

Distribution and abundance of birds relative to elevation and biogeoclimatic zones in coastal old-growth forests in southern British Columbia

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Abstract

This study examined birds and their association with forest structure and elevation in 1992 and 1993. The research sites were located in old-growth forest stands (251+ years) distributed between 400 and 1500 m elevation in south coastal British Columbia. The use of simple and multiple regressions revealed that the variation in mean abundance of most bird species was in part explained by elevation, and was likely due to stand structure and other factors (e.g., forage productivity) that vary with the elevational gradient. However, total bird abundance and richness responded weakly to elevation; instead, density of huge snags (≥ 100 cm DBH) per hectare more consistently accounted for the variation in these two measures.

Distributions of bird species are described according to two biogeoclimatic zones—the Coastal Western Hemlock and the Mountain Hemlock. Biogeoclimatic classification, which is based on plant associations and climate, is used for forest management in British Columbia. Mean abundance of 10 bird species differed significantly between the biogeoclimatic zones in at least one of the study years. Biogeoclimatic zones also effectively classified bird species into two different communities using multidimensional scaling and mean similarity analysis. However, richness and total bird abundance did not differ significantly between zones indicating that community structure was similar, although composition and dominance differed by zone. The authors, therefore, suggest that representation of old-growth forest by biogeoclimatic zone helps maintain bird diversity. To maintain the observed distributions of bird species, however, old-growth habitats should be represented over the entire elevational gradient and include variation in forest stand structure.

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Introduction

Occurrence of bird species correlates with vegetation structure (Roth 1976; Finch 1989, 1991). In turn, vegetation structure and several other factors, such as temperature and productivity, vary along the environmental gradient associated with elevation (Able and Noon 1976; Rahbek 1997; Hofer *et al.* 1999). Because elevation affects the condition of the physical environment and the kinds and amounts of resources available for breeding and foraging activities, the composition and structure of bird communities may change along elevational gradients (Able and Noon 1976; Cody 1981; Stevens 1992). Physical conditions become more adverse for some birds at higher elevations. As elevation increases, the availability of resources for birds diminishes reflecting differences in forest stand structure, site productivity, vegetation species composition, stand disturbance patterns, secondary biotic interactions, and available land area (Able and Noon 1976; Sabo 1980; McCoy 1990; Rahbek 1995; Hofer *et al.* 1999).

Previous forest harvesting in south coastal British Columbia has occurred mostly at lower elevations because of the ease of access and operations. Consequently, the Coastal Western Hemlock (CWH) and the Coastal Douglas-fir (CDF) biogeoclimatic zones, which occur at lower elevations, have experienced more harvesting than the upper elevation Mountain Hemlock (MH) zone (MacKinnon and Vold 1998). In general, biogeoclimatic zones are broad units within the biogeoclimatic classification system that consist of groupings of subzones with similar zonal plant associations and climate (Pojar *et al.* 1987). Subzones are described using regional climate and characteristic climax or near-climax plant associations that occur, or are expected to develop, on zonal sites (Pojar *et al.* 1987). Because of its influence on climate, elevation is also used to identify biogeoclimatic units (Green and Klinka 1994).

In the South Coast region, few studies have looked at the influence of elevation on bird species distributions or at the potential effects on bird communities of the concentrated pattern of harvesting at lower elevations (Wetmore and Booth 1986; Manning 2000). For example, little is known about the influence of factors which vary with elevation (e.g., forest stand structure) on bird species' distributions. Another unknown is whether the criteria used to classify zones also delineate shifts in bird communities and their habitats. In other North American regions, bird habitats have been effectively classified

In this study, we compared bird distributions during the breeding season according to the lower elevation CWH and the higher elevation MH, and to the elevational gradient across these units.

using vegetation zones along elevational gradients (Kendeigh and Fawver 1981; Finch 1989, 1991; Navarro 1992). Understanding the important relationships between bird communities, biogeoclimatic units, and elevation helps forest managers to maintain biodiversity.

In this study, we compared bird distributions during the breeding season according to two adjacent biogeoclimatic zones (the lower elevation CWH and the higher elevation MH) and the elevational gradient across these units. Our objectives were to:

- determine whether distributions of breeding bird species or bird communities change along elevational gradients and with forest stand structure;
- describe the distribution of breeding birds and bird communities according to two adjacent biogeoclimatic zones; and
- evaluate whether zones can provide an effective framework for managing bird habitats.

