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THE RELATIONSHIPS AMONG VEGETATION STRUCTURE,
WESTERN SPRUCE BUDWORM DENSITY,
AND AVIAN COMMUNITY COMPOSITION

By

Peter D. Hunt

B.S., Cornell University, 1986

Presented in partial fulfillment of the requirements

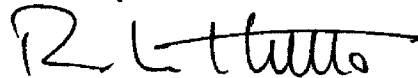
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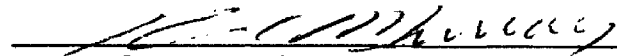
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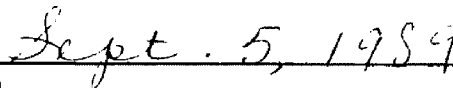
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The Relationships Among Vegetation Structure, Western Spruce Budworm Density, and Avian Community Composition

Director: Richard L. Hutto *RH*

I studied the relationship between local density of western spruce budworm (*Choristoneura occidentalis*) and the composition and diversity of western Montana bird communities. Fourteen study sites were chosen to include known variation in budworm outbreak intensity. I sampled bird and budworm populations during the summers of 1987 and 1988. All sites were predominantly Douglas-fir, and vegetation characteristics were measured at all sites. Vegetation characteristics were strongly influenced by elevation and slope, with ponderosa pine being replaced by spruce and fir at higher elevations: Douglas-fir was present throughout. Budworm density was not strongly influenced by any vegetative or topographic variables. Regressions on three measures of bird community diversity indicated that vegetation was a far better predictor of species richness than was budworm density. In particular, numbers of bird species per site increased with increasing densities of spruce/fir, larch/lodgepole, and shrubs, and decreased with increasing densities of ponderosa pine. Vegetation showed similar explanatory power when species were grouped into taxonomic/foraging guilds. Abundances of the more common bird species were also strongly influenced by the elevation/vegetation gradient, as well as by shrub density. Some species showed significant responses to budworm density, but many of these responses were negative, suggesting potentially spurious correlations. As a result, positive responses are viewed with a certain degree of skepticism, since they were both fewer and restricted to species whose habitat preferences may have confounded the analysis. Only one species, the Pine Siskin, showed evidence of responding numerically to budworm outbreaks, and further research into this species' actual use of budworm infested stands would be required before such a response could be reliably concluded. In addition, it was determined that budworm populations may not have been high enough to elicit avian population responses. On a broad, regional scale, vegetative variation was therefore more important than variation in food supply, with respect to the composition of bird communities.

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INTRODUCTION

The question of whether food supply is an important factor in determining avian community composition has received considerable debate in recent years. One side of the argument holds that because bird populations consume only a very small proportion of the food available to them (Lack 1954), food must be superabundant with respect to the needs of breeding birds. Thus, only under conditions of ecological stress, or "crunches", when food supplies are severely depressed, would one expect populations to be limited by their food supplies (Wiens 1977). The effect of "food crunches" has been confirmed in studies of wintering sparrow communities (Dunning and Brown 1982, Pulliam and Dunning 1987). In these studies, bird population sizes and species diversity were not influenced by changes in food supply unless food was severely limited (i.e., in years of very low summer rainfall). Thus, most studies of factors that determine avian community composition have down-played the importance of food supply and have emphasized the importance of the structure and species composition of the vegetation (MacArthur and MacArthur 1961, James 1971, Holmes and Robinson 1981, Rice et al 1984, Swift et al 1984, and many more). Such studies have found that vegetation characteristics can be important in predicting what bird species are present in area.

There is also evidence that food supplies can be limiting at the population level. In a study of Galapagos finches, drastically reduced food supplies due to drought resulted in population declines from deaths, emigration, and reproductive failure (Grant and Grant 1980). In addition, most species converged in foraging behaviors when food was limiting.

However, food can still be an important limiting factor when at high levels if a species has specialized food requirements or feeding behaviors. In such cases, species have been shown to respond numerically to increases or decreases in their food supply. Most numerical responses apply to birds feeding upon highly variable and unpredictable food sources. For instance, irruptive bird species have long been known to occur in areas of relatively high food density, given that food supplies in their normal geographic range are very low (Bock and Lepthien 1976, Widrelecher and Dragula 1984). Some irruptive species, notably crossbills (*Loxia* spp.), frequently breed after or during food irruptions, even when they are often far outside their normal breeding ranges (Catley and Hursthouse 1985). Such breeding is facilitated by high cone production within the breeding sites; and without a good cone crop the crossbills would presumably not be present in the community. In Europe, superabundant birch seed crops have been shown to be important to Redpolls (*Cardulis flammea*: Enemar et al. 1984), and Bramblings (*Fringilla montifringilla*: Jenni 1987), with both species showing dramatic population increases in high mast years.

In addition to seed crops, other major food sources that can show high variability are insect populations, especially forest "pests" that have a tendency to occur in outbreaks. Since the majority of birds feed primarily on insects, and

virtually all feed insects to their young, one would expect some bird species to respond numerically to insect population fluctuations. Such a numerical response has been shown in the Brambling, which was able to double its population during a mass outbreak of the moth, *Epirrita autumnata* (Enemar et al 1984).

In North America, various species of budworm (*Choristoneura*) are important defoliators in northern coniferous forests, and like other such insects, can show considerable variation in population densities, among both sites and years. Because of their tendency to form outbreaks, these species are considered serious pests throughout their range. Consequently, a great deal of primarily descriptive literature exists pertaining to bird predation on various species of budworm (Gage et al. 1970, Torgersen and Campbell 1982, Takekawa and Garton 1984). The intensity of predation is variable, but birds have been reported to consume up to 87% of the budworm population (Crawford et al 1983). However, it is frequently noted that bird predation is largely ineffective at very high budworm densities (Crawford and Jennings 1989).

Some insectivorous birds appear to be more important in budworm control than others, notably the Evening Grosbeak (*Coccothraustes vespertinus*) and several species of wood warblers (Morris et al 1958, Blais and Parks 1964, Morse 1978). The association of these birds with budworm may be so high that their local populations are greatly affected by changes in budworm density. Evening Grosbeaks were observed to increase in numbers during an outbreak in Quebec, and to decrease to pre-budworm levels after the outbreak died down (Blais and Parks 1964). An occurrence of polygyny in this species (Fee and Bekoff 1986) was also apparently tied to heavy infestation of budworm, suggesting that abundant

food supplies facilitated a greater than normal reproductive output. Similarly, populations of the Bay-breasted Warbler (*Dendroica castanea*) have been shown to track budworm populations closely (Morris et al 1958, Morse 1978). Both the Bay-breasted Warbler and its close relative the Cape May Warbler (*D. tigrina*) are often stated as being more common in areas with than in areas without budworm outbreaks (MacArthur 1958). Finally, Zach and Falls (1975) found that Ovenbirds (*Seiurus aurocapillus*) reduced territory sizes and increased territory packing when budworm was abundant, suggesting that a greater population size was supported. There was also some evidence that Ovenbird clutch size increased under conditions of high budworm density.

In addition, birds may respond functionally, rather than numerically, to changes in food supply. This has been shown for migrant warblers, which increased their foraging rates and had a greater food intake in areas with greater food abundance (Graber and Graber 1983). Ovenbirds were observed to forage higher in the foliage than normal when budworm populations were high (Zach and Falls 1975). Such functional responses also have been observed at the community level, with several species apparently responding in similar ways. After spraying to reduce arthropod abundance, Hunter and Witham (1985) found that birds shifted their foraging to unsprayed trees and became more generalized in foraging location. However, this pattern was not observed when spraying was more extensive and patches of unsprayed forest did not exist, suggesting that when birds are unable to escape in space, they do not modify their behaviors to any great extent.

Functional responses to budworm can also be detected at the community level, and are the result of several species' populations responding in the same fashion. Almost all species studied by Crawford and Jennings (1989) responded to higher budworm densities by consuming greater numbers of budworm larvae, as evidenced by stomach analyses. As a result, the insectivorous component of the avian community could be said to have shifted its foraging tactics.

Finally, whole communities may respond numerically to variations in food supply. This possibility is supported by work done by Brush and Stiles (1986) in the New Jersey pine barrens. They found that insect abundance was a better predictor of bird abundance than were vegetation characteristics. Hutto (1985a, 1985b) also found total bird abundance to be correlated with insect abundance, both overall and with respect to foraging height, and in different seasons and geographical locations. Outbreaks of the moth *Heterocampa guttivitta* resulted in population increases in several species of vireos and warblers in New Hampshire (Holmes et al. 1986), suggesting that such community-level responses may be limited to those species that actually forage on the food supply in question. Other than the studies cited above, little has been done relating avian community structure (as opposed to behavior) to food supply, but examples do exist in the literature for other groups of terrestrial vertebrates. Abramsky (1988) found that desert rodent communities became more speciose as productivity (itself a measure of the food available) increased, although there were limits imposed by the amount of cover. Abramsky's study further demonstrates that both food and vegetation may exert important influences on community structure.

Therefore, it would appear that evidence exists to support the hypothesis that food variability can be important in most years, and that populations can respond to increases as well as decreases in their food supplies. In particular, birds are able to respond to prey bases that are highly variable in space and time, such as forest defoliators, and such responses can be both numerical and functional.

With particular reference to the spruce budworm, some species (e.g., Evening Grosbeak and some wood warblers) may, to a certain extent, be budworm specialists. It is unclear to what extent such species might influence the composition and diversity of the avian community as a whole. Numeric responses to budworm may be less frequent than functional ones, since Crawford and Jennings (1989) found population increases in only two species, but increased budworm consumption in several. Thus, although budworm may be important, if not limiting to some species, on a community-wide level the effects of high prey densities may not be reflected in numeric terms.

The presence of functional and numerical responses to budworm outbreaks by birds may prove important in the field of forest management. Birds have long been recognized as important in controlling budworm (Gage et al. 1970, Torgersen and Campbell 1982, Crawford et al. 1983), but little research has been directed toward the question of how critical budworm is to birds. If, in fact, some species are highly dependent upon budworm outbreaks, they could be considered highly vulnerable to changes in budworm populations. In particular, budworm control measures, such as pesticide spraying, could have negative effects on these species. In compliance with the National Forest Management Act (1976), the Forest

Service is responsible for maintaining viable population sizes of all vertebrate species. Thus, information on the relationship between budworm and birds may prove useful to forest managers. In fact, it has been suggested (Crawford and Jennings 1989) that current management systems need to be modified to allow for the maintenance of bird diversity, which in the long run could result in reduced expenditures for budworm control.

