RELATIONSHIPS BETWEEN LOGGING METHODS, HABITAT STRUCTURE AND BIRD COMMUNITIES OF DRY INTERIOR DOUGLAS-FIR, PONDEROSA PINE FORESTS OF BRITISH COLUMBIA

K.H. Morgan
S.P. Wetmore
G.E.J. Smith
R.A. Keller

TECHNICAL REPORT SERIES No. 71
Pacific and Yukon Region 1989
Canadian Wildlife Service

Environment Canada | Environnement Canada
Canadian Wildlife Service | Service Canadien de la faune

Canada

TECHNICAL REPORT SERIES
CANADIAN WILDLIFE SERVICE

This series of reports, established in 1986, contains technical and scientific information from projects of the Canadian Wildlife Service. The reports are intended to make available material that either is of interest to a limited audience or is too extensive to be accommodated in scientific journals or in existing CWS series.

Demand for these Technical Reports is usually confined to specialists in the fields concerned. Consequently, they are produced regionally and in small quantities; they can be obtained only from the address given on the back of the title page. However, they are numbered nationally. The recommended citation appears on the title page.

Technical Reports are available in CWS libraries and are listed with the DOBIS system in major scientific libraries across Canada. They are printed in the official language chosen by the author to meet the language preference of the likely audience. **To determine whether there is significant demand for making the reports available in the second official language, CWS invites users to specify their official language preference. Requests for Technical Reports in the second official language should be sent to the address on the back of the title page.**

SÉRIE DE RAPPORTS TECHNIQUES
DU SERVICE CANADIEN DE LA FAUNE

Cette série de rapports donnant des informations scientifiques et techniques sur les projets du Service canadien de la faune (SCF) a démarré en 1986. L'objet de ces rapports est de promouvoir la diffusion d'études s'adressant à un public restreint ou trop volumineuses pour paraître dans une revue scientifique ou l'une des séries du SCF.

Ordinairement, seuls les spécialistes des sujets traités demandent ces rapports techniques. Ces documents ne sont donc produits qu'à l'échelon régional et en quantités limitées; ils ne peuvent être obtenus qu'à l'adresse figurant au dos de la page titre. Cependant, leur numérotage est effectué à l'échelle nationale. La citation recommandée apparaît à la page titre.

Ces rapports se trouvent dans les bibliothèques du SCF et figurent aussi dans les listes du système de référence DOBIS utilisé dans les principales bibliothèques scientifiques du Canada. Ils sont publiés dans la langue officielle choisie par l'auteur en fonction du public visé. **En vue de déterminer si la demande est suffisamment importante pour produire ces rapports dans la deuxième langue officielle, le SCF invite les usagers à lui indiquer leur langue officielle préférée. Il faut envoyer les demandes de rapports techniques dans la deuxième langue officielle à l'adresse indiquée au verso de la page titre.**

RELATIONSHIPS BETWEEN LOGGING METHODS, HABITAT STRUCTURE AND BIRD COMMUNITIES OF DRY INTERIOR DOUGLAS-FIR, PONDEROSA PINE FORESTS OF BRITISH COLUMBIA

K.H. Morgan
S.P. Wetmore
G.E.J. Smith
R.A. Keller

Technical Report Series No. 71
Pacific and Yukon Region 1989
Canadian Wildlife Service

This series may be cited as:

Morgan, K.H., S.P. Wetmore, G.E.J. Smith and R.A. Keller. 1989. Relationships between logging methods, habitat structure and bird communities of dry interior Douglas-fir, Ponderosa Pine forests of British Columbia. Technical Report Series No. 71. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Published by Authority of the
Minister of Environment
Canadian Wildlife Service

Minister of Supply and Services Canada 1989
Catalogue No. CW69-5/71E
ISBN 0-662-17079-2
ISSN 0831-6481

Copies may be obtained from:
Canadian Wildlife Service,
Pacific and Yukon Region
P.O. Box 340,
Delta, British Columbia,
Canada V4K 3Y3

ABSTRACT

The response of breeding birds to diameter limit and selection cutting of dry interior Douglas-fir (Pseudotsuga menziesii) and Ponderosa Pine (Pinus Ponderosa) forests was studied between 1983 and 1986. Multivariate analyses showed that the avifauna and the vegetation of the study areas near Princeton, B.C. were distinct from the birds and forests studied near Merritt, B.C. The responses of nesting and foraging guilds to habitat alterations predominantly followed expected trends. Neither logging method appeared to drastically harm the bird community. Opening up of the forest canopy resulted in a decline in several mature forest species, but overall tended to promote a more diverse avifauna. In general, the densities of birds showed little variation from year to year. Correlations between weather variables and groups of birds suggested that some of this yearly variation may have been due to temperature and precipitation patterns.

RÉSUMÉ

La réaction d'oiseaux nicheurs à des coupes au diamètre limite et d'écrémage pratiquées dans des peuplements secs de douglas taxifoliés bleus (Pseudotsuga menziesii) et de pins ponderosas (Pinus ponderosa) a été étudiés de 1983 à 1986. Des analyses multivariables ont montré que l'avifaune et la végétation des régions à l'étude situées près de Princeton en Colombie-Britannique étaient différentes des oiseaux et des forêts étudiées près de Merritt, également en Colombie-Britannique. Les réactions des guildes, sur le plan de la nidification et de la recherche de nourriture, aux modifications de l'habitat étaient en grande partie conformes aux tendances prévues. Aucune des deux méthodes d'exploitation n'a semblé avoir d'influence néfaste sur les oiseaux. L'ouvarture du couvert forestier a entra né de déclin de plusieurs essences arrivées à maturité, mais avait généralement tendance à favoriser la diversification de l'avifaune. En régle générale, les densités des différentes espèces d'oiseaux variaient très peu d'une année à l'autre. Des corrélations établies entre des variables météorologiques et des groupes d'oiseaux permettent de supposer qu'une partie de cette variabilité annuelle pourrait être attribuable aux régimes de la température et des précipitations.

INTRODUCTION

In the dry interior Douglas-fir and Ponderosa Pine forests of British Columbia, 2 methods of logging are frequently used: cutting on the basis of a minimum diameter, or as a percentage of various diameter classes. These methods are known as diameter limit logging and selection cutting, respectively.

The structure and species composition of coniferous and deciduous forests of North America have been and are being altered by logging and silvicultural practices. The alterations to the forest influence the distribution and abundance of birds by changing the structure of the vegetation and the availability of nest-sites, shelter and food. Alterations to the forest structure and the subsequent effects on the avifauna, may be severe following commercial clearcutting or more subtle when selectively logged or diameter limit cut (Freedman *et al*. 1981, Maurer *et al*. 1981, Mannan 1982, and Martin 1988).

According to the model of bird community structure in north temperate forests, developed by Holmes *et al*. (1986), each bird species seems to respond to its environment in a unique way, as determined by its evolutionary history and by a combination of different processes and factors that act on its populations. Some of these factors occur on a local scale (e.g. vegetation structure, food abundance), while others operate over large areas (e.g. weather conditions in areas where species over-winter).

PURPOSE OF THE STUDY

While there have been many studies in the United States examining the effects of forestry practices on bird communities, we are aware of only a few studies of this nature undertaken in Canada (Freeman *et al*. 1981, Welsh 1981, Wetmore *et al*. 1985, Morgan and Freedman 1986). In response to the need for information on the effects of logging in the dry interior of British Columbia, in 1983 the Canadian Wildlife Service initiated a study with the following objectives: i) to determine the densities of breeding bird species in logged and unlogged coniferous forests; ii) to analyze at the bird community, guild and species levels the response to differences and changes in vegetation; iii) to identify the habitat components that the avifauna was apparently responding to.

STUDY AREA

The study was conducted in 2 areas of southwestern British Columbia. Figure 1 provides a quick reference of the history of logging and bird surveys in each area. The Princeton study area was composed of 3 timber plots approximately 20 km south of Princeton. Elevations, slopes, aspects and biogeoclimatic zones and subzones of the study plots are listed in Table 1. Area 1 was logged during the winter of 1979-80 with a minimum size limit of 40 cm diameter at stump height (DSH) for Douglas-fir (Pseudotsuga menziesii) and Ponderosa Pine (Pinus Ponderosa) and 15 cm DSH on all other species. Area 2 was also logged during the winter of 1979-80. All Douglas-fir were left standing, while other species were cut to 15 cm DSH. At the onset of this study, area 3 was designated as the uncut control forest. However, during the summer of 1985, area 3 was logged, precluding any bird surveys that year. Timber was removed with a diameter limit of 35 cm DSH on Douglas-fir and Ponderosa Pine, and 15 cm DSH on all other species. This site was renamed area 4 and surveyed in 1986. All living and dead trees (above the appropriate DSH) are removed during a diameter limit cut. Consequently, most large snags and live trees with dead tops are removed, while deciduous species such as Trembling Aspen (Populus tremuloides) are left standing.

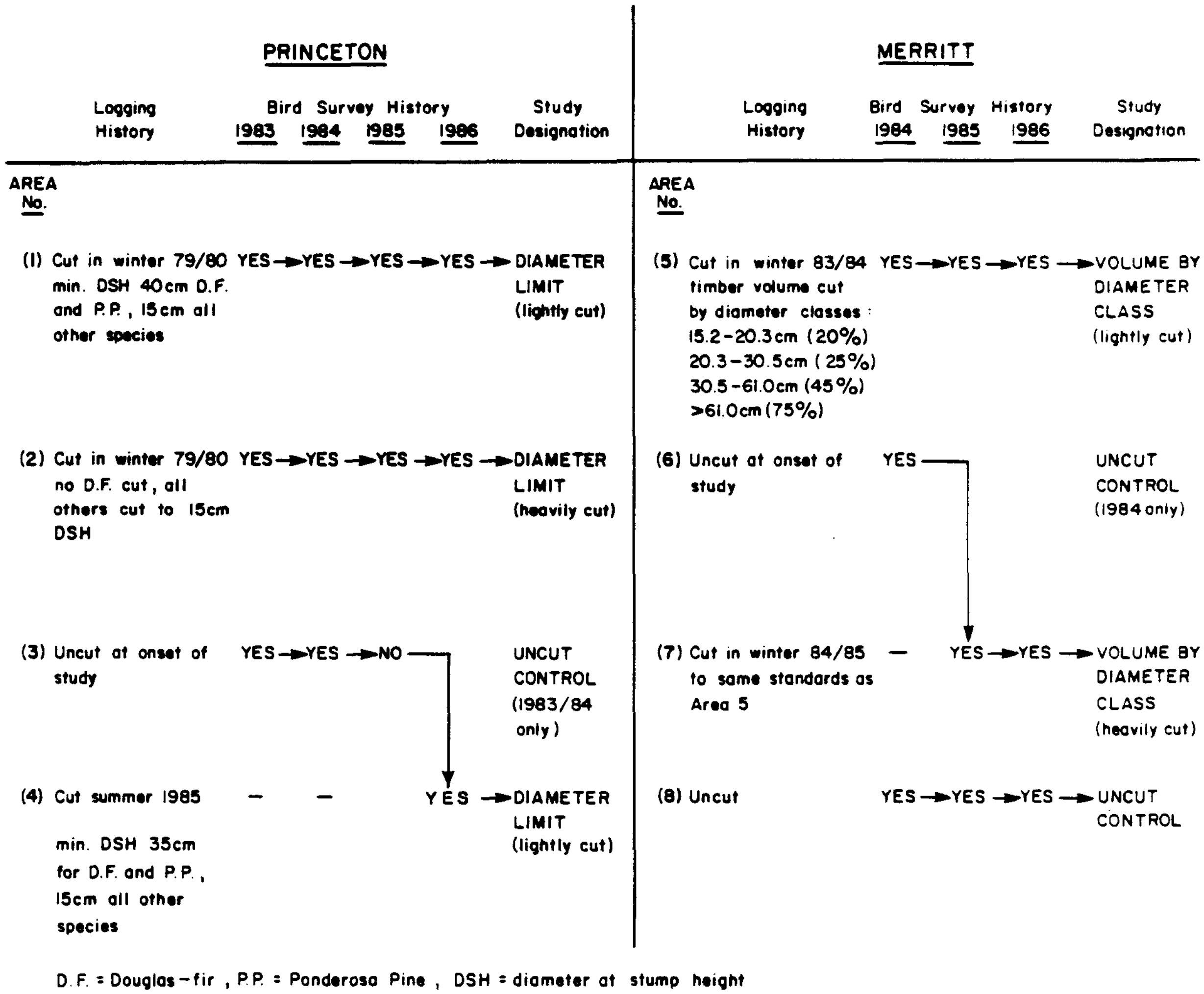


Figure 1. Flow chart summarizing the logging and bird survey histories of each study area.

Table 1. Description of the study area in Princeton (#1-4) and in Merritt (#5-8).