Study Area

We located our research sites within old-growth forest in the CWH and MH biogeoclimatic zones in the Lower Mainland and Sunshine Coast areas of the South Coast of British Columbia (Table 1). The elevation range in the CWH zone generally spans sea level to 900 m, while the adjacent MH zone is generally between 900 and 1800 m. These zones follow the coastline extending from southeastern Alaska to Oregon (Meidinger and Pojar 1991). Cool summers and mild winters characterize the CWH zone (mean annual precipitation: 214 cm; mean annual snowfall: 81 cm; and mean annual temperature: 9.2°C). The MH zone is typified by short, cool summers and long, wet winters with several months of heavy snowfall (mean annual precipitation: 295 cm; mean annual snowfall: 820 cm; and mean annual temperature: 5°C) (Meidinger and Pojar 1991). Tree species dominating the CWH zone include western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and



TABLE 1. Description of study areas used within biogeoclimatic zones to inventory relative abundance of birds

Zone	Subzone/ variant ^a	Study area	Total stands (1992)	Total stands (1993)	Survey points (1992)	Survey points (1993)	Elevation range (m)	Latitude	Longitude
CWH	vm1	Seymour Watershed (SY)	1	0	2	0	500	49°20'00"	122°43'45"
		Capilano (CP)	2	4	9	13	510–620	49°28'50"	122°02'15"
		Coquitlam (CQ1)	6	5	20	16	465–520	49°26'20"	122°02'40"
	vm2	Coquitlam (CQ2)	0	2	0	8	720–810	49°26'20"	122°02'40"
	ms1	Cheakamus (CHa) ^c	0	4	0	14	690–860	50°01'45"	122°57'00"
MH	mm1	Cypress (CY)	5	5	17	17	970–1150	49°28'00"	123°11'50"
		Garibaldi (GA)	0	4	0	12	1160–1475	49°45'15"	123°02'50"
		Seymour Mountain (SM)	2	2	10	8	1010–1030	49°22'10"	122°57'20"
	mm2	Cheakamus (CHb) ^c	0	3	0	8	970–1130	50°01'30"	122°58'50"
Tetrahedron (TE)		0	4	0	14	1020–1135	49°35'35"	123°38'15"	

^a CWHvm1: Coastal Western Hemlock very wet maritime (submontane).

CWHvm2: Coastal Western Hemlock very wet maritime (montane).

CWHms1: Coastal Western Hemlock moist submaritime (southern).

MHmm1: Mountain Hemlock moist maritime (windward).

MHmm2: Mountain Hemlock moist maritime (leeward).

The variant (number) further distinguishes differences in regional climates; for example, from drier to wetter, or 1 and 2, respectively.

^b Parkland at higher elevations (MMmmP1).

^c CHa and CHb are located within the same study area, but in different zones.

Pacific silver fir (*Abies amabilis*). The MH zone is dominated by mountain hemlock (*Tsuga mertensiana*), Pacific silver fir, and yellow-cedar (*Chamaecyparis nootkatensis*) (Meidinger and Pojar 1991). At high elevations, the MH zone is referred to as “Parkland” because the trees become clumped in irregular small patches that form mosaics with subalpine heath, meadow, and fen (Meidinger and Pojar 1991). Biogeoclimatic zones are generally not separated by narrow bands of transitional habitat. Boundaries are more often gradual, and elevational limits can vary by at least 100 m with aspect, latitude, and climate (Green and Klinka 1994). Our study area included a subset of those subzones found in the two zones (Table 1; Meidinger and Pojar 1991).

Methods

Avian Observations

In 1992 and 1993, we recorded both breeding and non-breeding bird behaviours at fixed 75-m-radius survey points (Verner 1985; Hutto *et al.* 1986). Survey points in each zone reflected various degrees of slope, but we avoided ridges, bluffs, or riparian areas adjacent to large rivers. Perimeters of adjacent survey points were at least 50 m apart to ensure their independence. All perimeters were a minimum of 50 m from any edge to reduce inclusion of edge species. We established two to five

survey points per forest stand, for a total of 58 survey points across 16 stands in 1992, and for a total of 110 survey points across 33 stands in 1993 (Table 1). Stands were distributed among study areas between 465 m and 1475 m. They were either delineated by natural features or, in contiguous forest, were separated by a minimum of 500 m. Study areas (five in 1992 and seven in 1993) were defined by major watersheds generally greater than 10 000 ha. Surveys were conducted within four hours of sunrise during May and June. Following a 2-minute rest period, trained observers recorded all visual and aural detections of birds during a 12-minute period. We undertook five replicate surveys in 1992, but we used only three replicates in 1993, covering more sites instead. In 1993, MH zone surveys started two weeks later because accessibility was reduced by a deeper snowpack and cooler weather. Observers were rotated between surveys to minimize observer bias.