The purpose of this study was to investigate the relationship between western spruce budworm (*C. occidentalis*) and the bird community within the coniferous forests of western Montana. Specifically, I addressed the following: (1) do any species respond numerically to variation in budworm density among sites, and (2) if any species shows a relationship, to what extent does that relationship influence the overall bird community composition?

METHODS

Due to time considerations, budworm densities varied primarily in space rather than in time, thus still allowing for comparisons between high and low levels of infestation. Despite its shortcomings, this approach, if adequately controlled, can yield conclusive and meaningful results, and is the same methodology used by Crawford and Jennings (1989).

Selection of Study Sites

Study sites were selected using maps of budworm occurrence prepared by the U.S. Forest Service. These maps were based on defoliation that was visible from the air, and indicated budworm infestation level as either non-detectable, light, moderate, or heavy. Using maps of the Garnet and Sapphire Mountains in western Montana, I selected a number of potential study sites in early 1987 and visited them to determine their suitability for study. Suitable sites were those that were predominately Douglas-fir, had enough area to set up a 1-km long transect, were relatively accessible, and appeared vegetatively similar to one another.

Twelve sites were eventually found during the 1987 field season, and selection was often hampered by inaccurate maps and inappropriate vegetation. Thus each site was only visited once for bird censusing in 1987. Two additional sites were chosen in 1988, and again other potential sites were found unsuitable

for various reasons. However, since most of the sites were already selected, I was able to visit each four times in 1988. The sites were located roughly in an east-west line stretching from near Avon, to Blue Mountain in Missoula (Figure 1). All satisfied my initial criteria for selection, and encompassed the complete range of budworm densities indicated on the maps.

Bird Censusing

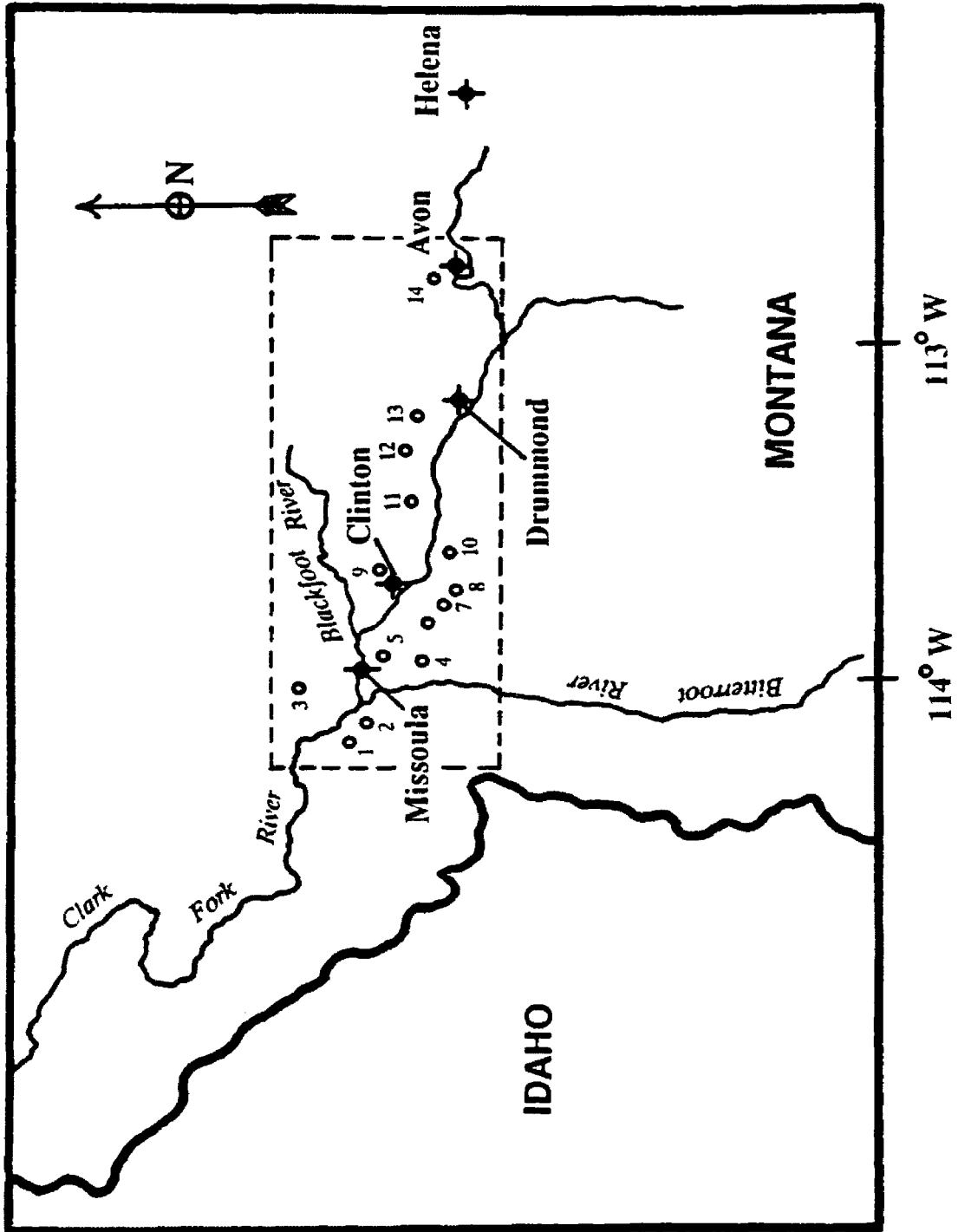
Bird communities were censused using a transect count method. During the period from early June to early July, 1 km long transects were walked at each site and all birds seen or heard were identified and counted. In addition, any species found on the site during the census period, but not actually recorded on the transect, was given a "+" on the data sheet. Censusing was limited to the time period between 0600 and 1200 hr, and when possible several sites were visited each morning. One transect was completed per site in 1987, and four in 1988. The 1987 counts, and the mean of the 1988 counts, were used as an index of abundance for a given bird species when sites were to be compared.

Budworm Sampling

Budworm density in each stand was estimated by clipping three 30 cm branch tips from the mid-crowns of a number of trees at each study site. The number of trees sampled in 1987 was 10 per site, whereas 20 trees were sampled in heavily invested areas in 1988 in an effort to reduce variance in the budworm density estimate. These clippings were then shaken into a bag, and the budworm

Figure 1. Location of study sites. Numbering: 1 - Blue Mountain High, 2 - Blue Mountain Low, 3 - Snowbowl, 4 - Miller Creek, 5 - Pattee Canyon, 6 - West Schwartz Creek High, 7 - West Schwartz Creek Low, 8 - Lower Schwartz Creek, 9 - Wallace Creek, 10 - Welch Gulch, 11 - Tenmile Creek, 12 - Mulkey Gulch, 13 - Rattler Gulch, 14 - Luke Mountain.

LOCATION OF STUDY SITES



larvae and pupae collected and counted. In 1988, I also counted other lepidopteran larvae, considering them a second category labeled "other". This method of estimating budworm density is well established (Carolin and Coulter 1972, Srivastava et al. 1984, Foltz and Torgersen 1985), and has been found to be as accurate as more tedious methods that involve transporting whole branch samples back to the laboratory for counting (Foltz and Torgersen 1985). Although the number of budworm per branch and the number per branch mass are well correlated (Hutto 1987), the branch samples from each tree were weighed so that a measure of budworm density per unit branch mass could be calculated for each stand. In order to retain comparability among sites, it was necessary to sample all the stands at the same time. Thus, all sampling was done in a three to four day period in early July, when all bird censusing had been completed.

In order to compare budworm densities between this and other studies, it was necessary to make crude conversions of densities per kilogram to densities per hectare and acre. To do so, I first converted numbers per kilogram to numbers per square meter of foliage using the data of Hutto (1987). These values were then converted to numbers per square foot of foliage. Morris (1955) estimated that 80 and 105 year old stands of spruce and fir contain 200,000 and 120,000 square feet of foliage per acre, respectively. Thus, since most trees on my study sites are in the 80 to 100 year age range, I used both of Morris' values to obtain budworm densities per acre for all sites. These values could then be converted to numbers per hectare for later comparisons.

Vegetation Measurement

Vegetation characteristics were recorded using a point-centered quarter method (Cottam and Curtis 1956). Sampling was done along the same transects used for bird censusing, with 10 points spaced roughly 100 m apart. Since many transect routes were along roads, points used for vegetation sampling were located at least 20 m to the side of the actual transect. This procedure allowed for a more accurate representation of the vegetation characteristics of each stand as a whole, rather than giving disproportionate weight to characteristics of the roadside edge. Similarly, since the main objective of the vegetation sampling was to characterize the coniferous habitat, points that fell in riparian areas were relocated. When present at a site, riparian habitat was limited in distribution, and thus not a major component of the stand.

At each of the 10 points, the following data were recorded: distance from center, diameter at breast height, and species of the nearest tree in each of four quarters around the sampling point; distance to and species of the nearest sapling or shrub in each quarter; and canopy cover. The latter was estimated by looking straight up through a 4 cm diameter tube at the canopy and estimating the percentage of the field of view occupied by vegetation. Other site characteristics such as elevation, slope, and aspect were recorded at every other sampling point. The distances and tree sizes recorded at each point were then used to calculate tree densities, dominance values, and importance values for each tree species at each site.

Statistical Analysis

Three criteria were used to select bird species for analysis. Initially, a number of species that were recorded from two or fewer sites, or that were recorded irregularly (mean number < 1) at all sites, were discarded. Of the remaining species, any that were still recorded at less than 50% of the sites were discarded if (1) they were more typical of riparian habitat at the edges of sites, or (2) they showed no apparent pattern in abundance. The species discarded in this manner were judged to be too rare or irregular to be used in the multivariate analyses which were to follow. The species remaining were thus those recorded in at least 50% of the sites. All further references to "mean abundance" refer to the mean abundances of these widespread species. Data on bird abundances and budworm densities were first tested with an ANOVA to determine if the study sites did indeed differ in these parameters. Vegetation data could not be tested in this way because the point-centered quarter method does not yield several values from which a mean can be calculated. In addition, the densities of a given tree species were transformed into relative densities by dividing them by the total tree density. In this way I hoped to get a more accurate picture of any effects of tree species composition. Both measures of tree density were used in analysis.