Area #	Location	Size (ha)	Elevation (m)	Slope (o)	Biogeoclimatic Zone (Mitchell & Green 1981)	Biogeoclimatic Subzone (Mitchell & Green 1981)
1	120 34'W, 49 17'N	97	900-1100	2-35	Interior Douglas-fir	Dry Western Montane
2	120 34'W, 49 16'N	50	1000-1250	0-11	Interior Douglas-fir	Dry Western Montane Interior Douglas-fir
					Montane Spruce	Dry Montane Spruce
3	120 34'W, 49 18'N	104	1100-1300	4-19	Interior Douglas-fir	Dry Western Montane Interior Douglas-fir
					Montane Spruce	Dry Montane Spruce
4	120 34'W, 49 18'N	104	1100-1300	4-19	Interior Douglas-fir	Dry Western Montane Interior Douglas-fir
					Montane Spruce	Dry Montane Spruce
5	120 55'W, 50 01'N	88	850-1050	4-22	Interior Douglas-fir	Dry Submontane Interior Douglas-fir and Very Dry Submontane Douglas-fir
6	120 56'W, 50 00'N	89	1000-1150	4-22	Interior Douglas-fir	Dry Submontane Interior Douglas-fir and Very Dry Submontane Douglas-fir
7	120 56'W, 50 00'N	89	1000-1150	4-22	Interior Douglas-fir	Dry Submontane Interior Douglas-fir and Very Dry Submontane Douglas-fir
8	121 02'W, 50 05'N	83	800-900	7-24	Interior Douglas-fir	Dry Submontane Interior Douglas-fir
					Ponderosa Pine-Bunchgrass	Very Dry Northern Ponderosa Pine-Bunchgrass, Forested

The Merritt study area was also composed of 3 timber plots. Areas 5 and 6 were approximately 16 km southwest of Merritt and area 8 was 17 km to the west. Elevations, slopes, aspects and biogeoclimatic zones and subzones for the Merritt study plots are also presented in Table 1. Area 5 was selection logged during the winter of 1983-84. The following percentages of the total volume, by diameter class, were removed: 15.2 - 20.3 cm (diameter at breast height, DBH) 20%, 20.3 - 30.5 25%, 30.5 - 61.0 45% and >61.0 75%. Area 6 was intact for the 1984 bird survey, but was then cut in the winter of 1985-86 to the same standards as area 5. Following logging, this site was renamed area 7 and was surveyed in 1985 and 1986. As with the Princeton study areas, most snags were cut. However, the selection process left some culls and trees with dead tops standing. In addition, species such as Trembling Aspen and willow (*Salix* spp.) were left uncut. Area 8, which is a British Columbia Ecological Reserve, served as the uncut control plot and remained intact for the duration of the study.

METHODS

Measurement of bird communities

The sampling unit was a series of 4 listening points 100 m apart along a straight line. Five sampling units were positioned in each study plot at least 150 m apart. Bird censuses were conducted between 0530 and 1130 from the last week of May through the first week of July. Sampling was not conducted in rain nor when the wind exceeded 10 kph. Singing males were counted at each listening point for 5 minutes following a 1 minute wait. In addition, obvious territorial behaviours such as display flights by hummingbirds (*Trochilidae*), and defence of nest cavities by swallows (*Hirundinidae*) were counted. The distance to each territorial male was measured with a hip chain or a range finder, or estimated to the nearest 5 m.

Each sampling unit was considered to be independent of the other units, as very few observations exceeded 75 m. We felt that this greatly limited the possibility of counting the same bird twice on adjoining units. As we averaged the data from the 4 listening points, there was no problem with dependence within a sampling unit. Population densities were estimated using the modified point-count, quadratic model method (Wetmore et al. 1985).

Bird density was expressed as the number of males/100 ha. Bird species diversity was calculated as $H' = -\sum pi\,(\ln pi)$ (Shannon and Weaver 1949), where pi is the proportion of the total number of individuals occurring as species i. Density and diversity were calculated using only those species with $\geq$0.1 males/100 ha. However, richness (the number of species) also included those that were present but with densities less than 0.1 males/100 ha.

Bird communities were divided into nesting and foraging guilds, modified from Franzreb and Ohmart (1978), Beedy (1981), Morrison (1981), Gruell et al. (1982), Mannan (1982), Airola and Barrett (1985), Repenning and Labisky (1985) and Holmes et al. (1986). The guild categories were i) foraging - ground searcher, foliage searcher, bark searcher and driller, flycatcher (and aerial pursuer), nectar feeder, and raptor; and ii) nesting - ground, canopy, and cavity. Two of the nesting guilds were further sub-divided into: low and high canopy nesters and primary (1') and secondary (2') cavity nesters. We defined low canopy nesters as those species that construct their nests above the ground, but normally below 3 m, whereas high canopy nesters seldom place their nests less than 3 m from the ground. Placement into the low or high canopy sub-guilds was based on Martin (1988) and on data in the British Columiba Nest Records Scheme, Royal British Columbia Museum. Placement of bird species into 1' or 2' cavity nester sub-guilds was based on Raphael and White (1984) and

Cannings *et al*. (1987). The bird communities were subdivided also into permanent residents and summer residents, according to Cannings *et al*. (1987).

Two species of flycatchers (Hammond's and Dusky) could not be accurately identified throughout the study, Others have experienced the same difficulty (Beedy 1981 and Mannan 1982). All records of these species have been lumped as *Empidonax* sp.

Measurement of study area vegetation

Twenty sampling points were established in each area (in the centre of each listening point). Vegetation sampling was conducted in a manner similar to that followed by Mannan (1982). All trees over 2.5 cm (DBH) were tallied in 0.07 ha circular plots (r=15 m). Trees were placed in diameter classes of: <10.0 cm, 10.0-20.0 cm, 20.1-40.0 cm, and >40.0 cm. Tree heights were estimated using a clinometer and placed in height classes: <10.0 m, 10.1-20.0 m, and >20.0 m. Canopy volume of all trees was estimated using the method described by Sturnam (1968). All standing dead trees (snags) over 10 cm DBH and over 3 m tall were included in the sampling.

Cover was estimated using the method described in Mannan (1982) using the following classes of vegetation: high coniferous and high deciduous trees (>10 m tall), mid coniferous and mid deciduous vegetation (1.3-10 m), low coniferous and low deciduous vegetation (0.2-1.29 m), herb and ground cover (<0.2 m), and logs (>0.1 m diameter). Total tree cover was the sum of high and mid cover (coniferous and deciduous). Total deciduous cover was the sum of high, mid and low deciduous cover. Total coniferous cover was the sum of high, mid and low coniferous cover.

Foliage height diversity was calculated using the Shannon-Weaver Index , where p_i = % high canopy cover (coniferous + deciduous), % mid canopy cover, % low canopy cover and % herb cover. Tree species diversity was calculated using the Shannon-Weaver Index where p_i = the stem density (living) of Douglas-fir, Pine species (Ponderosa and Lodgepole Pinus contorta)), Trembling Aspen, willow species and others. The ratios of deciduous to coniferous cover and the stem density of Trembling Aspen to Douglas-fir were also calculated.

Data analysis

Yearly variation in bird species densities

Yearly variation in species densities in each study area was examined using the method of Szaro and Balda (1986). In brief, the density of each species was classified into 1 of 4 categories: lowest density during the study, intermediate density during the study, highest density during the study and tied with another year. Areas with less than 3 years of data (3,4,6,7) were excluded from this analysis. If a species occurred only once during the study it was scored as having its highest density in that year and tied for lowest in each of the other years (Szaro and Balda 1986). Significant year to year variation was tested with the G-statistic (Zar 1974).

Effects of logging on guild proportions and species densities

As previously stated, areas 3 and 6 were cut part way through the study. This provided an opportunity to examine the effects of logging on bird communities. To test for significant differences, we ran a parametric two-way analysis of variance (ANOVA) on each of 9 guild proportions, immediately before and after logging. The guilds tested were: ground foragers, foliage foragers, bark foragers, flycatchers, ground nesters, low and high canopy nesters and 1' and 2' cavity nesters. We also ran ANOVA's on the densities of 5 species of birds expected to increase and 4 species of birds expected to decrease as a result of logging (from Peterson and Peterson 1983).

Bird - habitat relationships

The next step in the data analysis involved testing for relationships using Pearson product-moment correlation coefficients. Averaged vegetation variables and avian community data (taken from the same year as the vegetation survey was done) were tested for correlations. We used bird data from the appropriate years in this analysis due to the possibility of significant annual species density variations. Also, we had only sampled the vegetation once per site, and that the vegetation was constantly changing (albeit slowly), we felt that this was the best way of examining bird-habitat relationships.

The similarity between all study areas, for each year (by species density), was calculated using the coefficient of proportional similarity (PS) where:

$$PS = 2 \sum_{u=1}^{s} \frac{X_{iu}}{Z}, \frac{X_{ju}}{Z}$$

where $$Z = \sum_{i=1}^{s} (X_{iu} + X_{ju})$$

X_{iu} denotes the amount of species u in the entity i, and s is the total number of species in the 2 entities combined (Pielou 1977).

The resultant matrix of coefficients was used to run a cluster analysis using the unweighted pair group method on the arithmetic averages (UPGMA, Sneath and Sokal 1973). Similarities between 20 species of birds (all sites and years) were analyzed by running a cluster analysis (UPGMA) on the standardized densities. The standardization method used in this analysis was a species density in a particular area during a given year divided by the total density of that species during all years, on all sites. A third cluster analysis (UPGMA) was performed on the standardized densities (z-score) of 22 species of birds, averaged for each study area by the number of years and a fourth cluster analyses (UPGMA) was run on 23 standardized (z-score) vegetation variables from each area.

As a final examination of bird-habitat relationships, we ran a principal components analysis (PCA) on 9 vegetation variables from each area to determine the relationships of bird community indices and species densities in the "habitat space" (MacKenzie et al. 1982). We used the averaged vegetation values of each area in this analysis because PCA is inappropriate when there are many zero values and consequently little or no variation along a large part of the continuum (Pimentel 1979). The PCA produced multivariate principal components that were exact mathematical transformations of the original data, with the new multivariate variables being orthogonal (uncorrelated) to each other, and the eigenvalues (the variance along each principal axis) maximized (Morgan and Freedman 1986). The components were rotated using the varimax criterion of Kaiser (1958) in an attempt to improve the interpretation of the axes. We then correlated the averaged densities of the most common bird species against the principal components axes. We used the averaged species densities from each area in this analysis as we were only attempting to produce an approximate description of the average avifauna's response to the average vegetation of the entire area. Most likely the birds were responding to habitat features from an area much larger than that of the 15 m circular vegetation plots.

Bird density and climatic variability

Average monthly temperature and total precipitation from Princeton and Merritt (Monthly Record, Environment Canada, vols. 67-71) were tested with avian variables for correlations. For each year, we used the average of all bird data from the 4 Princeton study areas, and the average of the 4 Merritt sites, in the analyses with the climate variables.

Statistical analyses were performed at the University of Victoria using the SPSS statistical package.

RESULTS AND DISCUSSION

Total breeding bird densities ranged from 177 to 311 males/100 ha (Tables 2 and 3). These values are low compared with densities occurring in similar forests elsewhere. In Douglas-fir/Ponderosa Pine forests in northeastern Oregon, Mannan (1982) estimated densities between 509 and 705 males/100 ha. Szaro and Balda (1986) observed as many as 405 males/100 ha in northern Arizona Ponderosa Pine forests, while Franzreb (1975) reported between 1360 and 2161 individuals/100 ha in Ponderosa Pine/Douglas-fir stands in east-central Arizona.

Fifty-one species of breeding birds were observed in the Princeton areas, compared with 39 from Merritt. Eighteen species found in the Princeton study areas, were not encountered in Merritt, whereas 6 species were unique to Merritt. Table 4 summarizes some of the physical and biological characteristics of the study plots.

Yearly variation in bird species densities

In general, the bird densities and species composition in each study area varied relatively little from year to year. Much higher annual variation has been noted by numerous authors (Wiens 1975, Franzreb and Ohmart 1978, Holmes *et al*. 1986, Szaro and Balda 1986). The results of many studies have suggested that the relatively diverse avifaunas of coniferous forests are no more stable on an annual basis than the low diversity assemblages of open rangelands (James and Boecklen 1984, Wiens 1984, Noon *et al*. 1985). In

Table 2. Densities (males/100 ha) by year in the Princeton study plots. Density estimates were derived using the modified point count - quadratic equation model method. See below for explanation of codes. Scientific names of bird species are listed in Appendix 1.