Habitat Measurement

We recorded aspect, slope, and elevation, and measured overstorey tree canopy height at each survey point. We centred a 25-m-radius plot at the survey point, and visually estimated percent cover of overstorey tree canopy (> 10 m) and understorey layers of shrub and saplings (0.5–10 m tall), herbs and ferns, moss, and



downed wood. Next, we enlarged the plot into a 75-m-radius plot and divided it into 16 pie-shaped sections. We randomly selected three sections to count saplings (< 10 cm DBH) and trees and snags (≥ 10 cm DBH). Along the first 25 m of the right edge of each section, we used the line-transect method to measure pieces of downed wood (≥ 7 cm wide) that were intersected by the line (Marshall *et al.* 2000). For each survey point, we calculated: number of saplings, trees, and snags per hectare for diameter classes (10–29, 30–59, 60–99, ≥ 100 , ≥ 10 cm DBH), and volume of downed wood per hectare by piece size classes (7–29, 30–59, 60–99, ≥ 100 , ≥ 7 cm).

Analyses

We calculated mean abundance (mean detections per survey point) for each bird species from the replicate surveys conducted during the breeding period. We did not detect unusual fluctuations in abundance of any one species to justify eliminating counts for early or late migrants, although the later MH zone surveys in 1993 likely provided a seasonal adjustment for that year's weather. We used all recorded detections (song, call, and visual) to include different species that arrived and bred at different intervals or lacked distinguishable songs (e.g., chestnut-backed chickadee). For community measures we used the maximum abundance of each bird species per survey point from the replicate counts emphasizing total number of forest users at any one time during the breeding season. This included less common birds, migrants, and those of unknown breeding status, as well as breeders.

Mean and maximum abundance are relative measures. We analyzed each year separately reflecting the findings of Savard *et al.* (in press), who found that mean abundance of 11 bird species varied significantly from year to year between 1991 and 1993 using a sample of the same points. We used $\alpha = 0.05$ as our significance level for all analyses, but also report values between 0.05 and 0.10.

Elevation and Forest Stand Structure

First, we applied simple regression models (Model 1) to investigate whether the dependent variables of mean abundance (of each of 19 bird species per survey point), richness (maximum number of species per survey point), and total bird abundance (maximum number of individuals per survey point) increased or decreased with elevation (independent variable). The 19 bird species included those that occurred at 20% or more of the total survey points in either 1992 or 1993. Next, we

applied multiple regression models (Model 2) to test whether stand attributes or elevation influenced bird species distributions. We used the same dependent variables, but used as independent variables elevation and those stand attributes significantly correlated with the dependent variable being modelled. We controlled for multicollinearity among independent variables (Myers 1986) by eliminating the lesser of a significantly correlated pair (Pearson $r \geq 0.7$ and $P \leq 0.05$); if the lesser was elevation, we retained the elevation value instead. For the multiple regressions we used the maximum RSQUARE improvement technique (SAS Institute Inc. 1989), and chose the best-fit model for each dependent variable by using Mallows' (1973) C_p statistic of total squared error. This statistic is the sum-of-squares error for a model with p parameters (i.e., parameters are the stand attributes and elevation including the intercept). When the value of C_p is near p , the best-fit model is chosen because the parameter estimates are least biased.

We needed to eliminate certain survey points from our multiple regression analyses because they lacked some stand attribute data (18 survey points in 1992 and 7 in 1993). We expected elevation to remain or become a coefficient in Model 2, if factors associated with it were important influences on bird species distributions. We used the log+1 transformation ($\ln[Y+1]$) on the dependent variables throughout these analyses to produce normally distributed residuals with constant variance in the models.