Given that the sites differed in their bird populations, further analysis was undertaken to determine which factors were most important in contributing to differences among stands. Initially, correlation coefficients were calculated between all possible pairs of variables. High values in the correlation matrix were then tested for significance using linear regression. This phase of the analysis also served to determine which of the several site characteristics were most

important, thus allowing reduction of the number of variables involved in analysis. The next step involved calculating partial regression coefficients for use in path analysis (Sokal and Rohlf 1981). Partial regression is a multiple regression carried out after all dependent and independent variables have been standardized. This analysis yields standard partial regression coefficients (SPRCs), representing the relative strengths of the effects of the individual independent variables on a given dependent variable. SPRCs can then be used in path analysis, in which causal relationships are implied through a model of interrelationships among variables. This model is developed beforehand for the system involved, and the SPRCs are used to assess the strengths and significances of the several variables.

Part of the initial analysis involved categorizing bird abundances as common (2), uncommon (1), or rare (0), and placing these values in a species by site table. The rows and columns of this table were then rearranged until a pattern became apparent, a procedure known as the Braun-Blanquet approach (Gauch 1982). Once a pattern was discovered, I was able to determine what site characteristics, if any, were responsible for large-scale changes in bird abundances, and then use this information in the more rigid statistical procedures.

Other avenues of investigation involved grouping species into foraging guilds, on the assumption that some guilds would be more responsive to budworm density than others. Guild abundances were calculated by simply adding up the abundances of all the species in a guild. Correlation and partial regression coefficients were calculated for the guild abundances in the same way as for species abundances. Finally, I used clustering to group species and guilds based on similarities in their partial regression coefficients, under the assumption that

species which responded to habitat variables in similar ways would cluster together and possibly shed light on the factors that were most important in community organization.

RESULTS

Bird Abundance

Fifty-six species of birds were recorded over both field seasons and all study sites (Appendix 1). Of these, 34 occurred on fewer than 7 (=50%) of the sites in either year and were not considered in any further analysis. In addition, three species [Common Raven (*Corvus corax*), Northern Flicker (*Colaptes auratus*), and Red Crossbill (*Loxia curvirostra*)] were recorded at 9 or 10 sites in 1988. However, since these species were somewhat sporadic and because they are not known to consume budworm, they were eliminated from the analysis as well. Thus 19 species were recorded on at least 11 sites (75%) each. All of these species are primarily insectivorous during the breeding season. This collection of species represents a regularly occurring component of the overall avian community that can be tested for its responses to environmental variables. Mean abundances of these 19 species varied among sites (Table 1), and with the exception of the American Robin, the differences among sites were significant (ANOVA: all P-values <.018, American Robin: P=.067). Average numbers of species and individuals recorded per site also differed (Table 1) and were highly significant (ANOVA P=.002 (species), P=.001 (individuals)).

Table 1. Mean abundances of nineteen common bird species and measures of community diversity for all sites in 1988. Site numbers as in Figure 1. Species codes and diversity codes as follows: HIAFL - Hammond's Flycatcher, MOCH - Mountain Chickadee, RBNU - Red-breasted Nuthatch, GCKI - Golden-crowned Kinglet, RCKI - Ruby-crowned Kinglet, SMTH - Swainson's Thrush, AMRO - American Robin, SOVI - Solitary Vireo, WAVI - Warbling Vireo, OCWA - Orange-crowned Warbler, YRWA - Yellow-rumped Warbler, TOWA - Townsend's Warbler, MGWA - MacGillivray's Warbler, META - Western Tanager, CHSP - Chipping Sparrow, PEJU - Dark-eyed Junco, BHCO - Brown-headed Cowbird, PISI - Pine Siskin, EVGR - Evening Grosbeak, Nmean - Mean number of bird species, Ntot - Total number of bird species, Indiv - Mean number of individuals.

SPECIES	STUDY SITE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
HAFI	1.50	5.00	3.25	4.00	2.00	3.00	2.75	4.00	3.75	0.25	3.25	4.25	2.50	2.50
MOCH	1.75	2.50	2.00	0.75	2.75	2.25	1.25	0.75	0.50	3.50	1.25	1.25	2.25	2.00
RBNU	2.25	4.25	3.00	1.50	3.25	1.25	2.00	0.00	1.25	2.75	1.00	1.25	1.75	2.50
GCKI	1.75	0.00	0.25	3.75	0.00	0.75	1.25	0.75	1.50	1.00	1.25	1.50	2.25	0.75
RCKI	4.25	2.00	4.00	3.00	3.50	2.25	0.75	0.00	3.25	1.75	1.00	0.50	2.25	3.00
SMTH	2.25	0.75	2.00	4.50	2.75	2.00	4.00	3.50	3.25	1.25	4.00	3.50	3.25	2.75
AMRO	1.00	1.75	0.50	3.75	2.25	2.25	1.75	2.75	1.75	2.25	1.25	1.00	2.50	1.50
SOVI	1.50	1.50	2.75	0.75	1.00	0.50	0.00	0.75	0.25	0.75	0.00	0.00	0.25	0.75
WAVI	1.50	0.25	2.75	1.25	1.25	3.50	2.50	4.25	4.00	1.25	2.75	2.25	3.25	3.50
OCWA	0.75	0.25	0.75	0.50	1.00	1.75	0.25	0.25	1.50	1.50	1.25	1.00	0.00	0.00
YRWA	2.00	2.75	3.00	4.75	4.00	3.00	3.75	1.25	3.00	5.00	3.75	4.25	3.75	2.25
TOWA	6.50	0.00	2.75	4.75	1.00	6.25	7.50	4.50	5.75	0.25	0.00	0.25	0.00	0.00
MGWA	1.50	0.00	1.75	3.50	1.50	2.50	2.75	3.25	3.25	2.75	3.75	3.75	3.50	1.50
META	2.25	3.00	2.75	2.50	3.75	4.00	4.00	3.75	4.50	4.00	3.00	3.25	4.25	1.75
CHSP	3.50	5.00	5.25	3.00	5.75	5.50	5.75	4.25	7.00	6.50	5.50	5.50	5.75	4.25
DEJU	2.75	1.00	3.00	2.00	0.25	1.25	2.25	0.25	1.75	2.25	2.50	3.00	1.75	1.00
BHCO	0.00	1.35	3.00	1.00	0.50	1.75	0.25	1.00	0.25	1.50	0.75	0.25	1.25	1.25
PISI	4.50	7.00	5.50	10.00	3.75	8.50	4.25	7.00	8.00	4.75	7.00	2.50	9.75	8.25
EVGR	0.00	1.75	0.50	0.00	3.00	0.00	1.25	0.50	0.75	4.50	0.50	0.50	0.50	2.50
Nmean	22.00	17.00	18.75	20.50	19.00	21.00	19.25	18.75	20.25	18.50	16.75	16.25	18.00	19.50
Ntot	30	22	25	29	25	28	30	30	30	27	21	21	20	25
Indiv	47.25	47.25	52.50	60.50	47.50	56.00	52.75	48.00	59.00	51.25	45.75	42.75	53.25	44.25

Site Characteristics

Vegetation at all sites was characterized by relative densities of Douglas-fir of 47% or greater. In addition, Douglas-fir dominated other tree species at all sites, thus qualifying them as "Douglas-fir forests" in my view. From one to five other species of trees and tall shrubs occurred at each site, predominantly ponderosa pine and western larch, but also including lodgepole pine, Englemann spruce, subalpine fir, grand fir, western red-cedar, mountain maple, and serviceberry (Table 2). The latter three species were too rare to be included in the analysis. Several species of shrubs and young trees were recorded, but these were eventually all lumped together as a single variable to represent shrub density. Further manipulation of the data set involved lumping some tree species together. Specifically, Englemann spruce and the two true firs were combined to form the variable "spruce-fir density", and western larch and lodgepole pine were combined into "density of other conifers". To further reduce the variable list, and thus make later analysis more meaningful, canopy cover and total tree density were also removed from the data set, since both were highly correlated with Douglas-fir density (canopy: $r^2=.206$, $P=.038$; trees: $r^2=.76$, $P=.001$). Of the topographic variables, only elevation and slope were used in analysis (Table 2).

Spruce budworm densities ranged from 0 to 30.84 per kilogram in 1987 and 0 to 21.5 in 1988 (Table 3). Densities on any given tree were as high as 54.5 and 81.5, respectively. Although variances were high, there were significant differences among sites (ANOVA: $F=16.2$, $P=0$ (1987); $F=10.6$, $P=0$ (1988)). Densities of other lepidopteran larvae did not differ significantly among sites (ANOVA: $F=1.6$, $P=.08$), and were generally much lower than budworm densities when they were present.

Table 2. Vegetative and topographic features of all study sites. Tree species densities in trees/hectare. Site numbers as in Figure 1.

VARIABLE	STUDY SITE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Douglas-fir density	1233	309	601	935	530	651	685	850	253	485	867	638	948	333
Ponderosa pine density		342	100	24	255					59		36		
Western Larch Density	73		250			23	83		108	44				
Englemann spruce density	18					70	62						122	
<u>Abies</u> density	200								120					
Lodgepole pine density	128					186							153	272
Deciduous tree density	36		50								23			
Shrub density (/m ²)	0.81	0.92	1.00	2.37	4.53	7.30	1.69	0.80	1.43	1.73	1.18	0.98	0.49	0.05
Slope (degrees)	30.0	9.6	22.0	23.0	7.0	24.8	29.6	21.8	16.0	23.8	26.8	23.6	28.8	12.4
Elevation (feet)	5630	3740	4170	4140	4100	4820	4300	4000	4480	4470	4480	4860	5270	5670
Longitude (degrees W)	114.2	114.1	114.0	113.9	113.9	113.8	113.8	113.8	113.7	113.6	113.4	113.3	113.2	112.7

Table 3. Measures of insect abundance at all sites in 1987 and 1988. Site numbers as in Figure 1.

VARIABLE	STUDY SITE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1987 - budworm/kg	0.00	0.00	0.00	----	0.00	30.84	10.26	5.35	0.94	1.53	----	16.35	28.65	10.59
N	5	5	6		5	10	10	10	5	5		10	10	10
1988 - budworm/kg	0.00	0.00	0.00	0.00	0.00	21.50	4.54	7.09	0.65	1.91	8.22	7.17	17.83	6.89
variance						271.93	20.25	5.76	2.27	5.39	61.88	32.52	247.18	38.80
budworm/ha ₁ (x10 ³)	.1	.1	.1	.1	.1	2100	450	700	63	192	826	720	1800	692
budworm/ha ₂ (x10 ³)	.06	.06	.06	.06	.06	1300	280	428	39	115	496	432	1080	415
other leps/kg	0.00	0.40	0.00	0.00	0.00	0.82	0.68	0.35	0.33	0.31	0.85	1.19	0.00	0.00
N	10	10	10	10	10	20	20	10	10	10	20	20	20	10

1: budworm/ha calculated assuming stand age of 80 years.
 2: budworm/ha calculated assuming stand age of 105 years.