	Area 1				Area 2				Area 3		Area 4
Species	83	84	85	86	83	84	85	86	83	84	86
'Red-tailed Hawk 5/3	+										
'American Kestrel 5/5					+		+				
*Blue Grouse 2/1		0.3									
*Ruffed Grouse 2/1			+								
'Sora 1/1										+	
'Killdeer 1/1					10.3	3.2	5.1				
'Calliope Hummingbird 6/3			1.9								
'Red-naped Sapsucker 3/4	2.8	1.7	3.5		4.2	6.1	5.5		0.7	0.9	
*Hairy Woodpecker 3/4		7.4			4.0	2.5	7.9		3.9		
*Three-toed Woodpecker 3/4									+	+	
*Northern Flicker 1/4	2.3		2.9	1.5	5.8	7.3	4.6	1.5	0.6	0.7	
*Pileated Woodpecker 3/4			+						+		
'Olive-sided Flycatcher 4/3		+	+				+		+	+	
'Western Wood-Pewee 4/3		1.3	5.0			8.8	3.0	2.5			
'Willow Flycatcher 4/2					+						
'Empidonax sp. 4/2	3.4	4.3	8.6	10.4	13.3	13.9	11.1	12.6			
'Western Flycatcher 4/1	+				+						
'Tree Swallow 4/5							1.3				
*Gray Jay 2/3	1.4				1.4				2.9	3.6	
*American Crow 5/3	+				+				+		
*Common Raven 5/1	+				+					+	
*Mountain Chickadee 2/5	18.2	8.2	20.5	10.2	9.8		16.5		24.0	6.1	4.1
*Red-breasted Nuthatch 3/4	1.5	14.6	7.3	24.2		1.8	2.9	1.8	5.8	9.1	25.6
*Brown Creeper 3/5										1.7	
*Winter Wren 3/5									+		
*Golden-crowned Kinglet 2/3	33.6	15.0	12.0	4.0	12.8				38.4	44.0	8.0
*Ruby-crowned Kinglet 2/3	1.5	7.4			4.4	5.5	8.9	5.5	10.3	3.7	
'Mountain Bluebird 4/5		2.6			4.1	2.6	2.0				
*Townsend's Solitaire 1/1	8.8	4.6	3.7	8.2	0.7				4.4		3.7
'Swainson's Thrush 1/2	1.2		1.5	3.2	0.1		0.5	0.9	3.1	1.5	2.9
'American Robin 1/2	15.6	4.5	1.1	1.1	20.5	7.8	10.7	14.5		1.1	14.5
*European Starling 1/5					3.1	3.9	3.1	3.9			
'Solitary Vireo 2/3	18.8	21.4	34.2	12.8	3.4	2.1	1.7	2.1	1.7	6.4	6.4
'Warbling Vireo 2/2	11.7	9.1	14.6	18.3	24.8	27.4	26.3	30.1			1.8
'Orange-crowned Warbler 2/1	6.8	3.1	3.1	7.9	2.4	1.2	3.9	0.6	1.5		4.3
'Nashville Warbler 2/1										3.5	
'Yellow-rumped Warbler 2/3	33.1	29.3	28.8	32.8	8.4	15.7	12.6	26.7	49.9	40.9	39.6
'Townsend's Warbler 2/2	17.8	33.8	30.1	30.4		2.6	2.1	6.7	45.9	37.7	46.4
'MacGillivray's Warbler 2/2	+	+	+	+	+	+	+		+		
'Wilson's Warbler 2/1						+	+				
'Western Tanager 2/3	38.0	21.6	38.2	33.9	3.5			2.2	5.2	2.2	21.6
'Chipping Sparrow 1/2	13.9	12.6	20.5	28.4	15.0	23.7	21.5	28.4	3.8		25.3
'Vesper Sparrow					+						
*Song Sparrow 1/2					2.7	3.4	0.9				
'White-crowned Sparrow 1/2					+						
*Dark-eyed Junco 1/1	41.1	18.1	18.1	37.2	27.3	7.5	21.7	34.7	38.2	27.1	49.3
'Brown-headed Cowbird 1/6	5.6	9.7	5.6	1.4	11.6	13.9	7.8	11.1		4.2	
'Cassin's Finch 1/3		8.8	8.8			7.5	4.0	3.8		1.3	

Table 2. continued

	Area 1				Area 2				Area 3		Area 4	
Species	83	84	85	86	83	84	85	86	83	84	86	
*Red Crossbill 1/3	+		+						+			
'Pine Siskin 1/3		4.6	4.6		7.0	9.2	14.4		3.7			
*Evening Grosbeak 1/3			+									
Total Density	277.1	244.0	274.6	265.9	200.6	177.6	200.0	189.6	244.0	195.7	253.5	
Bird Species Diversity	2.58	2.81	2.71	2.49	2.83	2.78	2.86	2.37	2.23	2.16	2.24	
Richness (including +)	26	25	28	18	32	24	29	18	25	22	14	
Guild Densities												
Ground Foragers	88.5	62.9	66.8	81.0	104.1	78.2	94.3	98.8	53.8	35.9	95.7	
Foliage Gleaners	180.9	149.2	181.5	150.3	70.9	54.5	72.0	73.9	179.8	148.1	132.2	
Bark Probers	4.3	23.7	10.8	24.2	8.2	10.4	16.3	1.8	10.4	11.7	25.6	
Flycatchers	3.4	8.2	13.6	10.4	17.4	25.3	17.4	15.1	0.0	0.0	0.0	
Ground Nesters	56.7	26.1	24.9	53.3	40.7	11.9	30.7	35.3	44.1	30.6	57.3	
Low Canopy Nesters	63.6	64.3	76.4	91.8	76.4	78.8	73.1	93.2	52.8	40.3	90.9	40.3
High Canopy Nesters	126.4	109.4	133.5	83.5	40.9	48.8	44.6	42.8	112.1	102.1	75.6	
Primary Cavity	6.6	23.7	13.7	25.7	14.0	17.7	20.9	3.3	11.0	10.7	25.6	
Secondary Cavity	18.2	10.8	20.5	10.2	17.0	6.5	22.9	3.9	24.0	7.8	4.1	

+ = <0.1 males/100 ha.

After each species is a 2 digit code. The first number is its foraging guild, and the second is its nesting guild. * = permanent resident, ' = summer resident.

Foraging guilds: 1) ground forager, 2) foliage gleaner, 3) bark prober and driller, 4) flycatcher and aerial pursuit, 5) raptor, 6) nectar feeder.

Nesting guilds: 1) ground, rock, buildings, 2) canopy-low, 3) canopy-high, 4) cavity-primary, 5 cavity-secondary, 6) nest parasite.

Table 3. Densities (males/100 ha) by year in the Merritt study plots. Density estimates were derived using the modified point count - quadratic equation model method. See below for explanation of codes.

	Area 5			Area 6	Area 7		Area 8		
Species	84	85	86	84	85	86	84	85	86
'Red-tailed Hawk 5/3				+					
*Ruffed Grouse 2/1					+				
'Common Nighthawk 4/1							+		
'Calliope Hummingbird 6/3	5.7	3.8		1.9	3.8			5.7	
'Red-naped Sapsucker 3/4		0.9			0.9				
'Willaimson's Sapsucker 3/4				+					
*Hairy Woodpecker 3/4	2.5	2.5		2.5					
*Northern Flicker 1/4				0.7	3.6	2.2	0.7	0.7	0.7
'Olive-sided Flycatcher 4/3	+								
'Western Wood-Pewee 4/3	5.0			3.8			1.3		
'Empidonax sp. 4/2	20.3	13.4	16.7	10.2	28.8	20.0	27.8	25.6	23.3
*Clark's Nutcracker 2/3				+					
*Mountain Chickadee 2/5	10.2	31.8	11.5	4.1	31.1	14.3	2.0	44.3	14.3
*Red-breasted Nuthatch 3/4	3.7	1.8	19.4	12.8	9.1	20.1	7.3	5.5	33.3
*White-breasted Nuthatch 3/4	4.5	1.5		7.4	1.5		7.4	1.5	
*Golden-crowned Kinglet 2/3									16.0
*Ruby-crowned Kinglet 2/3				3.7				3.7	
'Townsend's Solitaire 1/1	8.2	9.1	6.6		8.2	7.3	3.7	10.1	10.1
'Swainson's Thrush 1/2	1.4	0.9	1.4	0.5	1.0	3.4	0.7	1.4	2.2
'American Robin 1/2	13.4	12.3	13.4	5.6	10.0	13.4	10.0	7.8	2.2
'Solitary Vireo 2/3	12.8	6.4	17.1	23.5	22.8	14.9	15.6	32.0	21.4
'Warbling Vireo 2/2		5.5	7.3	6.4	11.0	9.1	1.8	11.0	1.8
'Orange-crowned Warbler 2/1	2.4	1.2		1.8	4.3	0.6			
'Nashville Warbler 2/1	1.7	8.7	1.4		8.7		24.9	9.0	7.0
'Yellow Warbler 2/2					+				
'Yellow-rumped Warbler 2/3	33.7	36.7	36.9	36.4	31.7	37.2	40.1	41.6	41.4
'Townsend's Warbler 2/2	1.3			1.3		2.6	3.9		
'MacGillivray's Warbler 2/2							+		+
'Western Tanager 2/3	10.8	19.4	38.7	13.0	17.3	29.6	8.1	39.7	33.3
'Rufous-sided Towhee 1/1	+							+	
'Chipping Sparrow 1/2	33.2	39.2	26.3	17.4	47.4	40.8	45.8	38.4	44.0
*Song Sparrow 1/2		1.1							
'White-crowned Sparrow 1/2							+		
*Dark-eyed Junco 1/1	18.6	14.6	32.5	32.7	46.4	45.7	25.6	16.6	18.1
'Brown-headed Cowbird 1/6	23.6	9.7	8.9	1.4	16.7	11.1		2.8	
'Cassin's Finch 1/3	22.5	20.0	15.0	15.0	17.5	10.0	10.0	10.0	22.5
*Red Crossbill 1/3		+							
'Pine Siskin 1/3	13.4	27.2	7.4	18.4	9.2		9.2	3.8	9.2
*Evening Grosbeak 1/3				+					

Table 3. continued

Species	Area 5 84	Area 5 85	Area 5 86	Area 6 84	Area 7 85	Area 7 86	Area 8 84	Area 8 85	Area 8 86
Total Density	248.9	267.7	260.5	220.5	331.3	282.3	245.9	311.2	300.8
Bird Species Diversity	2.58	2.64	2.52	2.63	2.68	2.50	2.47	2.56	2.51
Richness (including +)	23	23	17	26	23	17	22	22	18
Guild Densities									
Ground Foragers	134.3	134.1	111.5	91.7	160.0	133.9	105.7	91.6	109.0
Foliage Gleaners	72.9	109.7	112.9	90.2	126.9	108.3	96.4	181.3	135.2
Bark Probers	10.7	6.7	19.4	22.7	11.5	20.1	14.7	7.0	33.3
Flycatchers	25.3	13.4	16.7	14.0	28.8	20.0	29.1	25.6	23.3
Ground Nesters	30.9	33.6	40.5	34.5	67.6	53.6	54.2	35.7	17.5
Low Canopy Nesters	69.6	72.4	65.1	41.4	98.2	89.3	90.0	84.2	73.5
High Canopy Nesters	103.9	113.5	115.1	115.7	102.3	91.7	84.3	136.5	143.8
Primary Cavity	10.7	6.7	19.4	23.4	15.1	22.3	15.4	7.7	34.0
Secondary Cavity	10.1	31.8	11.5	4.1	31.1	14.3	2.0	44.3	14.3

+ = <0.1 males/100 ha.

After each species is a 2 digit code. The first number is its foraging guild, and the second is its nesting guild. * = permanent residence, ' = summer residence.

Foraging guilds: 1) ground forager, 2) foliage gleaner, 3) bark prober and driller, 4) flycatcher and aerial pursuit, 5) raptor, 6) nectar feeder.

Nesting guilds: 1) ground, rock, buildings, 2) canopy-low, 3) canopy-high, 4) cavity-primary, 5) cavity-secondary, 6) nest parasite.

Table 4. Summary of habitat analysis.