Biogeoclimatic Zones

We used multidimensional scaling (MDS) and permutation testing (mean similarity analysis) as exploratory tools (Van Sickle 1997) to examine whether biogeoclimatic zones, which are defined *a priori* using one set of ecosystem attributes, are appropriate units for grouping bird communities defined using different biological attributes. For these tests we used mean abundance of each bird species per stand (based on maximum abundance per survey point) and then we calculated Renkonen Percent Similarity Indices between stands, where 0% is no similarity and 100% is complete overlap (Magurran 1988). Multidimensional scaling calculates the dissimilarities between the stands and plots them relative to one another and to each zone in a two-dimensional scatter plot. Permutation testing, using the same data set, computes whether bird communities are on average more similar within each zone than between the two zones. A significant result indicates that class structure for bird communities is effectively defined using zone.



We also tested whether the abundance of each of the 19 bird species observed and the richness and total bird abundance differed between zones with an analysis of variance (ANOVA) using a completely randomized design with sub-sampling (Steel *et al.* 1997). We eliminated the Cheakamus MHmm2 (CHb) stand from this analysis to produce the completely randomized design (see Table 1), and we rank-transformed variables to have normally distributed residuals with constant variance (Steel *et al.* 1997). Our sampling design was unbalanced; therefore, we report least-squares means (LSMEAN) and their associated standard errors, which estimate the marginal means expected under a balanced design (similar to arithmetic means for balanced designs) and matching what the ANOVA uses to test for treatment effects.

Results

Elevational Effects

We surveyed a broader geographic area in 1993 than in 1992; in 1993, the study area included 11 more stands in the MH zone and 6 more in the CWH zone (Table 1). Fifteen of the 37 bird species detected in 1992 and 20 of the 40 bird species detected in 1993 had less than five observations indicating they were incidental or rare (Table 2). This resulted in a total of 24 bird species being eliminated from individual analysis as they occurred at fewer than 20% of the point counts in either year (Table 2). Seven of the 24 species were detected only in MH zone, while four species occurred only in CWH zone.

TABLE 2. Bird species present at fewer than 20% of the survey points in either 1992 (58 survey points) or 1993 (110 survey points). Unless otherwise indicated with footnote markers (^a or ^b), the plus sign (+) designates fewer than five observations per zone per year.

Species	Scientific name	1992 (58 points)		1993 (110 points)	
		MH	CWH	MH	CWH
American goldfinch	<i>Carduelis tristis</i>				+
Band-tailed pigeon	<i>Columba fasciata</i>	+ ^a	+	+	
Black-throated gray warbler	<i>Dendroica nigrescens</i>		+		
Blue grouse	<i>Dendragapus obscurus</i>	+	+	+ ^a	+ ^a
Cedar waxwing	<i>Bombycilla cedrorum</i>	+			
Common raven	<i>Corvus corax</i>	+	+	+	+
Evening grosbeak	<i>Hesperiphona vespertina</i>	+	+	+	+
Fox sparrow	<i>Passerella iliaca</i>	+		+	
Hammond's flycatcher	<i>Empidonax hammondi</i>	+ ^a	+	+	+
MacGillivray's warbler	<i>Oporornis tolmiei</i>				+
Mountain chickadee	<i>Parus gambeli</i>			+	
Northern flicker	<i>Colaptes auratus</i>	+	+	+	
Northern goshawk	<i>Accipiter gentilis</i>		+	+	
Northern pygmy-owl	<i>Glaucidium gnoma</i>		+		+
Olive-sided flycatcher	<i>Contopus cooperi</i>	+ ^b	+	+	+
Pileated woodpecker	<i>Dryocopus pileatus</i>	+	+	+	
Pine grosbeak	<i>Pinicola enucleator</i>				+
Rufous hummingbird	<i>Selasphorus rufus</i>	+	+	+	+
Song sparrow	<i>Melospiza melodia</i>	+			
Three-toed woodpecker	<i>Picoides tridactylus</i>	+		+	
Western tanager	<i>Piranga ludoviciana</i>			+	+
Western wood pewee	<i>Contopus sordidulus</i>	+		+	
Wilson's warbler	<i>Wilsonia pusilla</i>	+	+	+	+
Yellow-rumped warbler	<i>Dendroica coronata</i>			+	

^a 6–10 observations.

^b 15 observations.



Mean abundance of many of the forest stand structural attributes in either 1992 or 1993 was correlated with elevation, indicating stand structure varied along the elevational gradient (Table 3). We eliminated 10–29 cm DBH snags and volume of downed wood per hectare in piece size classes 30–59 cm and ≥ 7 cm in 1992, and overstorey canopy height (m) in 1993, from their respective multiple regressions because they were highly correlated ($r \geq 0.7$ and $P \leq 0.05$) with elevation (Table 3). Thus, we cannot separate whether elevation or these stand attributes best explain the relationship since we did not identify causal factors.