Budworm densities at any given site were generally less in 1988 than 1987 and were highly correlated between years ($r^2=.94$, $P<.001$)

Relationships Among Site Variables

Pairs and groups of variables were analyzed with single and partial (multiple) regression. Some significant correlations between variables allowed for reduction of the variable list, but it is important to note that variables were only removed when I did not expect them to have influenced bird populations, and they were shown to be poorly correlated with bird populations.

In applying path analysis to my investigation of avian community structure, I first set up a model of the interrelationships among the eight site (=independent) variables. In this model, topographic features influence vegetation characteristics, and both topography and vegetation influence budworm densities (Figure 2). In addition, elevation and slope are not independent of one another, and the five vegetation variables are similarly interdependent. Such two-way correlations are traditionally represented by a double arrow in path diagrams, but are not shown in Figure 2 to maintain its clarity. Even in this form the path diagram is somewhat confusing and does not indicate the strengths or significances of any of the causal relationships.

Of the possible relationships shown in Figure 2, only two were found to be significant: the effect of slope on the density of Douglas-fir and the effect of slope on the the density of ponderosa pine (Table 4). In addition, a strong relationship was found between elevation and the combined densities of larch and lodgepole pine. Noting that SPRCs between tree densities were always lower than those

Figure 2. Path diagram depicting all potential causal relationships among site variables. Bidirectional arrows between variables on the same level (i.e. tree densities, topographic variables) have been omitted for clarity.

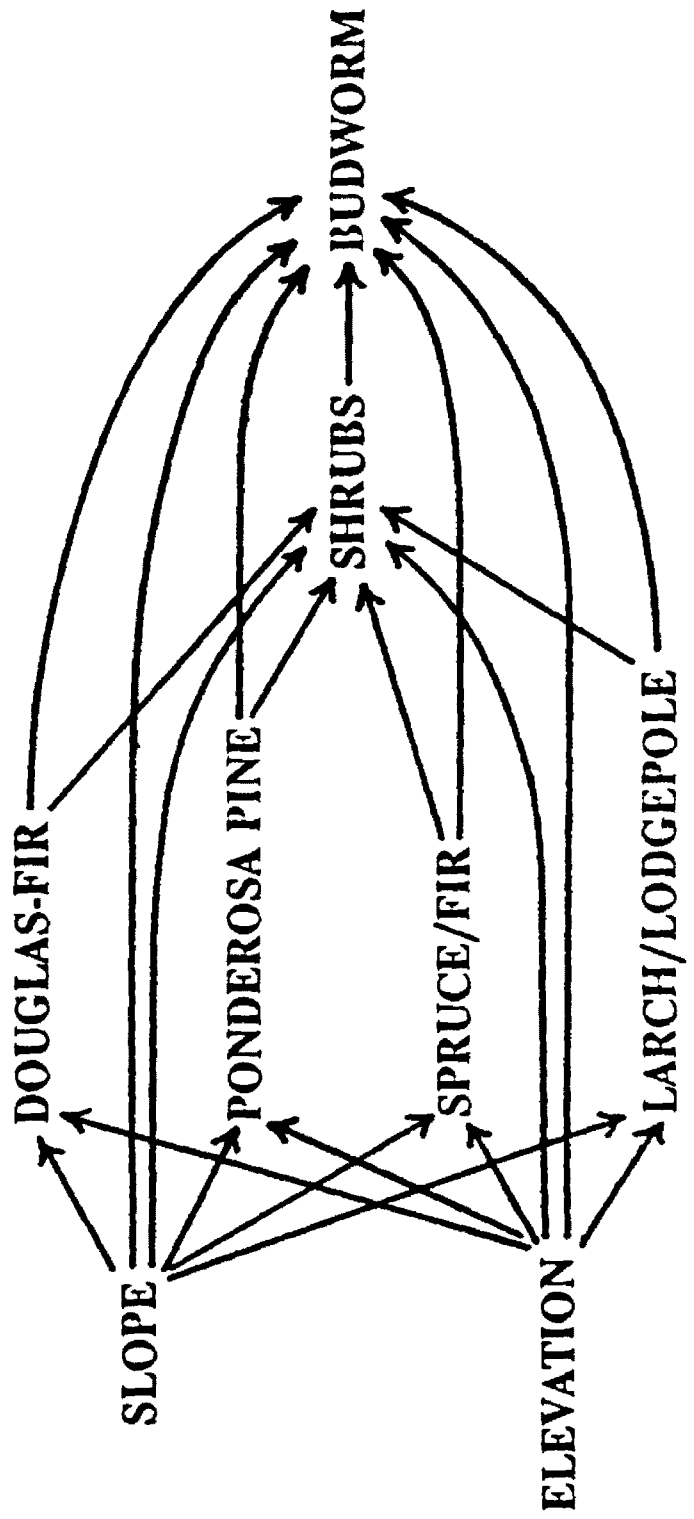


Table 4. Standardized partial regression coefficients among site variables: a) assuming interdependence among tree species' densities, b) assuming independence of tree species' densities.

"INDEPENDENT" VARIABLE	"DEPENDENT" VARIABLE					
	slope	Douglas- fir	ponderosa pine	spruce/ fir	larch/ lodgepole	shrub
a) elevation	.11	.23	-.42	.40	.59	-.37
slope		.78 *	-.78 *	.28	.13	-.16
Douglas-fir			.20	.22	-.35	.09
ponderosa pine		.22		.22	-.01	-.06
spruce/fir		.16	.14		.19	.10
larch/lodgepole		-.27	-.01	.20		.20
shrub		.04	-.02	.06	.10	
b) elevation	.11	.05	-.35 *	.47 *	.67 *	-.15
slope		.71 *	-.60 *	.29	-.07	-.09

* = significant at alpha = .05

between topographic and vegetation variables, I recalculated the SPRCs as if all tree species' densities were independent of each other by only including the two topographic variables in the model. In addition to reproducing the results of the first analysis, this analysis indicated that elevation was important in determining densities of ponderosa pine, spruce-fir, and other conifers. Neither model produced significant relationships for shrub or budworm densities. Although the independence assumptions of the second model are certainly invalid, I feel that the elevational relationships found make biological sense, and in any event simply accentuate trends already present in the first model. Thus I based the composite path diagram on the second model (Figure 3).

It is noteworthy that budworm density was not significantly affected by any of the other independent variables (Table 5), especially if one considers the insects' host preferences of Douglas-fir and true firs (USDA 1987). Thus, to get a better idea of what factors were affecting budworm populations on my sites, I turned to my original matrix of correlation coefficients. Simple regression of budworm densities against the other site variables revealed significant effects of three vegetation measures and longitude, and strong trends for elevation and slope. (Table 5). A closer look at this set of variables indicates that they are all interrelated along an elevational gradient: Englemann spruce and lodgepole pine increase with elevation and ponderosa pine decreases. Longitude and elevation were also highly correlated, due to the location of sites from west to east along a line approaching the continental divide. Looking at the SPRCs (Table 5), note that the highest coefficient is that of elevation, and although this relationship is not significant, it would appear to be more important than any of the others except

Figure 3. Path diagram depicting relationships among site variables. Numbers represent standardized partial regression coefficients. Significant coefficients ($P \leq .05$) are indicated by "*".

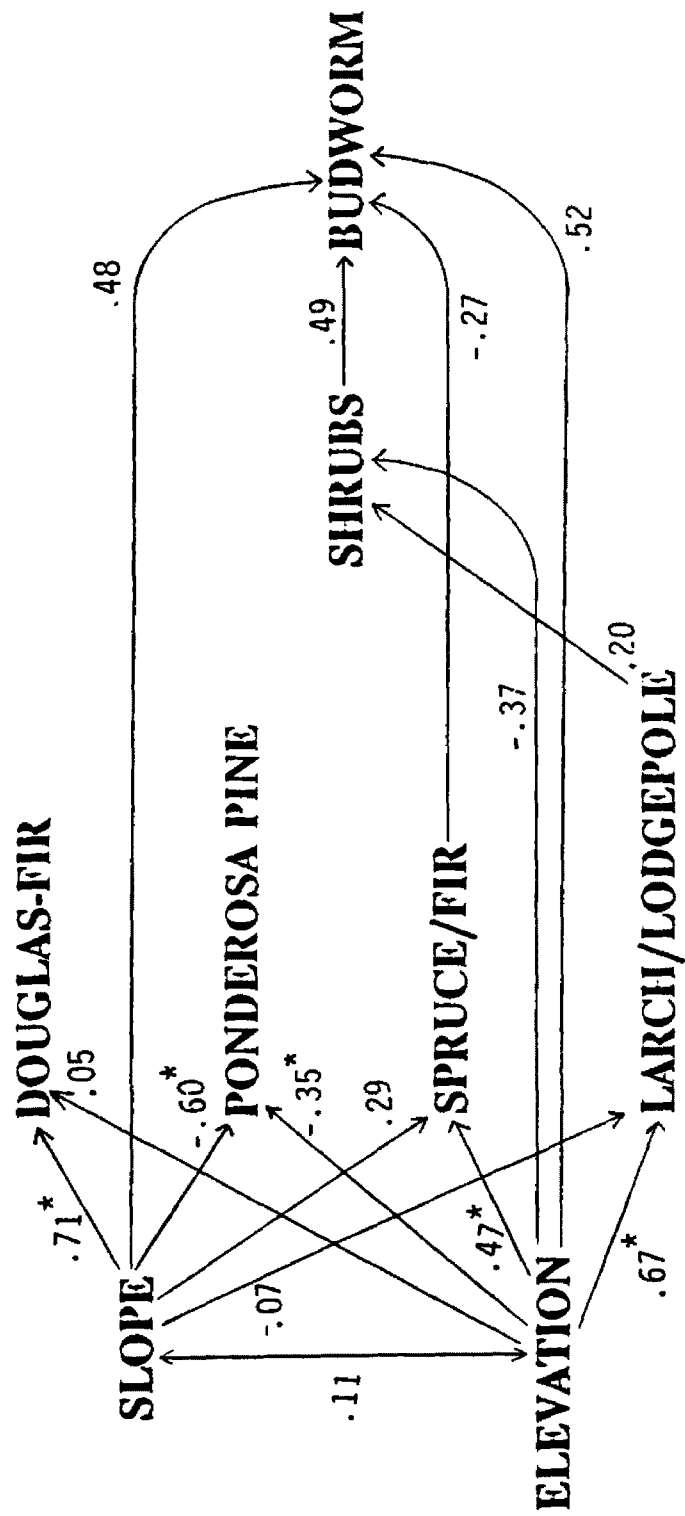


Table 5. Standardized partial regression coefficients and simple correlation coefficients for effects of vegetation and topography on western spruce budworm density.

