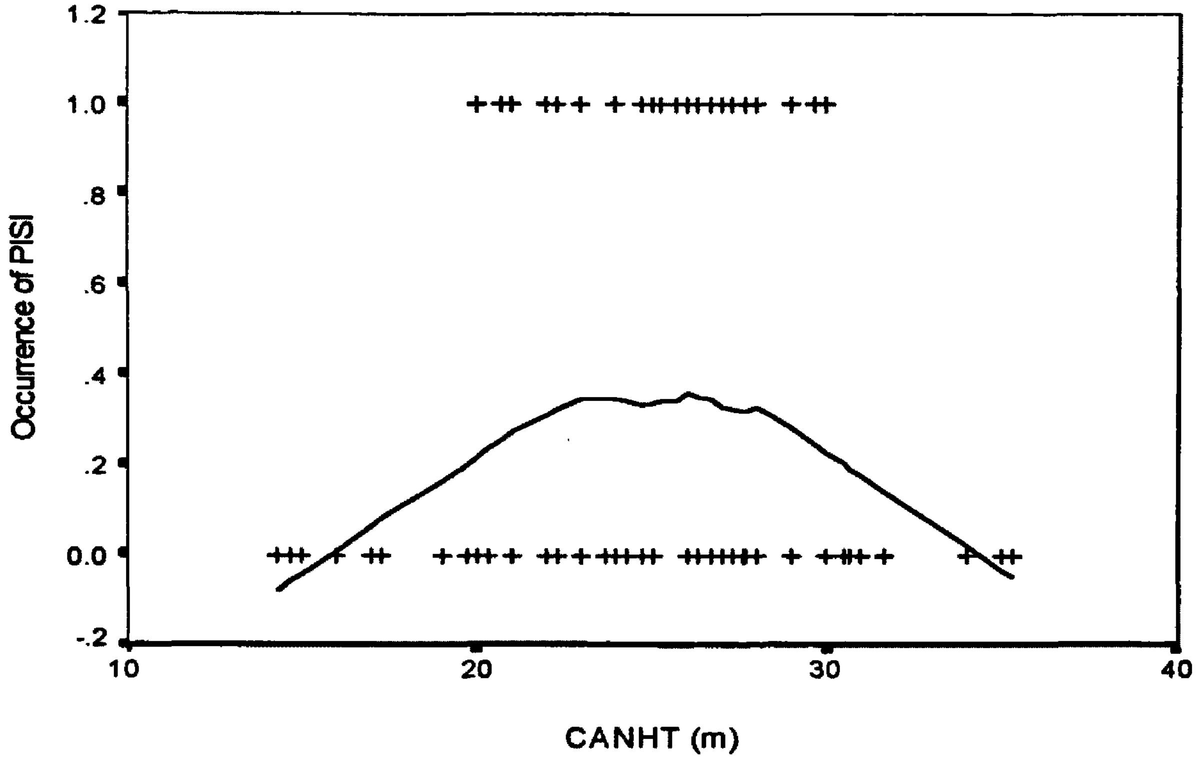


Figure 28. Univariate relationship of the Pine Siskin with typical canopy height (CANHT)