We fitted simple linear regression models (Model 1) as the pattern of the data did not appear obviously non-linear or segmented. The mean abundance of seven bird species decreased with increasing elevation, and

mean abundance of four bird species increased with increasing elevation in both 1992 and 1993 (Table 4). Mean abundance of four additional bird species showed a significant response to elevation, but only in one of the two years (Table 4). Using Model 1, elevation best explained the variation in mean abundance of Swainson's thrushes, Pacific-slope flycatchers, pine siskins, red-breasted nuthatches, and winter wrens (between 30–76% in either one or both years; Table 4). Elevation did not account for variation in the mean abundance of four species (red-breasted sapsucker, varied thrush, golden-crowned kinglet, and Vaux's swift) in either 1992 or 1993 with Model 1 (Table 4). Richness and total bird abundance for the elevational range tested showed weak declines with increasing elevation in 1993, but not in 1992 (Table 4).

TABLE 3. Correlations between each forest stand attribute and elevation ($P \leq 0.05$), where a minus sign (–) indicates a decrease and a plus sign (+) indicates an increase in the attribute as elevation increases

Attribute	Pearson correlation r with elevation	
	1992 ($n = 40$)	1993 ($n = 93$)
Slope (%)	ns	ns
Overstorey canopy height (m)	–0.61	–0.66
Overstorey canopy > 10 m (%)	–0.35	–0.27
Shrub and sapling layer 0.5–10 m (%)	ns	ns
Herb and fern layer < 0.5 m (%)	ns	ns
Moss layer (%)	ns	0.21
Total downed wood (%)	–0.65	–0.55
Trees per hectare (< 10 cm DBH)	–0.37	–0.50
Trees per hectare (10–29 cm DBH)	ns	+0.19 ^a
Trees per hectare (30–59 cm DBH)	+0.53	+0.48
Trees per hectare (60–99 cm DBH)	ns	ns
Trees per hectare (≥ 100 cm DBH)	–0.56	–0.65
Total trees per hectare (≥ 10 cm DBH)	+0.28 ^a	+0.35
Snags per hectare (10–29 cm DBH)	–0.67	–0.45
Snags per hectare (30–59 cm DBH)	ns	ns
Snags per hectare (60–99 cm DBH)	–0.51	–0.40
Snags per hectare (≥ 100 cm DBH)	–0.32	–0.47
Total snags per hectare (≥ 10 cm DBH)	ns	+0.20 ^a
Downed wood m ³ /ha (7–29 cm)	–0.37	–0.24
Downed wood m ³ /ha (30–59 cm)	–0.69	–0.34
Downed wood m ³ /ha (60–99 cm)	–0.41	–0.35
Downed wood m ³ /ha (≥ 100 cm)	–0.43	–0.44
Total downed wood m ³ /ha (≥ 7 cm)	–0.70	–0.56

^a $0.05 < P \leq 0.10$



TABLE 4. Regression models fitted to observed data. Model 1 is a simple regression model with elevation as the independent variable. Model 2 is a multiple regression model with elevation as one of a subset of independent variables from those variables significantly ($P \leq 0.05$, $* = 0.05 > P \leq 0.1$) correlated with the dependent variable (mean abundance of each bird species, richness, and total bird abundance). For 1992, $n = 40$, $df = 39$. For 1993, $n = 93$, $df = 92$. A minus sign (–) indicates a decrease and a plus sign (+) indicates an increase in mean abundance of the attribute as species' mean abundance increases. Habitat variables are listed in the order they are entered into the model.