VARIABLE	SPRC	SCC
elevation	.52	.38
slope	.48	.38
Douglas-fir	-.17	.19
ponderosa pine	-.04	-.42 *
spruce/fir	-.27	.14
larch/lodgepole	-.04	.27
shrub	.49	.37
lodgepole pine		.56 *
Englemann spruce		.74 *

* = significant at alpha = .05

shrub density. With regard to the latter, it is strongly, but not significantly, correlated with budworm density in both analyses, but I can think of no explanation for such a trend.

Avian Communities

Three measures of community composition were subjected to multiple regression as described above: mean number of individuals per transect, mean number of species per transect (species richness), and total number of species per site. Based on results from partial regression (Table 6), it would appear that vegetation characteristics have a major effect on species richness, but not on numbers of individuals or the total species pool. In most cases, however, note the similarity in trends for each community measure, if not the similarity of significance levels. The pattern between species richness and the independent variables is remarkably similar to that between budworm density and the same variables, with negative effects of ponderosa pine and positive effects of spruce-fir, other conifers, and shrub density. This time however, elevation had a negative effect, despite the vegetation's known response to elevation. This information on community structure can be incorporated into the path diagram presented earlier, resulting in the relationships shown in Figure 4.

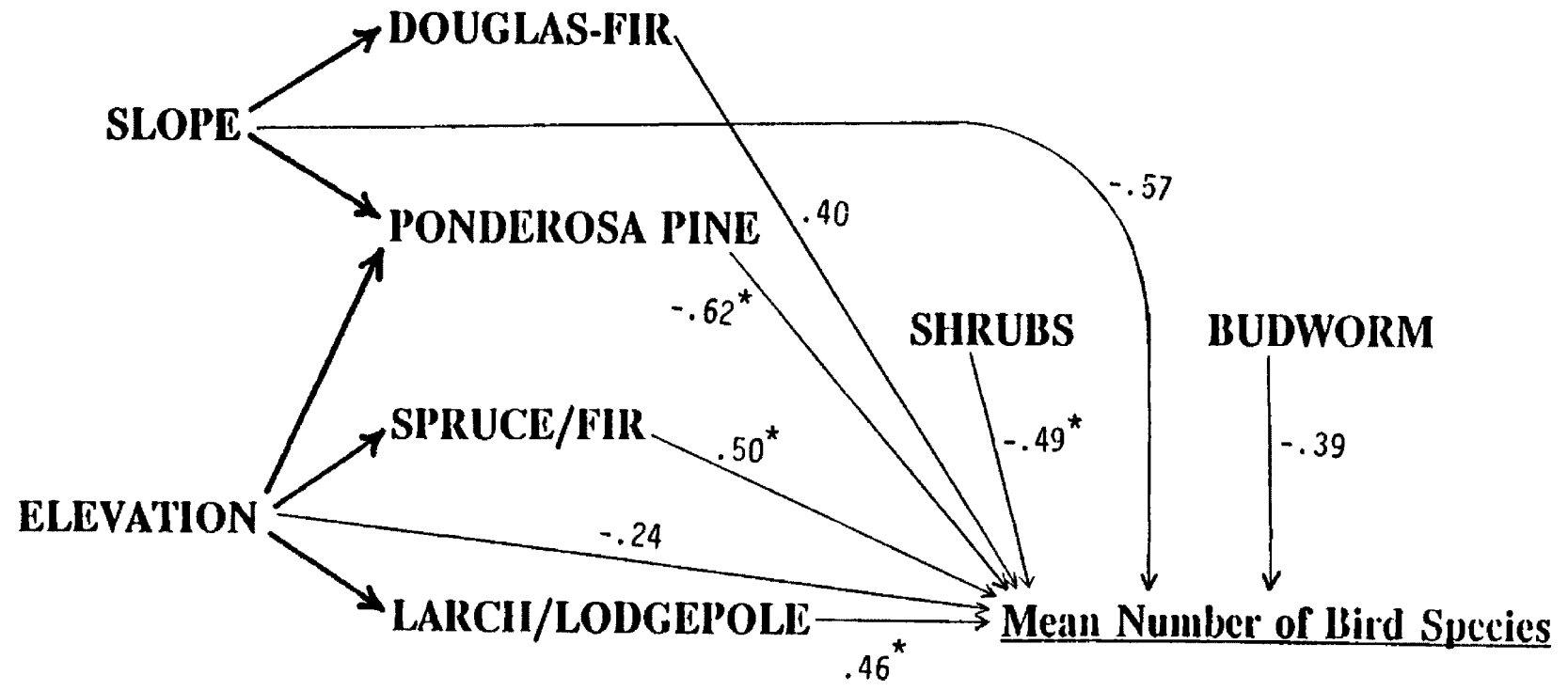
The avian community was also analyzed by calculating SPRCs for the 19 most common species (Appendix 2), and using these values to cluster bird species based on their habitat affinities. Clustering was performed using Euclidean least-squares distances and an average linkage algorithm. This was done under the assumption that species which responded similarly to a given variable or set of

Table 6. Standardized partial regression coefficients for effects of site variables on measures of community diversity.

VARIABLE	mean number of individuals	mean number of species	total number of species
budworm density	-.06	-.39	-.28
Douglas-fir	-.12	.40	.19
ponderosa pine	-.62	-.62 *	-.91 *
spruce/fir	.51	.50 *	.66
larch/lodgepole	.29	.46 *	.26
shrub	.29	.49 *	.21
elevation	-.92	-.24	-.74
slope	-.09	-.57	-.47

* = significant at alpha = .05

Figure 4. Path diagram depicting relationships between site variables and species richness. Numbers represent standardized partial regression coefficients. Significant coefficients ($P \leq .05$) are indicated by "*".

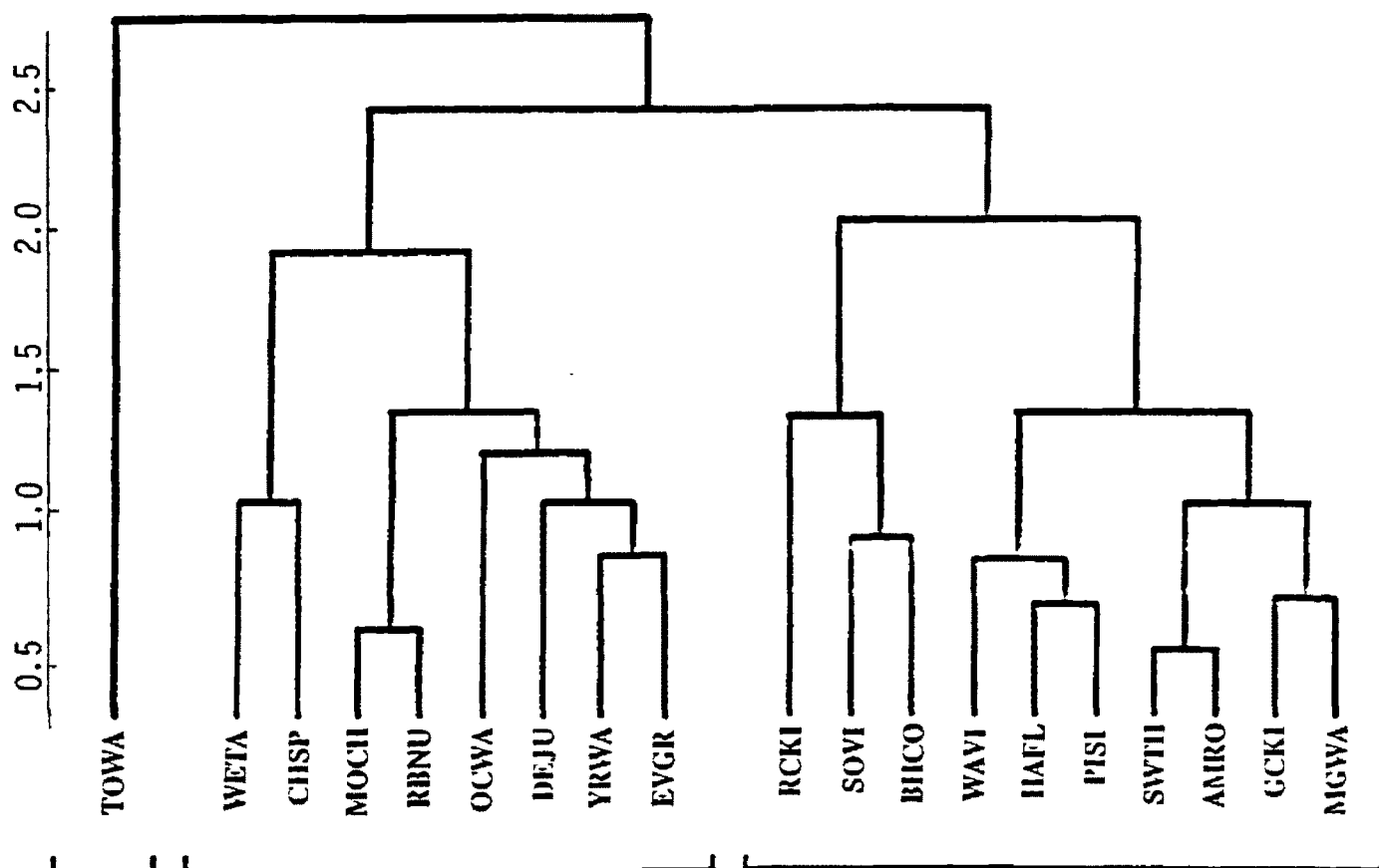


variables would be more similar to each other than to other species, and thus group together in the analysis. The clustering resulted in three primary groupings of species (Figure 5). Species in each of the clusters were compared to determine whether their SPRCs were of similar sign and magnitude, which would enable me to generalize about the group's response to habitat. Group A contains only Townsend's Warbler, which is characterized by strong positive responses to shrubs and spruce/fir and strong negative responses to elevation. Group B contains several species which show strong positive responses to ponderosa pine and negative responses to Douglas-fir, with the exceptions of Western Tanager and Chipping Sparrow. Group C contained those species that showed negative responses to ponderosa pine, exceptions being Ruby-crowned Kinglet, Solitary Vireo, and Brown-headed Cowbird. To make these clusters more meaningful, species that were "misclassified" were rearranged between groups B and C (Table 7). Partial regressions were then run on the summed abundances of the species in each group, the results of which supported the habitat relationships inferred from the original clusters (Figure 6).