Area	1	2	3	4	5	6	7	8
Basal Area (m^2/ha)	13.9	3.1	38.6	9.4	12.8	18.5	10.0	18.5
Canopy Volume (m^3/ha)	15899.3	2095.5	26515.8	10470.3	13306.0	14222.7	9059.2	11144.2
Tree Cover (%)	49.8	5.7	69.3	27.1	42.0	47.7	27.8	42.3
Ground Cover (%)	45.7	56.9	56.6	22.8	30.9	38.7	25.4	27.7
Log Cover (%)	4.1	3.2	6.0	6.2	2.8	2.3	5.9	4.8
Deciduous Cover (%)	13.5	2.5	4.4	1.1	14.0	12.2	9.8	20.6
Coniferous Cover (%)	50.3	6.1	76.3	28.3	42.8	52.0	31.5	47.4
# live stems/ha <10cm diam.	544.0	157.8	1013.8	374.0	311.2	269.4	255.7	218.4
# live stems/ha 10.1-20cm	182.4	33.9	310.7	147.1	182.5	163.4	142.2	99.0
# live stems/ha 20.1-40cm	105.3	11.9	209.9	58.6	66.5	65.7	58.7	64.2
# live stems/ha >40cm	5.7	7.1	49.5	9.1	18.3	35.2	14.1	49.4
# Douglas-fir/ha <10m tall	505.2	10.6	737.2	339.6	242.0	194.5	181.1	141.5
# Douglas-fir/ha 10.1-20m	216.5	10.6	203.7	109.0	121.0	52.4	33.3	60.1
# Douglas-fir/ha >20.1m	45.3	7.1	74.9	26.2	5.0	2.8	2.8	5.7
# Pine sp./ha <10m	5.6	136.6	121.7	52.3	155.7	148.6	120.3	122.4
# Pine sp./ha 10.1-20m	13.4	11.3	162.7	42.5	27.6	79.9	63.0	66.5
# Pine sp./ha >20.1 m	1.4	2.1	19.8	10.6	9.9	10.6	7.0	23.3
# Trembling Aspen/ha <10m	18.4	23.3	0.7	0.0	6.3	27.6	26.1	7.8
# Trembling Aspen/ha 10.1-20m	7.1	2.1	1.4	0.0	2.1	10.6	4.2	0.0
# Trembling Aspen/ha >20.1m	2.1	2.1	0.7	0.0	0.0	0.0	0.0	0.0
# Stems/ha other tree species	22.6	4.6	10.6	261.1	9.2	4.9	4.2	3.5
# Snags/ha	19.7	5.7	39.5	8.5	2.8	9.2	5.7	9.9
Foliage height diversity	1.29	0.52	1.26	1.18	1.32	1.27	1.26	1.37
Tree species diversity	0.39	0.88	0.99	0.64	0.78	0.95	0.93	0.82

Pine sp. - Lodgepole Pine in areas 1-4, Ponderosa Pine in areas 5-8.

contrast, Brewer (1963) concluded that temperate forest bird populations were relatively stable. Table 5 illustrates that in our study, only area 2 had significantly different annual densities. If we consider the overall annual variation of the 4 areas, the changes in density were not significant, suggesting that the avifauna of the forests we studied, were relatively stable.

Effects of logging on guild proportions and species densities

Areas 3(4) and 6(7) were not examined for annual variation due to the fact that they were logged part way through the study. Table 6 gives the proportions of total bird density for the foraging and nesting guilds in each area. The results of the analysis of variance of the pre- and post-logging guild proportions and the densities of 9 species of birds are presented in Table 7. In most cases, the changes agreed with trends observed by others. The proportion of ground foragers significantly increased following logging in both areas. This has been reported elsewhere (Flack 1976, Franzreb and Ohmart 1978, Maurer et al. 1981). This increase is a result of more foraging surfaces, more observation posts and greater protection of nest sites (Franzreb and Ohmart 1978).

There was only a slight decline in foliage searchers following logging of both areas. This differs from the pronounced post-logging changes others have noted. It is believed that foliage searchers decline following logging due to either the reduction in the total biomass of foliage (rather than a loss of tree volume or decreased foliage height diversity), or a decline in insect prey (Franzreb 1977, Franzreb and Ohmart 1978, Des Granges 1980).

Morrison (1981) found that with the removal of the deciduous portion of the canopy, some species (e.g. Orange-crowned and Wilson's warblers) shifted their foraging locations down from their "preferred" positions, rather than

Table 5. Patterns of bird densities on those study areas with at least three years of data (modified from Szaro and Balda 1986).

Area #	Number of Species					
Year	Lowest	2nd Lowest	2nd Highest	Highest	Tie	G-statistic
1						
1983	3	4	6	10	15	
1984	6	4	5	6	17	6.294 (ns)
1985	2	3	4	10	19	(12 df)
1986	4	3	4	6	21	(P=0.90)
2						
1983	8	3	8	14	7	
1984	3	3	6	7	21	26.633*
1985	3	9	5	9	14	(12 df)
1986	9	4	2	6	19	(P=0.009)

	Lowest	Intermediate	Highest	Tie	G-statistic
5					
1984	4	7	10	7	8.248 (ns)
1985	6	8	8	6	(6 df)
1986	10	2	7	9	(P=0.22)
7					
1984	6	1	10	11	9.765 (ns)
1985	5	5	10	8	(6 df)
1986	4	6	4	14	(P=0.13)
				Total	50.940 (ns) (36 df) (P=0.051)

* = significant ($P<0.05$), ns = not significant, df = degrees of freedom

Table 6. Proportions of major nesting and foraging guilds, expressed as a percentage of the total bird density in each area.

Area	1				2				3		4	5			6	7		8		
Guild / Year	83	84	85	86	83	84	85	86	83	84	86	84	85	86	84	85	86	84	85	86
a) Foraging																				
Ground foragers	32	24	23	31	48	44	40	52	21	18	38	49	40	40	33	46	47	39	28	33
Foliage gleaners	65	63	68	56	39	36	43	39	75	76	52	35	51	46	50	41	38	43	60	48
Bark probers/drillers	2	10	4	9	4	6	8	1	4	6	10	4	3	8	10	4	7	6	2	11
Flycatchers/ aerial pursuit	1	3	5	4	9	14	9	8	0	0	0	10	5	6	6	9	7	12	8	8
b) Nesting																				
Ground	20	11	9	20	20	7	15	19	18	16	22	12	13	16	16	20	19	23	12	12
Low canopy	23	26	28	34	38	44	37	49	22	21	36	28	27	25	19	30	32	34	27	24
High canopy	46	45	49	31	20	27	22	23	46	52	30	42	42	44	52	31	32	36	44	48
Primary cavity	2	10	5	10	7	10	11	2	4	5	10	4	2	8	11	5	8	6	2	11
Secondary cavity	7	4	7	4	9	4	11	2	10	4	2	4	12	4	2	9	5	1	14	5

Some minor guilds are not reported here, consequently the sum of the proportions does not always equal 100.

Table 7. Results of the analysis of variance tests on the guild proportions and species densities observed in areas 3 and 5, before and after logging. Following cutting, the areas were renamed areas 4 and 7, respectively.

	Area 3/4		Area 6/7	
Foraging Guild	Trend	P	Trend	P
(% of total bird density)				
Ground	Increased	.001*	Increased	.006*
Foliage	Decreased	.382	Decreased	.991
Bark	Increased	.128	Decreased	.804
Flycatch	-		Increased	.237
Nesting				
(% of total bird density)				
Ground	Increased	.004*	Increased	.102
Low Canopy	Increased	.001*	Increased	.019*
High Canopy	Decreased	.144	Decreased	.094
1' cavity	Increased	.104	Increased	.853
2' cavity	Decreased	.428	Decreased	.975
# Expected to increase due to logging				
(density)				
Dark-eyed Junco	Increased	.004*	Increased	.258
Chipping Sparrow	Increased	.001*	Increased	.036*
American Robin	Increased	.009*	Increased	.008*
Swainson's Thrush	Increased.	.367	Increased	.008*
Western Tanager	Increased	.027*	Increased	.100
# Expected to decrease due to logging				
(density)				
Red-breasted Nuthatch	Increased	.055	Decreased	.333
Solitary Vireo	No change	1.000	Decreased	.466
Townsend's Warbler	Increased	.365	Decreased	.667
Golden-crowned Kinglet	Decreased	.005*	-	

Note: we compared the densities of area 3 (1984) with area 4 (1986), and area 6 (1984) with area 7 (1985).

* = significant at $p<0.05$.
- = not present on site.
= species sensitive to logging identified in Peterson and Peterson (1983).

abandoning the site. A similar response on our post-logging sites, could offset the effects of the habitat changes, producing the minor changes we noted in the proportion of foliage foragers.

Bark drillers and probers either decline following logging due to a lack of foraging substrates (Franzreb and Ohmart 1978) or became more abundant, due to increased foraging substrate on the ground, increased ease of access to the logs and increased insect prey (Conner and Crawford 1974, Anderson 1979). Our results were inconsistent; the proportions of this guild increased slightly on the Princeton site and showed a small decline in Merritt.

Flycatchers were absent from area 3(4). Although the proportions of this group of birds increased following logging in Merritt, the change was not significant. Noon et al. (1979), and Maurer et al. (1981) observed that flycatchers disappeared completely following total clearcutting, either due to a lack of perch sites, or because of a shift in insect species or density. However, many authors have reported that flycatchers were more abundant in forests with openings (natural or man-made) than in forests without such openings. This has been attributed to a greater abundance of insects, availability of open perches, and room for aerial pursuit (Haapanen 1965, Kilgore 1971, Franzreb and Ohmart 1978, Beedy 1981 and Mannan 1982).

Variation in nesting guild proportions may more closely reflect habitat changes than foraging guilds do. Martin (1988) felt that species richness and density may be less correlated with foliage for foraging because foliage is only an index of food availability and actual distribution of food may be only loosely correlated with foliage. Martin continued by stating that foliage is a much more direct assay of nest sites because it provides the substrate for the nest and the cover to protect the nest from predators and weather.

Ground nesters tend to benefit from logging, due to a reduction in canopy cover, greater shrub cover and increased log cover (Flack 1976 and Morgan 1984). Table 7 shows that while ground nesters increased significantly in the Princeton area, there was only a slight change in Merritt. This variable response may have been due to the differences in logging treatments. The limited amount of timber removed from the Merritt area may have been insufficient to benefit ground nesters.

Low canopy nesters increased significantly in both areas. A reduction in the tree canopy would likely attract higher densities of species that prefer to nest in low shrubs, beneath a partial canopy, such as Dusky Flycatcher, American Robin and Chipping Sparrow (Johnson 1963, Mannan 1982, Szaro and Balda 1986 and Cannings _et al_. 1987).

Due to the removal of the canopy nesting substrate, we expected to see a sharp decline in the proportion of high canopy nesters. If certain birds were capable of modifying their concept of the "right" nesting height, as Morrison (1981) noted with the shifting of foraging heights, they could exploit altered habitats. Flexibility such as this, by high canopy nesters could produce the less-than-expected responses of this guild to logging.

The abundance of cavity nesters usually declines following logging, primarily due to the loss of suitable nest sites (Flack 1976, Webb 1977, Mannan 1982, Peterson and Peterson 1983, and Raphael and White 1984). Our results did not follow observed trends. Following logging, the proportion of 1' cavity nesters increased very slightly, while 2' cavity nesters showed a slight decline. We can offer no explanation for these results.

Bird species expected to increase due to logging all showed significant increases (Table 7). However, of the 4 species that were expected to decline post-cutting, only Golden-crowned Kinglets responded as predicted. The changes in the densities of the other 3 species were inconsistent; showing increases on the site that was most intensely logged, while declining slightly on the selection cut area. Conceivably, annual variations masked the expected post-cutting declines.

According to Webb et al. (1977) the avifauna in unlogged forests are not supplanted by a totally different fauna after logging. Others have found similar results, concluding that the effects of forest practices vary with the type and age of the stands, the silvicultural method employed and the intensity of application of the treatments and that no intensity or method can be selected as being better or worse (Webb 1977, Freedman et al. 1981, Maurer et al. 1981, Szaro and Balda 1986). Our results support these conclusions. While some species were absent following logging, resulting in a decline in species richness, other species were found only on the altered sites. Overall, total bird density and bird species diversity increased on both sites following logging.

The positive relationships between the extent of forest fragmentation and the degree of nest parasitism and nest predation are areas of concern to Brittingham and Temple (1983), Wilcover (1985) and Martin (1988). As forests become more fragmented due to logging, a larger portion of forest interiors become available to nest parasites (e.g. Brown-headed Cowbird) and predators. This may result in lower reproductive success and/or the loss of certain sensitive species. In our study, Cowbirds were more numerous on the more open sites and increased in density after logging of area 6 (Tables 2 and 3).

The logging methods (and intensities) studied here, appear not to have dramatically harmed the avian community. However, if the current practice of forest fragmentation results in increased nest parasitism and/or predation, we suggest that there will be dramatic changes in the bird species composition of North American forests.

Bird-habitat relationships

Table 8 shows the results of the correlations between avian and habitat variables. Bird species diversity was significantly ($p<0.02$) correlated with the number of Trembling Aspen present. As the ratio of Douglas-fir to Trembling Aspen increased there was a significant ($p<.01$), negative relationship with the diversity of birds. Many authors (Odum 1950, Winternitz 1976, Winkler and Dana 1977, and Beedy 1981) have noted that stands dominated by coniferous trees usually supported a less diverse bird population, than either mixed or deciduous dominated forests.

Ground foragers were negatively associated with developed stands (i.e. dense canopy cover, high stem density and high basal area), whereas foliage searchers appeared to prefer such forests. This supports the finding of others (Franzreb and Ohmart 1978, Maurer et al. 1981, and Morgan and Freedman 1986).

Flycatchers appeared to be less numerous in stands where Douglas-fir dominated, and on sites where there was a high density of stems less than 10 cm in diameter. Such stands as these, may have been less suitable because of insufficient perches, restricted mobility, or inappropriate insect prey.

Low canopy nesters were negatively associated with stand development, whereas increasing tree cover appeared to promote higher numbers of high canopy nesters. Franzreb and Ohmart (1978) similarly found that low canopy nesters were more abundant on disturbed sites, while high canopy nesters were more common on uncut stands.