Avian Guilds

To determine how various subsets of the community responded to habitat variables, avian communities were subdivided into 17 taxonomic/foraging guilds containing one to six species (Table 8). When used in analysis, a guild variable was assigned a value equal to the sum of the mean abundances of the species it contained. Multiple regressions were performed on the guild data, and several significant relationships were discovered (Table 9 - due to space considerations,

Figure 5. Clustering of bird species based on standardized partial regression coefficients for site variables.



A MOIST/DENSE
(SPRUCE/FIR)

B DRY/OPEN
(PONDEROSA PINE)

C MOIST/DENSE
(DOUGLAS-FIR)

Table 7. Revised groupings of bird species based on comparisons of standardized partial regression coefficients within the groups defined in Figure 5.

GROUP A (Moist/dense, spruce/fir)

Townsend's Warbler

GROUP B (Dry/open, ponderosa pine)

Chipping Sparrow
Mountain Chickadee
Red-breasted Nuthatch
Orange-crowned Warbler
Dark-eyed Junco
Yellow-rumped Warbler
Evening Grosbeak
Solitary Vireo
Brown-headed Cowbird

GROUP C (Moist/dense, Douglas-fir)

Western Tanager
Ruby-crowned Kinglet
Warbling Vireo
Hammond's Flycatcher
Pine Siskin
Swainson's Thrush
American Robin
Golden-crowned Kinglet
MacGillivray's Warbler

Figure 6. Path diagram depicting relationships between site variables and the three habitat groups shown in Table 7. Numbers are significant ($P \leq .05$) standardized partial regression coefficients.

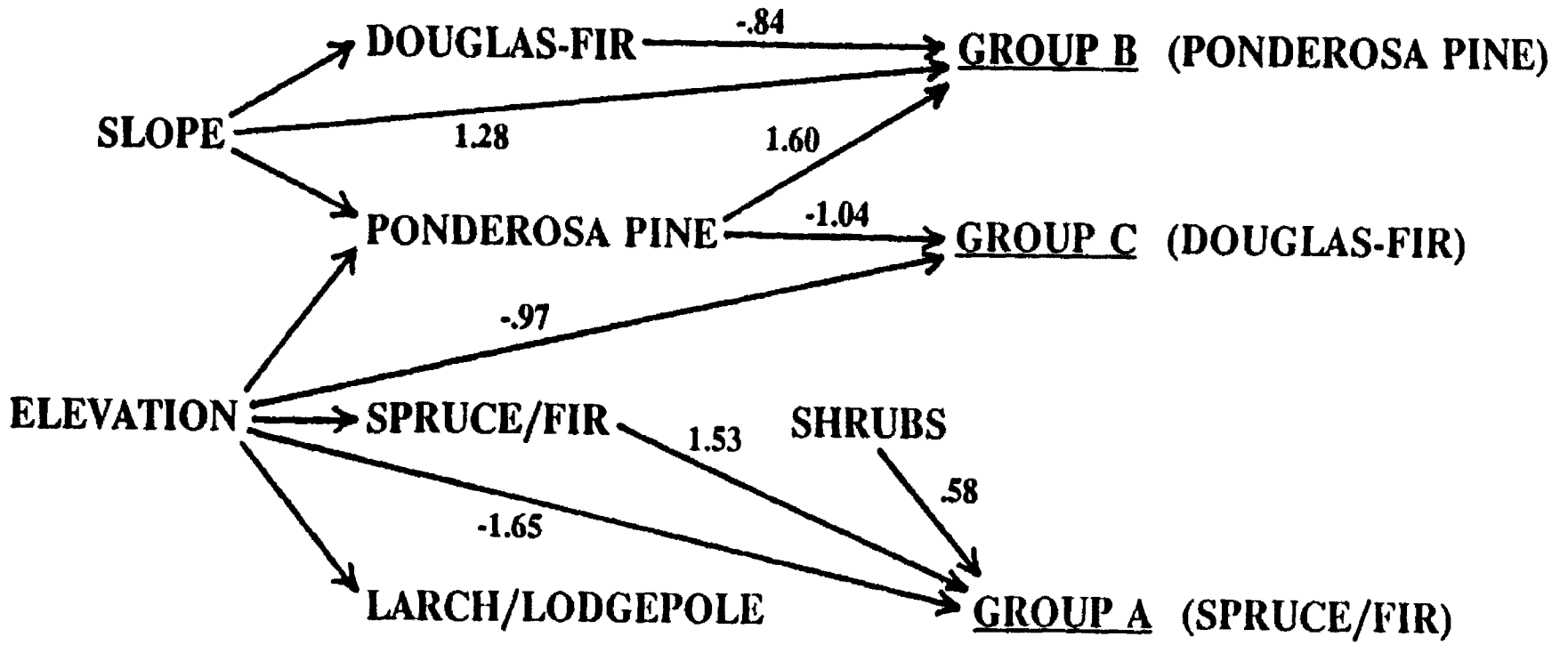


Table 8. Species composing the guilds and subguilds used in analysis, with identifying codes. Species codes as in Table 1.

FLYC = Flycatchers: HAFL

BARK = Bark foragers: MOCH
RBNU

ABIN = Arboreal Insectivores

KING = Kinglets: GCKI
RCKI

VIREO = Vireos: SOVI
WAVI

WARB = Warblers and Tanager: YRWA
TOWA
WETA

SMIN = Small Insectivores: MOCH
KING

GLEAN = Gleaners: KING
VIREO
WARB

SEED = Seed-eaters: BHCO
PISI
EVGR

GROU = Ground foragers

THRU = Thrushes: SWTH
AMRO

SPAR = Sparrows: CHSP
DEJU

GRWA = Ground Warblers: OCWA
MGWA

SMGR = Small ground foragers: SPAR
GRWA

Table 9. Significant ($P \leq .05$) standardized partial regression coefficients between site variables and guild abundances. Guild abbreviations as in Table 8.

VARIABLE	BARK	ABIN	VIREO	WARB	GLEAN	GROU	SPAR	GRWA	SMGR
Douglas-fir							-1.21		
ponderosa pine	1.31			-.56	-.71			-.79	
spruce/fir		.61		.62	.65				
larch/lodgepole			.94			-.69		-.59	
shrub		.53		.57	.43				
elevation	.65	-.63	-1.27	-.61	-.75				
slope	.76						1.46		

only SPRCs significant at .05 are presented. All guild results can be found in Appendix 3). As in the community analysis, budworm density did not prove to be an important variable, whereas vegetation and topography were often important "determinants" of a guild's abundance. Guilds that showed several significant relationships included bark foragers, arboreal gleaning insectivores, and ground foragers. One guild, the nomadic seed-eaters, proved to be a poor combination, in that the two species in it showed opposite trends in all variables. On average, however, the species in a guild showed at least a 50% similarity in their population trends, lending support to the use of guilds in the analysis. No path diagrams are presented for guilds, simply because of the number that would be involved, and because combining all the guilds into one diagram would make its interpretation difficult.

Individual Species

Of the 19 species used in the analysis, 13 showed at least one significant response to a site characteristic (Table 10). Of these, 11 responded to vegetation, 4 to topography, and 5 to budworm density. Most species responded to a given variable in the same manner as the guild to which they were assigned. Of the vegetation variables, densities of ponderosa pine and "other conifers" were important to the most species. Interestingly enough, most species that responded to budworm density did so in a negative fashion, although I suspect that the confounding effects of vegetation were not totally separated out.

Species abundances were also analyzed using simple regression in an attempt to sort out the more obvious effects of the site variables, regardless of

Table 10. Significant ($P \leq .05$) standardized partial regression coefficients between site variables and twelve common bird species. Species codes as in Table 1.

VARIABLE	MOCH	RBNU	RCKI	SOVI	WAVI	OCWA	TOWA	MGWA	WETA	CHSP	DEJU	BHCO
budworm		-0.37	-0.60	-0.41	0.67						-0.62	
Douglas-fir				0.46						-1.20		
ponderosa pine	1.20	1.22		0.60	-1.08			-0.89				
spruce/fir							1.53		0.73			-0.61
larch/lodgepole		0.32	0.66	1.04				-0.59				1.07
shrub						0.84	0.58					
elevation		0.45			-1.00		-1.65					
slope		0.60									1.49	

any relationships among the latter. This analysis revealed numerous significant effects of ponderosa pine density and budworm density (Table 11). As has been indicated earlier, several species respond negatively to high densities of ponderosa pine, and these species are probably responsible for several of the broader trends in guilds and communities described above. More interesting for the purposes of this study are the species that responded to budworm density. This list can be reduced by eliminating those species that responded negatively to ponderosa pine density, since the negative correlation between budworm and pine could have caused a spurious correlation between budworm and those species' abundances. When those species are removed, one species remains - the Pine Siskin. Siskins showed a positive response to increasing levels of budworm infestation ($r^2=.15$, $P=.066$). This relationship is supported to some extent by the multiple regression for this species, in which the coefficient for budworm is among the highest, and its significance is the highest of all eight variables ($t=1.5, P=.09$).

One species, the Townsend's Warbler, was not analyzed in the same way as the others because of complications arising from its geographic range. According to Skaar (1985), Townsend's Warblers reach their eastern limits within the longitudinal range of my study sites. When the abundances of Townsend's Warblers are examined in Table 1, it would appear that the limit is reached between sites 10 and 12. due to my experience with the species at these sites over the two years, I chose to draw the line between sites 10 and 11. Once the confounding effects of longitude were removed, analysis of Townsend's Warbler abundance proceeded as for the other species, but using only the 10 westernmost sites. All subsequent results reported for Townsend's Warbler were obtained using this methodology.

Table 11. Correlation coefficients between bird abundances and ponderosa pine and spruce budworm densities. Species codes as in Table 1.

VARIABLE	budworm	MOCH	RBNU	GCKI	SOVI	WAVI	TOWA	MGWA	PISI	EVGR
ponderosa pine	-.42*	.49*	.78*	-.53*	.47*	-.64*	-.40	-.72*	-.24	.40
budworm		.07	-.45*	.02	-.46	.52*	-.03	.36	.39	-.30

* = significant at alpha = .05

Partial regression revealed strong relationships between Townsend's Warbler and spruce-fir ($t=13.44$, $P=.024$), shrub density ($t=6.37$, $P=.05$), and elevation ($t=11.54$, $P=.027$). Interestingly enough, the relationship with elevation is negative. Simple regression produced no significant results, although a strong negative trend existed for ponderosa pine, and strong positive trends were found for budworm and elevation.

DISCUSSION

The Site Variables

Vegetation on the sites used in this study was typically Douglas-fir/ponderosa pine or Douglas-fir/alpine conifers, with ponderosa pine dropping out as elevation increased. As the dominant tree species at all sites, Douglas-fir showed few significant responses to physiographic variables, and its density varied very little when compared with other tree species. Higher elevation sites were characterized by higher densities of spruce, fir, larch, and lodgepole pine, and tended to have a slightly higher overall tree density. Lower elevation sites tended to be flatter and have higher densities of ponderosa pine. Lodgepole pine, Englemann spruce, and subalpine fir never occurred on the lower sites. Understory composition was predominantly low deciduous shrubs, although young conifers were usually present in low densities. Shrub densities were not strongly influenced by any other vegetative or topographic variables. Although spruce budworm densities were expected to respond to densities of their host trees, particularly Douglas-fir and true firs, this was not observed. In fact, there were no significant interactions between budworm density and the other site variables. However, there is an indication that elevation may be important, and if so, then vegetation effects are probably closely tied in as well.

Community composition

Food supply, measured in terms of spruce budworm density, had no effects on the numbers of species or individuals at a given site. Rather, vegetation characteristics proved to be relatively important, particularly with respect to species richness. In particular, tree and shrub densities affected the mean number of species per transect at a given site, but not the total number found at that site over two summers. The principal difference between the mean and total number of species is the absence of rare or hard to find species on most transects. Thus, the mean reflects the number of common species present at a site, which can include species that are considered rare at a different site. In this sense, the mean species richness can be interpretable in terms of changes in species' abundances, with a speciose site possessing species that are considered rare at less speciose sites. Therefore, the results of my analysis indicate that richness increases with increasing densities of shrubs, spruce-fir, and larch/lodgepole, and decreases with increasing density of ponderosa pine. If rare species are becoming more common under the above conditions, there must be an explanation for the lack of strong correlations between number of individuals and site variables. I suspect that some species, particularly those that show a positive response to ponderosa pine, must be decreasing in abundance at the more speciose sites, but not declining to the extent that they become rare.

The importance of ponderosa pine and spruce/fir in determining species richness is reiterated by analyses at the other levels of organization investigated: guilds and individual species. In particular, the species clusters based upon SPRCs indicate that there are groups of species, at a level "above" the foraging guild,

which respond similarly to habitat parameters. The existence of a spruce/fir group and a ponderosa pine group supports my earlier contention that changes in species richness, but not in total bird abundance, result from declines in the populations of one group and increases in another.

That different bird species "prefer" different tree species has been well documented (Balda 1969, Franzreb 1974, Holmes and Robinson 1981, Rice et al 1984). Many of these studies have been conducted in deciduous habitats, and their results are thus not directly applicable to the system under investigation. However, Franzreb (1974, 1981) reports that several species preferentially avoid ponderosa pine and key in on Douglas-fir, spruce, and fir. Interestingly, one such species is the Mountain Chickadee, which this study found to be strongly associated with ponderosa pine. On the other hand, Balda (1969) failed to note avoidance of ponderosa pine by birds, suggesting that habitat selection is strongly influenced by multiple factors operating in concert. In addition, it is quite likely that communities in different geographic regions will have different sets of habitat requirements, thus explaining the differing results of Franzreb and Balda (both working in Arizona) and those of this study in Montana.

Guilds

Results on the guild level were generally similar to those for the community as a whole, as redefined by the three habitat groups. The most speciose and abundant guild, canopy gleaners (in whole or in part), responded to vegetation in much the same way as did species richness. Other guilds were likewise comparable to one of the three habitat groups, although some (i.e. flycatchers,

finches) showed no significant responses to any habitat characteristics. No doubt some of these results can be explained through the foraging strategy of the birds within a given guild. For example, the proportional lack of foliage on ponderosa pine (when compared with spruce and fir; Franzreb 1974) may explain why gleaning insectivores are less abundant in areas dominated by this species. There is simply not enough substrate to support as high a population. Similarly, ground foragers, such as sparrows and juncos, may be responding in exactly the opposite fashion, that is preferring ponderosa pine, because of the relative openness of the habitat. Thus vegetation composition and structure, both known to be important to birds, are in a sense highly correlated.

Although vegetation was of primary importance in determining guild abundances, there is some evidence that budworm has some influence at this level. However, most of the significant SPRCs involving budworm are negative, as are many of those SPRCs that merely suggest a relationship. Such a result is in strong disagreement with any previously known relationships between insects and birds, and I can see no logical explanation for such findings. It is highly unlikely that a species or group of species would decrease in abundance as its food supply increases. I thus suspect that the negative correlations involving budworm are spurious, somehow being maintained through the partial regression analysis. Similarly, if one assumes the negative effects to be spurious, the even fewer positive relationships should be viewed with the same or greater skepticism. Skepticism conceivably could be applied to any vegetational effects as well, but I believe that since these are of higher significance, and are far more prevalent and consistent, they accurately reflect the role of habitat at all levels.

Individual species

Much of what has been said about communities and guilds can be equally valid for the many species under study. All have habitat preferences and respond in different ways to varying habitat parameters. Suffice it to say that the nineteen common bird species fall into the three habitat groups discussed earlier: spruce/fir, Douglas-fir, and ponderosa pine. The more important subject of this section is the role of spruce budworm.

That budworm is important to some species in eastern North America has already been mentioned, and it would not be unexpected to find similar relationships in the West. Strong relationships were found between budworm and a number of bird species, but the problems inherent in concluding that budworm has an effect have already been discussed. Of the species showing strong positive responses to budworm, only two will be considered in any greater detail: the Warbling Vireo and the Pine Siskin.

The Warbling Vireo was the only species to respond positively and significantly to budworm densities after partial regression. If, for the moment, one assumed this correlation to be meaningful, it would be necessary to explain it. Warbling Vireos are primarily a riparian or edge species in western Montana, hence their negative relationship with ponderosa pine. Thus they would not normally encounter spruce budworm on a regular basis, and may not even forage extensively in the budworm's host species (pers. obs.). Thus I am fairly confident that this species' response to budworm is spurious, perhaps driven by the absence

of budworm in ponderosa pine dominated stands. A similar scenario could be concocted for the MacGillivray's Warbler, another species showing strong budworm affinity.

The Pine Siskin is another matter entirely. Although its trends are never significant, they are consistent between years and analyses, and were maintained throughout the series of variable list reductions preceding the final regression model. I would not be surprised, therefore, if siskins do in fact respond numerically to budworm infestation. The nomadic flocking behavior of this species would make it more able to discover infestations than other species, particularly those showing strong philopatry. In this sense, siskins are similar to eastern populations of the Evening Grosbeak, which show much stronger nomadism and population fluctuation than their western counterparts (pers. obs., Christmas Bird Count data). In addition, siskins have been shown to concentrate in areas of higher than normal food supply (Rolad et al. 1986). In the latter case, siskins were locally abundant in areas with high winter moth densities, and appeared to key in on areas of heavy defoliation.

The response of siskins to moths necessitates the introduction of the problem of scale. Rolad's study was done at the level of individual trees, and not between larger areas with varying infestation levels. Since budworm is patchily distributed within a stand, the community/population approach may not be appropriate to test for budworm effects. Instead, more detailed information about the distribution of a population within the habitat would potentially show the effects of patchiness, in this case of budworm. In the present study, budworm levels were relatively low, in that extensive defoliation was not observed. For

budworm effects to be observable at this level, infestations would have to be larger and broader in geographical coverage.

Summary

Regarding the relative importances of food and vegetation to avian community composition, the results presented herein must be viewed in terms of the actual scope of the study. Due to more extensive variation in vegetation than was expected, birds' responses to vegetation may have obscured any similar responses to budworm densities. Thus, it is important to note that, according to this analysis, vegetation is more important than budworm given that sites are as vegetatively dissimilar as the series that I considered. Perhaps if a similar study were conducted in a more narrowly defined range of habitat types, effects of food density, should they exist, would be detectable.

The problem of habitat variability can be considered another example of the scale problem discussed above. If sites vary in vegetative characteristics, any comparisons among them are done on a broad, regional scale (i.e. western Montana), and any conclusions cannot be localized to any smaller subset of the regional habitat type. If, however, sites are similar, conclusions refer directly to a much more specific set of habitat parameters, and cannot necessarily be applied on a regional basis (Wiens 1981, Wiens et al. 1987). Since both applications cannot be undertaken simultaneously without requiring prohibitive sample sizes, one must choose which scale is to be concentrated upon. Wiens et al (1987) suggest that, if one wishes to correlate bird abundance with habitat characteristics,

the "best" approach involves having several sites on a regional scale, but with replication within each site. Thus, this study should be interpreted in terms of a primarily regional scale, if not a broader, biogeographical one (i.e. Townsend's Warbler).

On this regional scale, budworm densities were not found to be important to bird species which occurred over a relatively wide range of habitat types. Given that the common species under study tended to show some preferences for certain components of the regional habitat mosaic, response to budworm may have been obscured by vegetative "noise". However, because these same bird species were found regularly on most sites, one could reasonably conclude that they are not so highly tied to habitat variables as to be specialized on a more narrowly defined habitat type. In such a case it is perhaps more reasonable to examine community structure on a regional scale, since vegetative variation is greater than variation in food supply, and is thus more likely to have effects on bird populations.

A second consideration that is important when considering the conclusions of this study is the comparability between this and the other budworm studies referred to. In most eastern studies, where avian responses to budworm are well documented, budworm densities are reported per unit area (either land or foliage), whereas I calculated them per unit foliage mass. Although I have already indicated that these two measures yield comparable estimates, it is difficult to directly compare my data with those of other researchers. Examination of the data of various studies reveals densities ranging from 240,000 to 14,000,000 per hectare (Crawford and Jennings 1989), 1000 to 8,000,000 per acre (Morris et al. 1958), and 30 to 500 per 15 inch twig (Dowden et al. 1953).