Although we tested bird density, species richness and the proportion of bark foragers, ground nesters, and primary and secondary cavity nesters with the habitat variables listed in Table 8, we found no significant relationships.

Table 8. Summary of results of correlation analysis between average avian community and habitat variables. Only significant correlation results are listed. See below for acronym definitions.

Habitat variable	BSD	Foraging guilds (% of total) Ground	Foliage	Flycatch	Nesting guilds (% of total) Low canopy	High canopy
FHDI						
TSDI						
BAAR		-.849***	.727*			
CAVO		-.865***	.811**		-.766*	.728*
TRCO		-.810**	.704*		-.801**	.834***
DECO						
COCO		-.819**			-.787*	.805**
COCO/DECO				-.761*		
GRCO						
LOCO						
ST. <10 cm dbh		-.852***	.904***	-.730*		
ST. 10-20 cm dbh		-.779*	.770*		-.740*	
ST. 20-40 cm dbh		-.870***	.867***			
ST. >40 cm dbh						
ST. <10 m tall		-.845***	.870***			
ST. 10-20 m tall	-.711*	-.881***	.885***			
ST. >20 m tall	-.732*	-.862***	.902***			
# snags			.932***			
Total stems		-.862***	.882***			
# Tr. Aspen	.802**					
# Pine						
# Douglas-fir		-.825**	.909***	-.792**		
# D.-fir/ # Tr. Aspen	-953.***					

p,.01 ***, p<.02 **, p<.05 *

FHDI = Foliage Height Diversity, TSDI = Tree Species Diversity, BAAR = Basal Area, CAVO = Canopy Volume, TRCO = Total Tree Cover, DECO = Deciduous Cover, COCO = Coniferous Cover, COCO/DECO = Ratio of Coniferous Cover to Deciduous Cover, GRCO = Ground Cover, LOCO = Log Cover, ST. = Number of Stems/ha # D.-fir/# Tr. Aspen = Ratio of the Number of Stems/ha of Douglas-fir to Trembling Aspen.

BSD = Bird Species Diversity

Table 9 shows the results of the correlation analyses between bird species and the same habitat variables. In summary, Northern Flicker, Red-naped Sapsucker, Hairy Woodpecker, American Robin, Solitary Vireo, Warbling Vireo, Orange-crowned Warbler, Chipping Sparrow and Cassin's Finch appeared to be associated with more open areas, with abundant low shrubs and/or a high number of deciduous trees. In contrast, Red-breasted Nuthatch, Swainson's Thrush, Yellow-rumped Warbler, Townsend's Warbler and Pine Siskin appeared to be associated with a wide range of habitats, from stands of mixed deciduous and coniferous trees to those forests dominated by conifers. Generally, these results support the observations of others (e.g. Franzreb 1978, Kroodsma 1982, Peterson and Peterson 1983, Szaro and Balda 1986, and Cannings et al. 1987). Other bird species were tested for habitat associations, but we did not find significant correlations. This may suggest that many species of birds have broad habitat requirements.

Figure 2 displays the results of the cluster analysis by area by year, based on proportional similarity coefficients. If vegetation characteristics are more important than year to year variability of extrinsic factors (e.g. weather), in determining the size and composition of the avifauna, then the study areas should cluster by vegetation similarity. With the exception of those sites modified by logging, an area should be most similar to itself, from year to year. However, if extrinsic factors are more important than the vegetation, then the study sites should cluster by years (Szaro and Balda 1986). Our results (Fig. 2) initially suggested a compromise between the 2 hypotheses; some pairing occurred between the same years, and others between the same area. However, by examining each of the first order linkages (i.e. when only 2 lines are linked), 6 out of 8 involved the same areas (e.g. area 8 1985 and area 8 1986). This strongly supports the hypothesis that the

Table 9. Summary of results of correlation analyses between average bird density and habitat variables. Only significant correlations results are listed. See below for acronym definitions.

Bird species	NOFL	RNSA	HAWO	RBNU	SWTH	AMRO	SOVI	WAVI	OCWA	YRWA	TOWA	CHSP	CAFI	PISI
Habitat variable														
FHDI	-.79**	-.86***						-.83**		.85***				
TSDI									-.77*					
BAAR						-.87***				.73*				
CAVO						-.82**				.73*				
TRCO						-.85***				.76*				
DECO							.83***						.74*	
COCO						-.87***		-.71*		.78*				
COCO/DECO					.76*						.88***			
GRCO			.86***	-.79**								.76*		
LOCO					.92***									-.86***
ST. <10cm dbh						-.71*					.73*	-.75*		
ST. 10-20cm														
ST. 20-40cm						-.81**								
ST. >40cm						-.76*			-.74*					
ST. <10m tall						-.72*						-.72*		
ST. 10-20m						-.78*								
ST. 20m						-.72*					.75*	-.71*		
# Snags						-.83**								
Total stems												-.71*		
# Tr. Aspen														
# Pine									-.86***					
Douglas-fir											.78*			
D.-fir/Tr.Asp.					.76*			-.74*		.71*	.76*			

p<.01 = ***, p<.02 = **, p<.05 = *

FHDI=Foliage Height Diversity, TSDI=Tree Species Diversity, BAAR=Basal Area, CAVO=Canopy Volume, TRCO=Total Tree Cover, DECO=Deciduous Cover, COCO=Coniferous Cover, COCO/DECO=Ratio of Coniferous Cover to Dedicuous Cover, GRCO=Ground Cover, LOCO=Log Cover, ST.=Number of Stems/ha.

NOFL=Northern Flicker, RNSA=Red-naped Sapsucker, HAWO=Hairy Woodpecker, RBNU=Red-breasted Nuthatch, SWTH=Swainson's Thrush, AMRO=American Robin, SOVI=Solitary Vireo, WAVI=Warbling Vireo, OCWA=Orange-crowned Warbler, YRWA=Yellow-rumped Warbler, TOWA=Townsend's Warbler, CHSP=Chipping Sparrow, CAFI=Cassin's Finch, PISI=Pine Siskin.

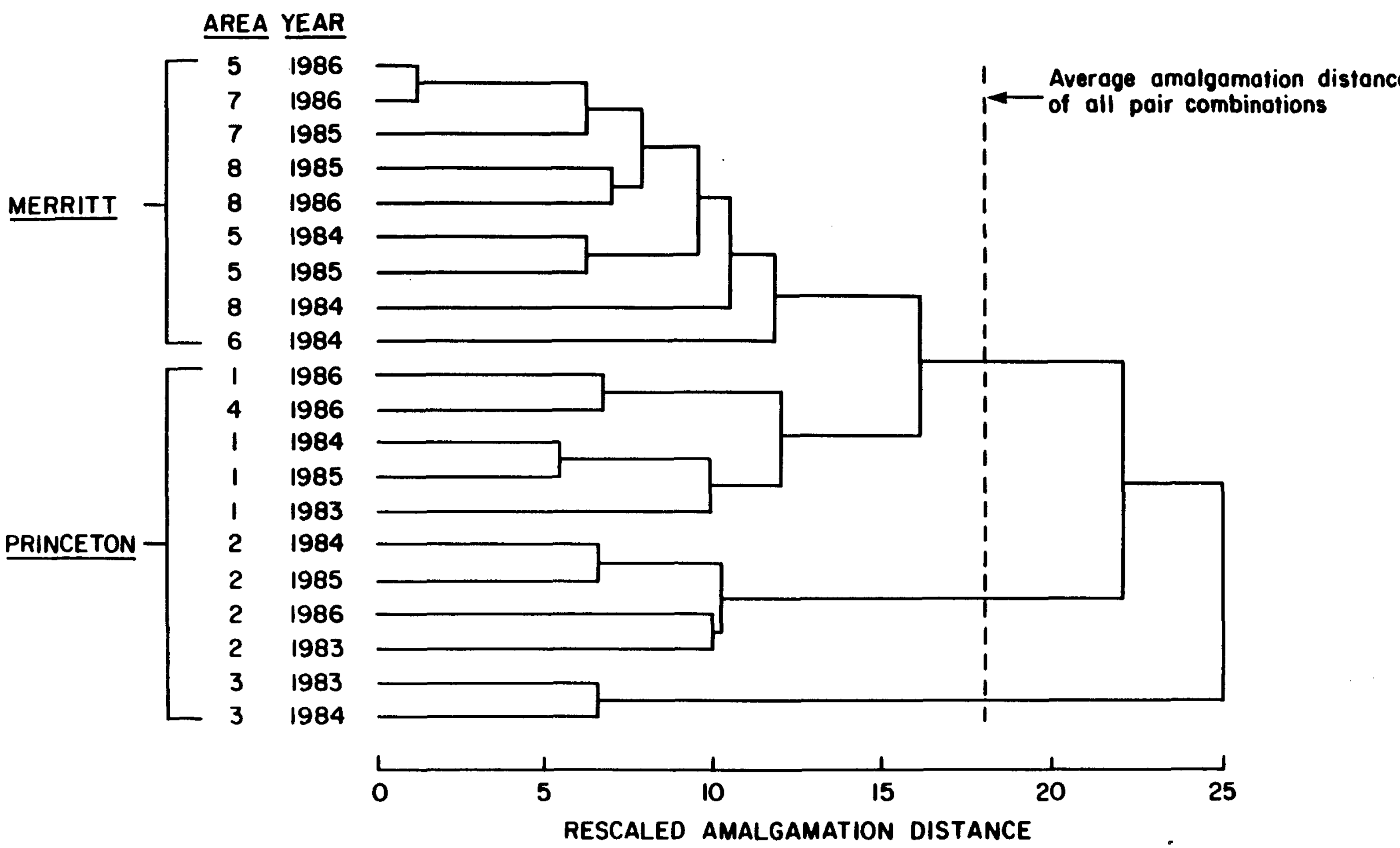


Figure 2. Cluster analysis dendrogam of coefficients of proportional similarities based on the densities of all species of birds observed on all sites from 1983 to 1986.

composition of the bird community was largely controlled by the vegetation. Szaro and Balda (1986) came to the same conclusion.

Determining where an area enters the cluster (greater or less than the mean linkage distance between all pair combinations) is a way to distinguish distinct groupings (Holmes et al. 1979). Figure 2 indicates that areas 2 and 3 were quite distinct from the others in terms of avian communities. Area 2, the most heavily cut stand, with numerous Trembling Aspen, and pockets of shrubby mixed deciduous and isolated large Douglas-fir, supported the most diverse bird community. Area 3 on the other hand, was uncut and the most "coniferous" of all the stands, having the highest conifer cover, the densest canopy volume, and the greatest number of coniferous stems. This site had the lowest diversity of birds. This again supports the observation that the avifauna of conifer forests are frequently less diverse than that occurring in mixed or pure deciduous forests.

The first linkage to the left of the mean linkage line, is where the Princeton areas join those from Merritt. This suggests that in terms of species composition and densities, the Princeton and Merritt areas had dissimilar avian communities.

Figure 3 shows the results of the cluster analysis of the standardized densities of the 20 most common species of birds. This figure shows 3 groupings of birds. From top to bottom, group 1 represents a spectrum of bird species from those associated with open, mixed deciduous/coniferous habitats (the first 5 species), through those species found in a broad range of habitats (the next 4 species), to those species more frequently associated with coniferous forests (the next 4 species) (Johnson 1963, Meslow and White 1975, Mannan 1977, Manuwal and Munger 1978, Beedy 1981, Holmes and Robinson 1981, Mannan 1982, Franzreb 1983, Peterson and Peterson 1983, Szaro and Balda 1986, and Cannings et al. 1987). Group 2 is made up of species strongly associated with deciduous vegetation, especially Trembling Aspen, in either edge situations, or in open habitats (James 1971, Kilham 1971, Conner et al. 1975, Crockett and Hadow 1975, Galli et al. 1976, Franzreb 1978, and Keisker 1987). The 3 species making up group 3 are considered by many authors to represent species of mature forests (Kessler 1980, Vermeer 1980, Kroodsma 1982, and Peterson and Peterson 1983).

Further evidence supporting the hypothesis that habitat characteristics, to a large extent, control the species composition and density of birds, is illustrated in Figures 4a and 4b. Figure 4a represents the clustering of areas based upon standardized vegetation variables, and Figure 4b is based upon standardized average densities of the 19 most common species of birds. The linkage patterns are extremely similar. Again, areas 2 and 3 appear to be most dissimilar, in terms of vegetation and birds. In addition, Figures 4a and 4b show that the Princeton study areas were more-or-less distinct from the Merritt sites.