However, after converting budworm per kilogram to budworm per hectare (Table 3), one can directly compare my results with those reported above. It is important to note, however, that the conversions are not highly accurate, but at least give an idea of the magnitude of the range in budworm densities. Assuming either an 80 or 105 year old forest, minimum densities ranged from 1000 to 600 per hectare (respectively) and maximum densities in 1988 ranged from 2,100,000 to 1,300,000. Maximum densities in 1987 were between 3,000,000 and 2,500,000. These values for maximum density are comparable to the 1,700,000 per hectare reported for transitional levels of infestation by Crawford and Jennings (1989). Thus, the possibility exists that the budworm densities obtained during this study were not of the magnitude necessary to elicit responses in bird populations. Further evidence toward this conclusion can be obtained by comparing my data with that of Morris et al. (1958). In that study, Bay-breasted Warblers did not show a response until budworm numbers jumped from below 500 per acre to over 2,000,000 per acre within a year. My converted data indicate a range of roughly 30 to 700,000 per acre (intermediate between values for 80 and 105 year old stands), certainly not of the magnitude reported by Morris et al. (1958). Therefore, given relatively low levels of budworm infestation, and little overall variation in budworm densities among sites, the existing variation in other habitat characteristics becomes more important to avian communities and populations in western Montana. However, the possibility still exists that future outbreaks could be of sufficient magnitude to result in population increases in some species.

Appendix 1. Mean abundances (N=4) of all bird species recorded during 1988. Site numbers as in Figure 1.

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Sharp-shinned Hawk									0.25					
Cooper's Hawk							0.25	+						
Northern Goshawk				0.25										+
Red-tailed Hawk				+	0.25						0.25		0.25	
Ruffed Grouse	0.25	+			0.50		0.25	+	0.25					
Mourning Dove		0.25											0.25	
Barred Owl							0.75							
Calliope Hummingbird	0.75					1.25		+			0.25			
Red-naped Sapsucker						+							0.25	+
Hairy Woodpecker		0.25	0.50							0.25			0.25	
Northern Flicker	1.00	0.25	0.25	0.50		0.50		0.25		0.75		0.50	0.25	1.50
Pileated Woodpecker									0.50	0.25				
Olive-sided Flycatcher	+					0.25								
Western Wood-Pewee		1.00												
Hammond's Flycatcher	1.50	5.00	3.25	4.00	2.00	3.00	2.75	4.00	3.75	0.25	3.25	4.25	2.50	2.50
Willow Flycatcher				0.25					+					
Stellar's Jay	+							+						
Gray Jay	0.25			0.25	0.25					0.75			0.75	0.25
Clark's Nutcracker	0.25											0.25		0.50
Common Raven	+		+	1.25	0.50	0.75	+	0.25			0.25			0.50
Black-capped Chickadee			1.75		0.50		0.75	+	0.25					
Mountain Chickadee	1.75	2.50	2.00	0.75	2.75	2.25	1.25	0.75	0.50	3.50	1.25	1.25	2.25	2.00
Red-breasted Nuthatch	2.25	4.25	3.00	1.50	3.25	1.25	2.00		1.25	2.75	1.00	1.25	1.75	2.50
Brown Creeper									0.25					
Winter Wren	1.00			0.25			0.25		0.50					
Golden-crowned Kinglet	1.75		0.25	3.75		0.75	1.25	0.75	1.50	1.00	1.25	1.50	2.25	0.75
Ruby-crowned Kinglet	4.25	2.00	4.00	3.00	3.50	2.25	0.75		3.25	1.75	1.00	0.50	2.25	3.00
Townsend's Solitaire	0.25					0.75		+	+	+				
Swainson's Thrush	2.25	0.75	2.00	4.50	2.75	2.00	4.00	3.50	3.25	1.25	4.00	3.50	3.25	3.75
Hermit Thrush				0.25	0.25					0.50	1.25	2.25	0.50	

Appendix 1 (continued)

SPECIES	STUDY SITE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
American Robin	1.00	1.75	0.50	3.75	2.25	2.25	1.75	2.75	1.75	2.25	1.25	1.00	2.50	1.50
Varied Thrush	1.00													
Solitary Vireo	1.50	1.50	2.75	0.75	1.00	0.50		0.75	0.25	0.75			0.25	0.75
Warbling Vireo	1.50	0.25	2.75	1.25	1.25	3.50	2.50	4.25	4.00	1.25	2.75	2.25	3.25	3.50
Orange-crowned Warbler	0.75	0.25	0.75	0.50	1.00	1.75	0.25	0.25	1.50	1.50	1.25	1.00		
Nashville Warbler				0.25		0.25	1.00	2.50						
Yellow Warbler								0.25	0.50					
Yellow-rumped Warbler	2.00	2.75	3.00	4.75	4.00	3.00	3.75	1.25	3.00	5.00	3.75	4.25	3.75	2.25
Townsend's Warbler	6.50		2.75	4.75	1.00	6.25	7.50	4.50	5.75	0.25		0.25		
American Redstart					0.25		0.50	2.00						
MacGillivray's Warbler	1.50		1.75	3.50	1.50	2.50	2.75	3.25	3.25	2.75	3.75	3.75	3.50	1.50
Western Tanager	2.25	3.00	2.75	2.50	3.75	4.00	4.00	3.75	4.50	4.00	3.00	3.25	4.25	1.75
Black-headed Grosbeak							+							
Lazuli Bunting			+	0.25										0.50
Rufous-sided Towhee						+			0.75					
Chipping Sparrow	3.50	5.00	5.25	3.00	5.75	5.50	5.75	4.25	7.00	6.50	5.50	5.50	5.75	4.25
Dark-eyed Junco	2.75	1.00	3.00	2.00	0.25	1.25	2.25	0.25	1.75	2.25	2.50	3.00	1.75	1.00
Lincoln's Sparrow													+	
Song Sparrow								0.25						
Brown-headed Cowbird		1.25	3.00	1.00	0.50	1.75	0.25	1.00	0.25	1.50	0.75	0.25	1.25	1.25
Cassin's Finch	0.25						0.25	+	0.25					0.50
Red Crossbill	0.75	5.50	1.25	2.00	2.00		0.50		0.50	0.75			+	
Pine Siskin	4.50	7.00	5.50	10.00	3.75	8.50	4.25	7.00	8.00	4.75	7.00	2.50	9.75	8.25
Evening Grosbeak		1.75	0.50		3.00		1.25	0.50	0.75	4.50	0.50	0.50	0.50	2.50

+ = Species recorded at site but never on official transect count.

Appendix 2. Standardized partial regression coefficients between site variables and mean abundances of common bird species. Species codes as in Table 1.

SPECIES	Budworm	Douglas-fir	Ponderosa pine	Spruce/fir	Larch/lodgepole	Shrub	Elevation	Slope	overall r^2	F value (df 8,5)
HAFI	.56	.19	-.24	.18	.01	-.47	-.83	-.61	.41	.445
MOCH	-.05	-.33	1.20	-.38	.12	.31	.78	.81	.67	1.278
RBNU	-.37	-.31	1.22	-.15	.32	.07	.45	.60	.94	9.409
GCKI	-.20	.30	-.55	.10	-.38	-.03	.13	-.06	.53	.710
RCKI	-.36	.34	.12	.22	.66	.31	.86	-.41	.83	3.011
SWTH	.25	.42	-.70	.10	-.46	-.34	-.41	-.63	.54	.733
AMRO	.28	.47	-.60	.12	-.34	.15	-.41	-.78	.46	.537
SOVI	-.41	.47	.60	-.22	1.04	-.03	-.37	.05	.91	6.686
WAVI	.67	.06	-1.08	.44	.24	-.29	-1.00	-.66	.85	3.652
OCWA	-.44	-.65	-.15	.08	-.35	.84	.32	.58	.62	1.022
YRWA	-.44	-.65	.45	-.46	-.61	.51	.78	1.17	.58	.873
TOWA	-.13	.30	-.45	1.53	.13	.58	-1.65	.46	.99	69.810 (df 8,1)
MGWA	.18	-.07	-.89	-.05	-.55	-.14	-.11	.05	.86	3.797
WETA	.51	-.67	-.18	.73	-.44	.07	-.60	.24	.76	2.007
CHSP	.21	-1.20	.16	.39	-.34	.06	-.04	.71	.67	1.262
DEJU	-.62	-.50	.41	-.27	.04	.07	.51	1.49	.78	2.187
BHCO	.25	.14	.33	-.61	1.07	-.11	-.60	.27	.83	3.084
PISI	.70	.43	-.62	.27	.34	-.33	-.76	-.98	.45	.519
EVGR	-.39	-.64	.41	-.38	-.29	.20	.75	.42	.54	.738

Appendix 3. Standardized partial regression coefficients between site variables and guild abundances. Guild abbreviations as in Table 8.

GUILD	Budworm	Douglas-fir	Ponderosa pine	Spruce/fir	Larch/lodgepole	Shrub	Elevation	Slope	overall r^2	F value (df 8,5)
FLYC	.56	.19	-.24	.18	.01	-.47	-.83	-.61	.41	.445
BARK	-.25	-.35	1.31	-.27	.25	.19	.65	.76	.86	3.946
ABIN	-.39	-.02	-.49	.61	.40	.53	-.63	.12	.89	5.269
KING	-.56	.44	-.23	.23	.30	.23	.15	-.36	.55	.760
VIREO	.42	.37	-.70	.31	.94	-.31	-1.27	-.64	.76	2.030
WARB	-.32	-.30	-.56	.62	-.04	.57	-.61	.35	.90	5.904
SMIN	-.55	.26	.35	.03	.34	.36	.50	.05	.55	.765
GLEAN	-.36	.05	-.71	.65	.35	.43	-.75	-.60	.91	6.095
FINCH	.48	.06	-.40	.05	.17	-.22	-.33	-.75	.30	.270
GROU	.24	-.54	-.61	.14	-.69	.16	-.08	.49	.76	2.016
THRU	.32	.55	-.80	.14	-.50	-.13	-.51	-.87	.64	1.101
SPAR	-.23	-1.21	.38	.12	-.23	.10	.29	1.46	.68	1.329
GRWA	-.04	-.33	-.79	-.01	-.59	.35	.05	.29	.78	2.259
SMGR	-.16	-.91	-.21	.07	-.47	.25	.20	1.05	.66	1.191
SEED	.49	.10	-.24	-.14	.47	-.22	-.46	-.56	.37	.373

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