In a final attempt to examine the relationships between habitat structure and the avian community, we analyzed a portion of the vegetation data using principal components analysis (PCA). We reduced the number of variables considerably due to redundancy caused by variable inter-correlations. However, the results of this analysis should be considered descriptive, rather than mathematically rigorous, due to the small sample size. Table 10 shows that the first component accounted for 38.4% of the habitat variation, and loaded heavily on total conifer cover, the density of Douglas-fir stems and the density of snags. The second component represented a gradient from open stands with abundant herb and ground cover, to dense mixed stands with an evenly developed foliage profile (i.e. high foliage height diversity). The second component accounted for an additional 24.2% of the variation. PCA

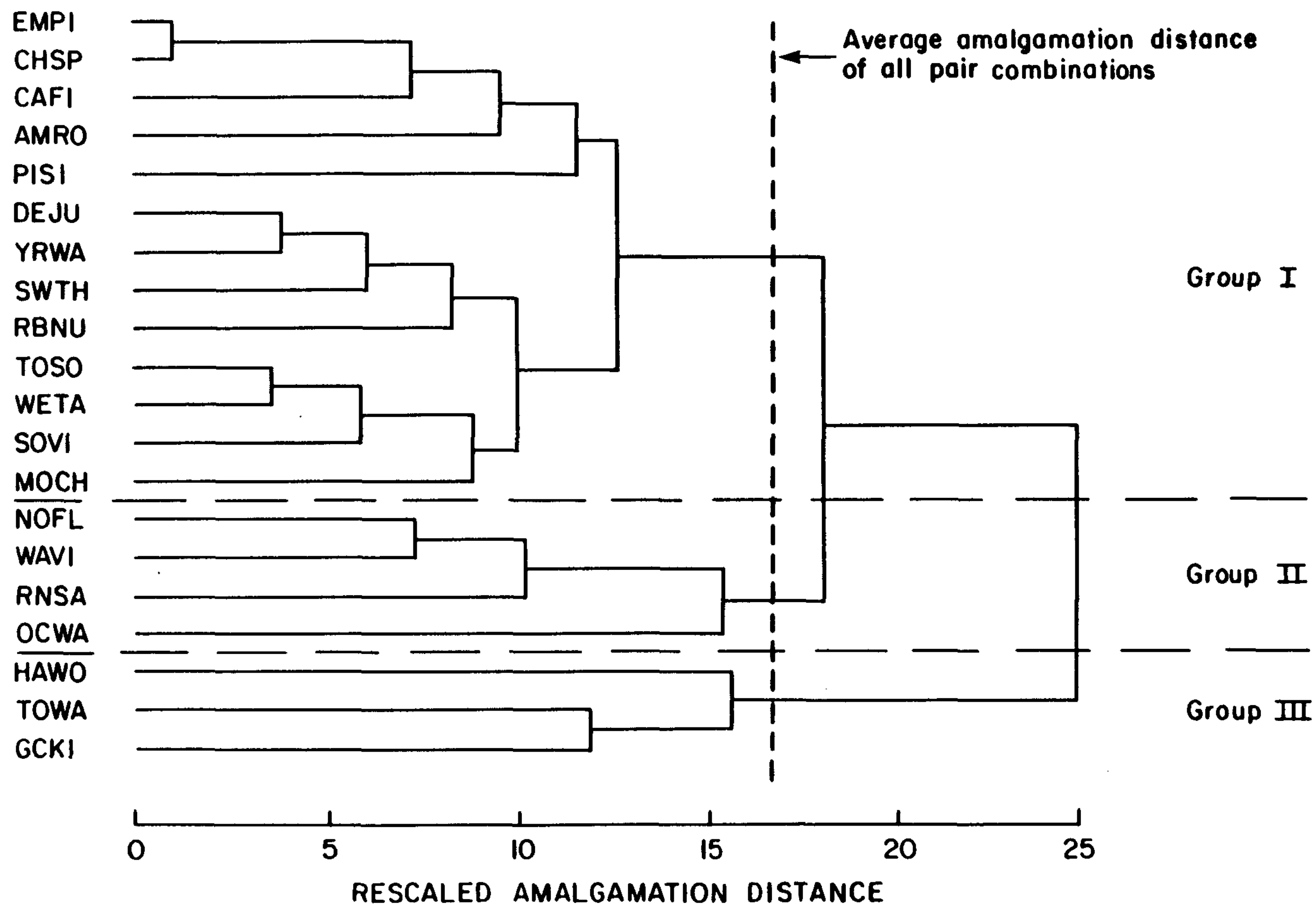
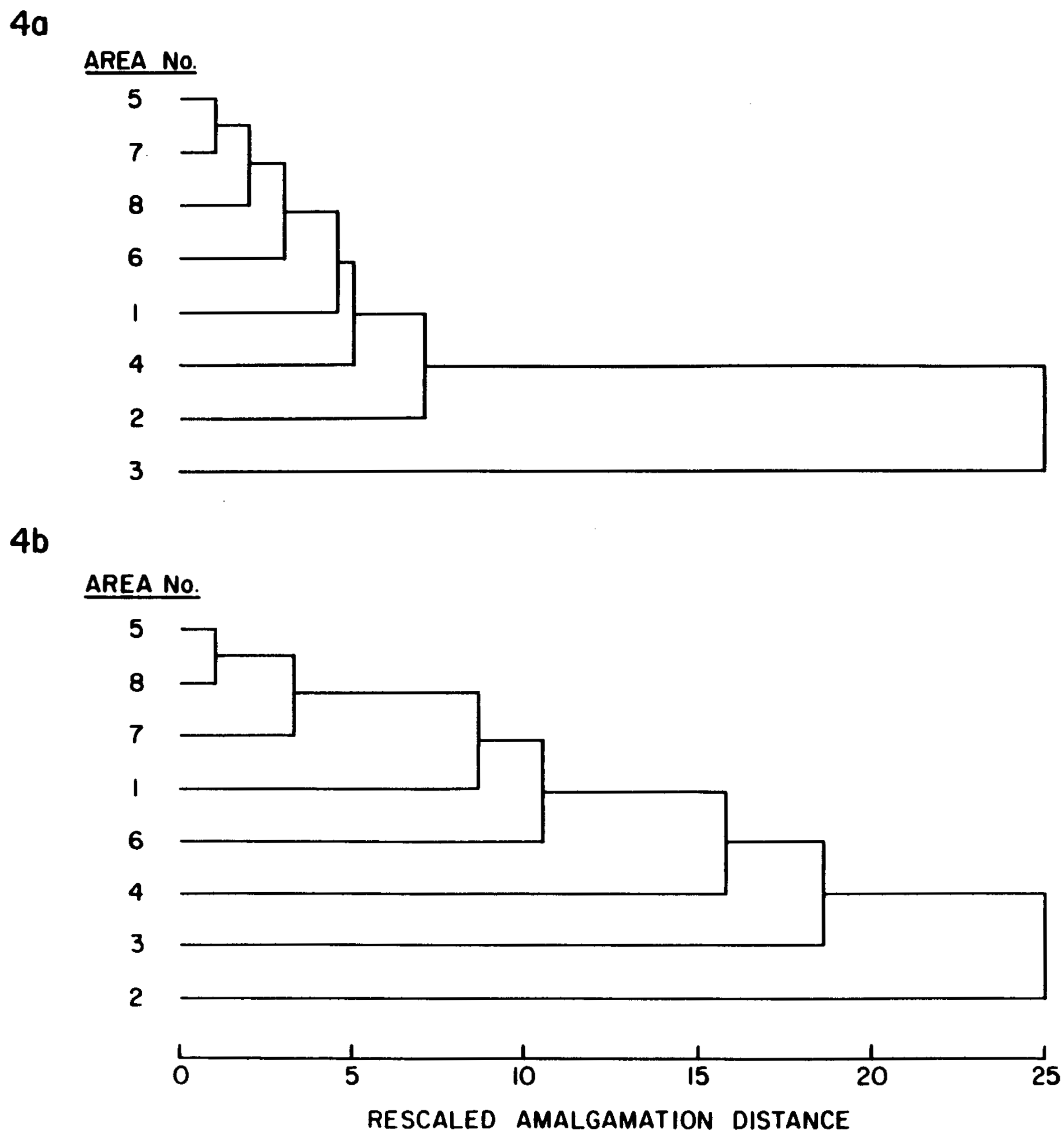


Figure 3. Cluster analysis of dendrogram of bird species densities in Princeton and Merritt from 1983 to 1986.



Figures 4a and 4b. Cluster analysis dendrograms based upon average vegetation variables (4a) and average bird species densities (4b).

Table 10. Results of principal components analysis of vegetation variables.

	Component		
	I	II	III
Eigenvalue	3.457	2.177	1.617
% of total variance explained	38.4	24.2	18.0
Cumulative %	38.4	62.6	80.6
<u>Components loading on variables</u>			
Number of Douglas-fir stems/ha	.8995	-.1985	-.0113
Number of Trembling Aspen stems/ha	-.5291	-.0553	.5976
Number of pine stems/ha	.3839	.0328	.2963
Number of snags/ha	.8887	-.3915	.1622
% Ground cover	.1943	-.8028	.5257
% Log cover	.5096	-.0647	-.7377
% Total coniferous cover	.8945	.2388	.3648
% Total deciduous cover	.0057	.8071	.4380
Foliage height diversity	.5769	.7890	.0231

axis 3 loaded only percent log cover, and accounted for another 18.0% of the variation, for a cumulative total of 80.6%.

The factor scores of each component upon each area were used to quantify a particular site's position on each axis. These scores were then correlated with avian variables (Table 11 and Figures 5 and 6). The positions of high canopy nesters and foliage searches in Figure 5 suggests that birds in these guilds were associated primarily with coniferous forests. In contrast, ground foragers, and low canopy nesters appeared to be associated with open stands and dense growths of low vegetation, while ground nesters appeared to select relatively undisturbed sites, (i.e. low log cover).

Figure 6 shows the apparent habitat associations of 10 species of birds. This figure shows a gradient from dense, undisturbed coniferous stand species (Golden-crowned Kinglet and Townsend's Warbler) to those species more frequently occurring in open to shrubby habitats (American Robin and Chipping Sparrow). The 10 remaining species listed in Table 11 were not significantly correlated with any of the PCA axes. This suggests that: we did not include the appropriate variables in the analysis, we did not measure the habitat on a fine enough scale, or that these species have broad habitat tolerances, allowing them to exploit a wide range of environment.

Bird density and climatic variability

The average temperatures and precipitation totals by season that occurred during the study period are presented in Table 12. These data were regressed against 9 avian variables (Table 13). Raphael and White (1984) and Szaro and Balda (1986) observed significant negative correlations between precipitation and cavity nesters, summer residents and permanent residents. Permanent residents, adapted to winter conditions, may be less affected by summer weather than the tropically derived and perhaps more physiologically sensitive

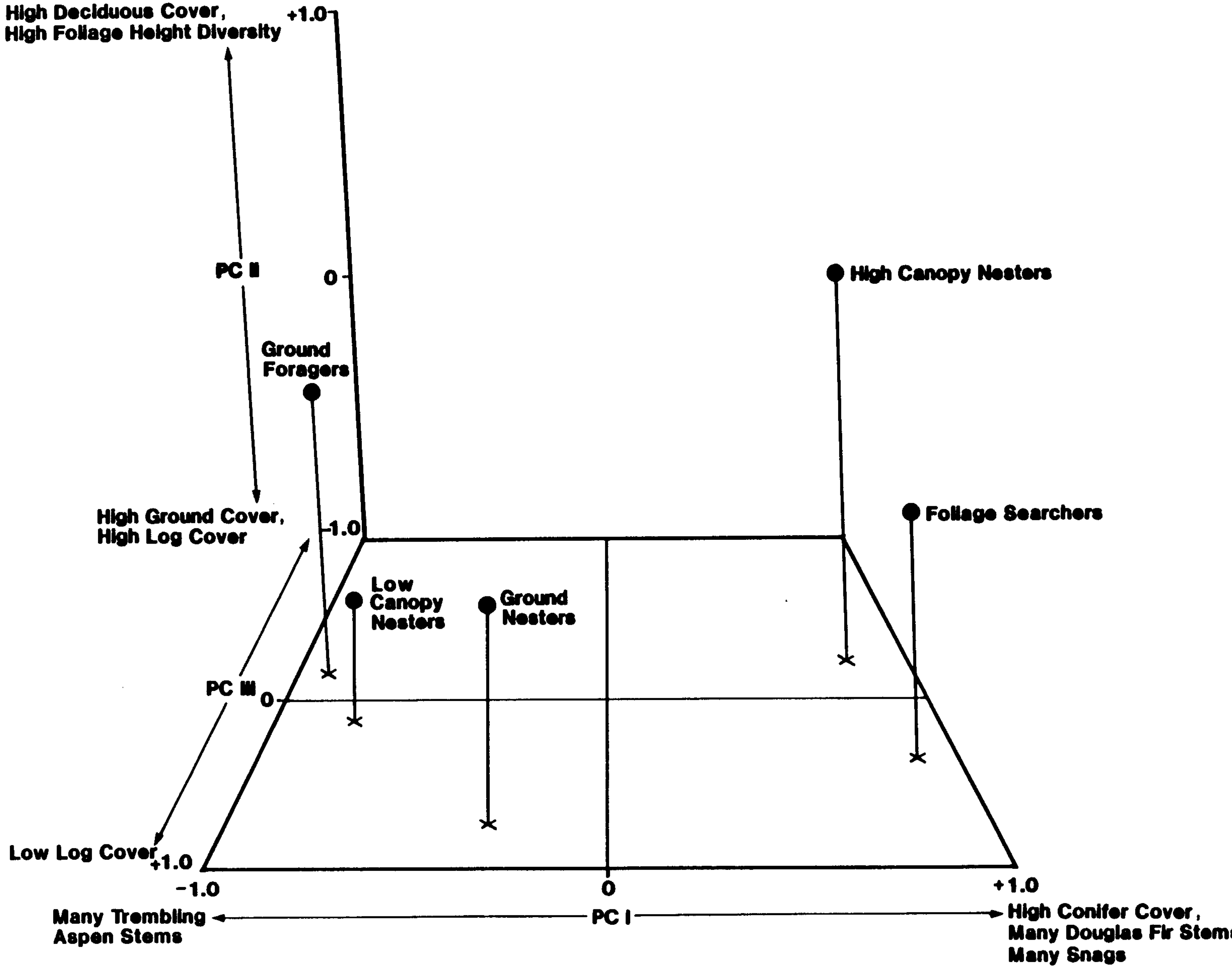


Figure 5. Correlations between guild proportions (nesting and foraging) and site factor scores of the habitat principal components. Only those guilds that were significantly correlated with 1 principal component axis have been included here. Each axis has been scaled according to the percentage of the habitat variation it explains.

Table 11. Correlations between guild proportions and species densities with principal component axes.

	PC I	PC II	PC III
<u>Foraging guilds</u> (% of total density)			
Ground foragers	-.889**	-.069	-.193
Foliage searchers	.874**	-.058	.360
Bark probers and drillers	-.158	.195	.099
Flycatchers	-.486	.148	-.667
<u>Nesting guilds</u> (% of total density)			
Ground nesters	-.309	-.143	.742*
Low canopy nesters	-.746*	-.513	.112
High canopy nesters	.776*	.512	-.260
1^{o} cavity nesters	-.349	-.061	-.083
2^{o} cavity nesters	.202	-.062	-.067
<u>Average species densities</u>			
Red-naped Sapsucker	-.252	-.742*	-.411
Hairy Woodpecker	.279	-.618	-.675
Northern Flicker	-.310	-.649	-.386
Empidonax sp.	-.430	-.507	-.352
Mountain Chickadee	.129	.512	.128
Red-breasted Nuthatch	-.316	.447	.625
Golden-crowned Kinglet	.845**	-.298	.419
Townsend's Solitaire	-.204	.688	.287
Swainson's Thrush	.075	.099	.956***
American Robin	-.922**	-.147	.112
Solitary Vireo	-.018	.779*	-.386
Warbling Vireo	-.401	-.608	-.543
Orange-crowned Warbler	-.247	-.232	.216
Yellow-rumped Warbler	.493	.606	.542
Townsend's Warbler	.379	-.315	.745*
Western Tanager	-.264	.725*	.177
Chipping Sparrow	-.722*	.540	.014
Dark-eyed Junco	-.197	-.070	.589
Cassin's Finch	-.218	.724*	-.509
Pine Siskin	-.073	.346	-.763*

P<.001 ***, p<.01 **, p<.05 *

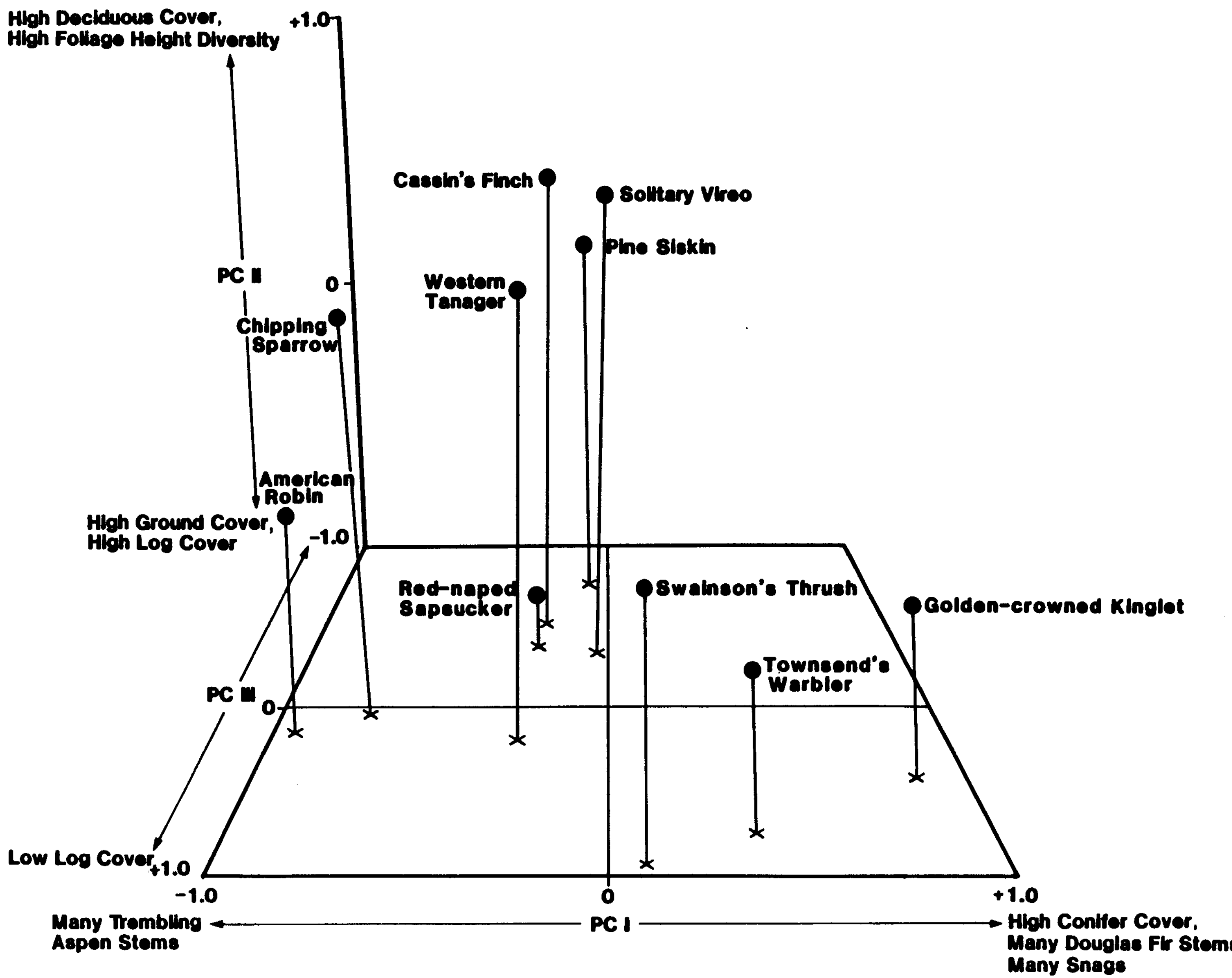


Figure 6. Correlations between bird species densities and site factor scores of the habitat principal components. Only those species that were significantly correlated with 1 principal component axis have been included here. Each axis has been scaled according to the percentage of the habitat variation it explains.

Table 12. Average temperatures and total precipitation by season that occurred during the study. A "+" or "-" after each value indicates whether above or below the 10 year average.

	Temperature (°C)			Precipitation (cm)		
	Winter	Spring	Breeding season	Winter	Spring	Breeding season
Princeton						
1982/1983	-2.9+	9.4+	14.9+	151.7-	33.4-	78.2+
1983/1984	-3.2+	7.0-	15.8+	117.6-	34.0-	50.0+
1984/1985	-5.9-	9.1+	17.3+	115.4-	35.2-	15.0-
1985/1986	-6.8-	8.6+	15.6+	167.0-	39.6+	77.4+
Merritt						
1983/1984	-1.4+	8.2-	16.9+	83.0-	33.8+	36.8-
1984/1985	-4.7-	10.2+	18.1+	125.1-	37.0+	34.8-
1985/1986	-5.6-	9.5+	16.6+	109.5-	60.8+	149.3+

Winter = November through February
Spring (migratory period) = April and May (most migrants arrive during this period (Cannings et al. 1987))
Breeding Season - June and July

Table 13. Results of correlation analyses between avian variables and climatic data. Only significant correlations are listed. See Tables 2 and 3 for designation of cavity and non-cavity nesters and permanent and summer residents.

	Average temperature			Total precipitation			
	Winter	Spring	Breeding Season	Winter	Spring	Breeding Season	Spring + Breeding Season
Bird density		.869**					
Bird species diversity	-.782*					-.855**	-.879***
Species richness							
Density of cavity nesters		.755*					
Density of non-cavity nesters		.814*					
Density of permanent residents							
Density of summer residents			.870**				
Permanent residents/ total density			-.785*				
Summer residents/ total density			.785*				

Note: The bird variables used in these analyses were the average values for that year for all of the Princeton study areas and all of the Merritt areas.

p<.01***
p<.02**
p<.05*

summer residents (Holmes et al. 1986). In our study, we did not find any significant relationships between groups of birds (e.g. summer residents) and total precipitation. However, we did observe a strong negative association ($p<0.01$) between the diversity of birds and the total precipitation during the migration period and the breeding season. Average spring temperature appeared to be more closely associated with the density of birds. The densities of cavity and non-cavity nesters were significantly correlated ($p<0.05$) with the average spring temperature, while increasing breeding season temperatures appeared to significantly ($p<0.05$) promote higher densities of summer residents. The negative association between the proportion of permanent residents and temperature was likely related more to the higher density of summer residents, rather than an actual drop in permanent resident numbers. While these results do suggest a link between climate variability and population levels, we must caution the reader that we did not have site specific weather data, thereby preventing more rigorous analyses.

CONCLUSIONS

The results of this study showed that the forests and associated avifauna of Princeton and Merritt were similar, and yet distinct enough to be separated by various statistical methods. Over the duration of the study, total bird densities remained relatively stable, but there was considerable year to year variation at the species level.

Changes brought about by logging were only in part predictable. This suggested that many of the species were more adaptable to the altered vegetation, than we expected. Neither logging method studied here appeared to be overly harmful, in comparison to what might have occurred to the avifauna if the stands had been clearcut. By cutting only a portion of the conifers, and by leaving most deciduous trees standing, the forests took on a park-like appeareance that attracted a wide range of birds. Open-habitat species, species associated with varying degrees of canopy closures, edge specialists and many cavity nesters exploited these modified habitats.

We observed that seasonal weather patterns appeared to affect the densities of certain groupings of birds. These associations might either mask or exaggerate the bird communities' responses to habitat modifications. For example, the inconsistent response by cavity nesters to logging, may have been as much a response to weather variability as to habitat alteration. We suggest that weather parameters should be monitored and included in all investigations examining the relationships between the avifauna and their habitat. We also recommend that studies such as this, should be of a longer duration, so that seasonal avian and climatic variability can be adequately assessed.

The results of many of the analyses strongly suggested that the diversity and density of the bird community were largely controlled by the structure and composition of the forest. On a regional level, it would appear that a mosaic of forest types and ages, with an abundant deciduous component would support the richest avifauna. However, this will open up a greater proportion of the interior of forests, allowing higher nest parasitism and predation (as well as adversely affecting those species requiring large tracts of uncut forest). The long-term effects of forest fragmentation are unknown, but most likely will result in a very different regional avifauna.

ACKNOWLEDGEMENTS

We wish to thank T. Bekhuys, B. Booth, R. Heggs, A. Hetherington, B. Jedrejewska, W. Jedrejewska, C. Samper Kutschbach, and D. Smith, for their assistance in collecting the field data. We also express our thanks to Weyerhaeuser Canada in Princeton and Balco Industries in Merritt, for allowing access to the study areas. M. Darveau and J-P. Savard kindly reviewed this manuscript. A special thanks goes to B. Forer for his invaluable assistance in the analysis of the data.

LITERATURE CITED

Airola, D.A. and R.H. Barrett. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. Condor 87:205-216.

Anderson, S.H. 1979. Changes in forest bird species composition caused by transmission line corridor cuts. American Birds 33: 3-6.

Beedy, E.C. 1981. Bird communities and forest structure in Sierra Nevada of California. Condor 83: 97-105.

Brewer, R. 1963. Stability in bird populations. Occasional Papers of the Adams Center for Ecological Study 7: 1-12.

Brittingham, M.C. and S.A. Temple. 1983. Have Cowbirds caused forest songbirds to decline? Bioscience 33: 31-35.

Cannings, R.A., R.J. Cannings and S.G. Cannings. 1987. Birds of the Okanagan Valley, British Columbia. Royal British Columbia Museum, Victoria, B.C.

Conner, R.N. and H.S. Crawford. 1974. Woodpecker foraging in Appalachian clearcuts. J. Forestry 72: 564-566.

Conner, R.N., R.G. Hooper, H.S. Crawford and H.S. Mosby. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. J. Wildl. Manage. 39: 144-150.

Crockett, A.B. and H.H. Hadow. 1975. Nest site selection by Williamson's and Red-naped sapsuckers. Condor 77: 365-370.

Des Granges, J.L. 1980. Avian community structure of six forest stands in La Mauricie National Park, Quebec. Occaisonal Paper 41. Canadian Wildlife Service.

Flack, J.A.D. 1976. Bird populations of aspen forests in western North America. Ornith. Monogr. 19. Amer. Ornith. Union.

Franzreb, K.E. 1975. Avian densities in a mixed-coniferous forest, Thomas Creek, White Mountains, Arizon. Western Birds 6: 101-105.

Franzreb, K.E. 1977. Bird population changes after timber harvesting of a mixed conifer forest in Arizona. USDA Forest Service Research Paper RM-184.

Franzreb, K.E. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forests. Wilson Bulletin 90: 221-238.

Franzreb, K.E. 1983. A comparison of avian foraging behavior in unlogged and logged mixed-coniferous forest. Wilson Bulletin 95: 60-76.

Franzreb, K.E. and R.D. Ohmart. 1978. The effect of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80: 431-441.

Freedman, B., C. Beauchamp, I.A. McLaren and S.I. Tingley. 1981. Forestry management practices and populations of breeding birds in a hardwood forest in Nova Scotia. Can. Field-Nat. 95: 307-311.

Galli, A.E., C.F. Leck and R.T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93: 356-364.

Gruell, G.E., W.C. Schmidt, S.F. Arno and W.J. Reich. 1982. Seventy years of vegetative change in a managed Ponderosa Pine forest in western Montana - implications for resource management. USDA Forest Service General Technical Report INT-130. Intermountain Forest and Range Experiment Station. Ogden, Utah.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession I. Ann. Zool. Fenn. 2: 153-196.

Holmes, R.T., R.E. Bonney Jr. and S.W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60: 512-520.

Holmes, R.T. and S. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwood forest. Oecologia 48: 31-35.

Holmes, R.T., T.W. Sherry and F.W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecol. Monogr. 56: 201-220.

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83: 215-236.

James, F.C. and W.J. Boecklen. 1984. Interspecific morphological relationships and densities of birds. pp. 458-477 in: Ecological communities: conceptual issues and the evidence. D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle eds. Princeton Univ. Press, Princeton, New Jersey.

Johnson, N.K. 1963. Biosystematics of sibling species of flycatchers in the Empidonax hammondii-oberholseri-wright complex. Univ. Calif. Publ. Zool. 66: 79-238.

Kaiser, H.F. 1958. The varimax criterion for analytic rotation in factor analysis. Psychometrika 23: 187-200.

Karr, J.R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70: 348-357.

Keisker, D.G. 1987. Nest tree selection by primary cavity-nesting birds in south-central British Columbia. B.C. Min. Env. and Parks, Victoria, B.C. Wildlife Report R-13.

Kessler, W.B. 1980. Bird populations of riparian habitats in the Tongass National Forest of southeast Alaska. USDA Forest Service, Ketchikan, Alaska. Unpublished paper.

Kilgore, B.M. 1971. Response of breeding bird populations to habitat changes in a Giant Sequoia forest. Amer. Midl. Nat. 85: 135-152.

Kilham, L. 1971. Reproductive behavior of Yellow-bellied Sapsuckers I. Preference for nesting in Fomes-infected aspens and nest hole interrelations with flying squirrels, raccoons and other animals. Wilson Bulletin 83: 159-171.

Kroodsma, R.L. 1982. Edge effect on breeding forest birds along a power line corridor. J. Appl. Ecol. 19: 361-370.

MacKenzie, D.I., S.G. Sealy and G.D. Sutherland. 1982. Nest site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. Can. J. Zoo. 60: 2212-2223.

Mannan, R.W. 1977. Use of snags by birds, Douglas-fir region, western Oregon. M.Sc. thesis, Oregon State Univ., Corvallis, Oregon.

Mannan, R.W. 1982. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. Ph.D. thesis, Oregon State Univ. Eugene, Oregon.

Manuwal, D.A. and G. Munger. 1978. The effect of timber harvest on bird populations in the Douglas-fir forests of Washington State. Final report to U.S. Forest Service. Univ. Washington, Seattle, Washington.

Martin, T.E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? Ecology 69: 74-84.

Maurer, B.A., L.B. McArthur and R.C. Whitmore. 1981. Effect of logging on guild structure of a forest bird community in West Virginia. American Birds 35: 11-13.

Meslow, E.C. and H.M. Wight. 1975. Avifauna and succession in Douglas-fir forests of the Pacific. pp. 266-271 in: Symposium on management of forest and range habitats for nongame birds. USDA Forest Service General Technical Report WO-1. Tucson, Arizona.

Mitchell, W.R. and R.E. Green. 1981. Identification and interpretation of ecosystems of the western Kamloops forest region. vols. 1 and 2. B.C. Min. Forests, Victoria, B.C.

Morgan, K.H. 1984. Breeding bird communities of a post-clearcutting secondary succession in a Nova Scotia hardwood forest. M.Sc. thesis, Dalhousie Univ., Halifax, Nova Scotia.

Morgan, K.H. and B. Freedman. 1986. Breeding bird communities in a hardwood forest succession in Nova Scotia. Can. Field-Nat. 100: 506-519.

Morrison, M.L. 1981. The structure of western warbler assemblages: analysis of foraging behaviour and habitat selection in Oregon. Auk 98: 578-588.

Noon, B.R., V.P. Bingman and J.P. Noon. 1979. The effects of changes in habitat on northern hardwood forest bird communities. pp. 33-48 in: Management of north central and the northeastern forests for nongame birds. USDA Forest Service General Technical Report NC-51. North Central Forest Experiment Station. St. Paul, Minn.

Noon, B.R., D.K. Dawson and J.P. Kelly 1985. A search for stability gradients in North American breeding bird communities. Auk 102: 64-81.

Odum, E.P. 1950. Bird populations of the highlands Plateau in relation to plant succession and avian invasion. Ecology 31: 587-605.

Peterson, E.B. and N.M. Peterson. 1983. Summer bird densities in relation to forest types in western North America: annotated bibliography and analysis of literature. Canadian Wildlife Service, Delta, B.C.

Pielou, E.C. 1977. Mathematical Ecology. J. Wiley and Sons, New York.

Pimentel, R.A. 1979. Morphometrics. The Multivariate Analysis of Biological Data. Kendal-Hunt Publ. Co., Iowa.

Raphael, M.G. and M. White. 1984. Use of snags by cavity-nesting birds in Sierra Nevada. Wildl. Monogr. 86: 1-66.

Repenning, R.W. and R.F. Labisky. 1985. Effects of even-age timber management on bird communities of the Longleaf Pine forest in northern Florida. J. Wildl. Manag. 49: 1088-1098.

Shannon, C.W. and W. Weaver. 1949. The Matematical Theory of Communication. Univ. Illinois Press, Urbana.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical Taxonomy. W.H. Freeman, San Francisco.

Sturnam, W.A. 1968. Description and analysis of breeding habitats of the chickadees Parus atricapillus and P. rufescens. Ecology 49: 418-431.

Szaro, R.C. and R.P. Balda. 1986. Relationships among weather, habitat structure, and Ponderosa Pine forest birds. J. Wildl. Manag. 50: 253-260.

Verner, J. 1980. Bird communities of mixed-conifer forests of the Sierra Nevada. pp. 198-223 in: Proceedings of the workshop, Management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86. Intermountain Forest and Range Experiment Station. Ogden, Utah.

Webb, W.L. 1977. Songbird management in a northern hardwood forest. pp. 439-448 in: Transactions of the 42nd North American Wildlife and Natural Resources Conference. K. Sabol ed. Wildlife Management Institute, Washington, D.C.

Webb, W.L., D.F. Behrend and B. Saisorn. 1977. Effects of logging on songbird populations in a northern hardwood forest. Wildl. Monogr. 55: 1-6.

Welsh, D.A. 1981. Impact on bird populations of harvesting the boreal mixed wood forest. pp. 155-167 in: Boreal mixedwood symposium O-P-9. Canadian Forest Dept. Envir.

Wetmore, S.P., R.A. Keller and G.E.J. Smith. 1985. Effects of logging on bird populations in British Columbia as determined by a modified point-count method. Can. Field-Nat. 99: 224-233.

Wiens, J.A. 1975. Avian communities, energetics, and functions in coniferous forest habitats. pp. 226-265 in: Symposium on management of forests and range habitats for nongame birds. USDA Forest Service General Technical Report WO-1, Tucson, Arizona.

Wiens, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. pp. 439-457 in: Ecological communities: conceptual issues and the evidence. D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle eds. Princeton Univ. Press. Princeton, New Jersey.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66: 1211-1214.

Winkler, D.W. and G. Dana. 1977. Summer birds of a lodgepole-aspen forest in the southern Warner Mountains, California. West. Birds. 8: 45-62.

Winternitz, B.L. 1976. Temporal change and habitat preference of some montain breeding birds. Condor 78: 383-393.

Zar. J.H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix 1. Scientific names and acronyms of all bird species mentioned in the text.

Red-tailed Hawk	*Buteo jamaicensis*	RTHA
American Kestrel	*Falco sparverius*	AMKE
Blue Grouse	*Dendragapus obscurus*	BLGR
Ruffed Grouse	*Bonasa umbellus*	RUGR
Sora	*Porzana carolina*	SORA
Killdeer	*Characrius vociferus*	KILL
Common Nighthawk	*Chrodeiles minor*	CONI
Calliope Hummingbird	*Stellula calliope*	CAHU
Red-naped Sapsucker	*Sphyrapicus nuchalis*	RNSA
Williamson's Sapsucker	*Sphyrapicus thyroideus*	WISA
Hairy Woodpecker	*Picoides villosus*	HAWO
Three-toed Woodpecker	*Picoides tridactylus*	TTWO
Northern Flicker	*Colaptes auratus*	NOFL
Pileated Woodpecker	*Dryocopus pileatus*	PIWO
Olive-sided Flycatcher	*Contopus borealis*	OSFL
Western Wood-Pewee	*Contopus sordidulus*	WWPE
Willow Flycatcher	*Empidonax traillii*	WIFL
Hammond's Flycatcher	*Empidonax hammondii*	HAFL
Dusky Flycatcher	*Empidonax oberholseri*	DUFL
Western Flycatcher	*Empidonax difficilis*	WEFL
Tree Swallow	*Tachycineta bicolor*	TESW
Gray Jay	*Perisoreus canadensis*	GRJA
Clark's Nutcracker	*Nucifraga columbiana*	CLNU
American Crow	*Corvus brachyrhynchos*	AMCR
Common Raven	*Corvus corax*	CORA
Mountain Chickadee	*Parus gambeli*	MOCH
Red-breasted Nuthatch	*Sitta canadensis*	RBNU
White-breasted Nuthatch	*Sitta carolinensis*	WBNU
Brown Creeper	*Certhia americana*	BRCR
Winter Wren	*Troglodytes troglodytes*	WIWR
Golden-crowned Kinglet	*Regulus satrapa*	GCKI
Ruby-crowned Kinglet	*Regulus calendula*	RCKI
Mountain Bluebird	*Sialia currucoides*	MOBL
Townsend's Solitaire	*Myadestes townsendi*	TOSO
Swainson's Thrush	*Catharus ustulatus*	SWTH
American Robin	*Turdus migratorius*	AMRO
European Starling	*Sturnus vulgaris*	EUST
Solitary Vireo	*Vireo solitarius*	SOVI
Warbling Vireo	*Vireo gilvus*	WAVI
Orange-crowned Warbler	*Vermivora celata*	OCWA
Nashville Warbler	*Vermivora ruficapilla*	NAWA
Yellow Warbler	*Dendroica petechia*	YEWA
Yellow-rumped Warbler	*Dendroica coronata*	YRWA
Townsend's Warbler	*Dendroica townsendi*	TOWA
MacGillivray's Warbler	*Oporonis tolmiei*	MAWA
Wilson's Warbler	*Wilsonia pusilla*	WIWA
Western Tanager	*Piranga ludoviciana*	WETA
Rufous-sided Towhee	*Pipilo erythrophthalmus*	RSTO
Chipping Sparrow	*Spizella passerina*	CHSP
Vesper Sparrow	*Pooecetes gramineus*	VESP
Song Sparrow	*Melospiza melodia*	SOSP

Appendix 1. continued

White-crowned Sparrow	Zonotrichia leucophrys	WCSP
Dark-eyed Junco	Junco hyemalis	DEJU
Brown-headed Cowbird	Molothrus ater	BHCO
Cassin's Finch	Carpodacus cassinii	CAFI
Red Crossbill	Loxia curvirostra	RECR
Pine Siskin	Carduelis pinus	PISI
Evening Grosbeak	Coccothraustes vespertinus	EVGR