Species	Model 1		Model 2			
	1992 R^2	1993 R^2	1992 R^2	Variables ^a	1993 R^2	Variables ^a
Swainson's thrush <i>Catharus ustulatus</i>	76 (–)	28 (–)	89	+sapling, +treelarge, +treehuge +cwdhuge, +cwdsml, –elev, +height	32	+sapling, +snaglarge, –elev, +overstorey
Pacific-slope flycatcher <i>Empidonax difficilis</i>	71 (–)	60 (–)	74	–elev, +overstorey	61	+treehuge, –elev
American robin <i>Turdus migratorius</i>	15 (–)	11 (–)	20	–elev, +overstorey	11	+cwdhuge, –elev
Hairy woodpecker <i>Picoides villosus</i>	12 (–)	9 (–)	24	–elev, –herb	11	+snaglarge, –elev
Winter wren <i>Troglodytes troglodytes</i>	51 (–)	30 (–)	66	–treemed, +snaghuge, +cwdlarge, –elev	49	–treemed, +treehuge, +snaghuge, +snaglarge, +overstorey
Steller's jay <i>Cyanocitta stelleri</i>	15 (–)	14 (–)	38	+snaglarge, +height, +moss	17	+cwdsml, –elev
Chestnut-backed chickadee <i>Parus rufescens</i>	14 (–)	11 (–)	37	+treehuge, –slope	17	+snaghuge, +snaglarge, –elev
Pine siskin <i>Carduelis pinus</i>	42 (+)	16 (+)	45	+treelarge, +elev	31	–treelarge, –snaghuge, –cwd- total, +elev, –overstorey
Red-breasted nuthatch <i>Sitta canadensis</i>	32 (+)	16 (+)	40	+treelarge, +elev	32	–sapling, +treelarge, –cwd- small, –cwdtotal, +elev
Gray jay <i>Perisoreus canadensis</i>	12 (+)	10 (+)	12	+elev	22	–slope, +elev, –overstorey, +herb, –% cwd
Dark-eyed junco <i>Junco hyemalis</i>	12 (+)	19 (+)	53	+saplings, +height, +overstorey	52	–treehuge, –snaglarge, +cwdlarge, +cwdsml, +slope, –overstorey, +herb, –%cwd
Red crossbill <i>Loxia curvirostra</i>	16 (+)	ns ^b	30	+elev, –overstorey, –moss	11	+understorey, +elev
Townsend's warbler <i>Dendroica townsendi</i>	10 (+)	ns	30	+elev, +herb	24	+slope, –moss
Brown creeper <i>Certhia americana</i>	8.0*(–)	24 (–)	41	+snaghuge, +snaglarge, +cwdsml, +elev, +%cwd	37	–sapling, +treemed, +treehuge, +snaghuge, +slope, –elev, –moss



TABLE 4. Continued

Species	Model 1		Model 2			
	1992 R ²	1993 R ²	1992 R ²	Variables ^a	1993 R ²	Variables ^a
Hermit thrush <i>Catharus guttatus</i>	7.7*(+)	14 (+)	27	–snaghuge, +understorey, +elev	27	–snaglarge, –snagsmall, –cwdsml, –cwdtotal, +elev, +understorey
Red-breasted sapsucker <i>Sphyrapicus ruber</i>	ns	ns	50	–treetotal, +cwdlarge, –moss, +elev	18	–cwdtotal, +understorey, –elev
Varied thrush <i>Ixoreus naevius</i>	ns	ns	34	–slope, +height, +elev	14	+treelarge, +snaglarge, +cwdlarge
Golden-crowned kinglet <i>Regulus satrapa</i>	8.3*(+)	ns	8.0*(+)		37	+snaglarge, +cwdlarge, +overstorey, –understorey, +moss, +elev
Vaux's swift <i>Chaetura vauxi</i>	ns	ns	ns		16	+treelarge, +cwdsml, –under- storey
Total bird abundance	7.0*(+)	6 (–)	41	+snaghuge, +elev	22	–treetotal, +snaghuge, +cwdsml
Richness	ns	8 (–)	14	+snaghuge	15	–treetotal, +snaghuge, –elev

^a Coding for forest structure variables as described in the methods section of this document: snag = stems per hectare; tree = stems per hectare; cwd = wood volume (m³) per hectare or % cover; height = tree (m; huge = ≥ 100 cm; large = 60–99 cm; medium = 30–59 cm; small = 7 (or 10)–29 cm; total = ≥ 7 (or 10) cm; overstorey = % overstorey canopy; understorey = % shrubs and saplings in 2.1–10 m layer; sapling = < 10 cm trees; elev = elevation.

^b ns = not significant.

Using the Model 2 regressions, the best-fit models retained elevation in combination with one or more stand structural attributes for 17 of the 19 bird species in at least one of the two study years. Although elevation was not significant in Model 1, it was included in the best-fit Model 2 regressions for varied thrushes in 1992 and golden-crowned kinglets in 1993 (Table 4). Dark-eyed junco was the only species for which elevation was included in Model 1, but not Model 2 (Table 4). Using Model 2, elevation accounted for variation in total bird abundance in 1992 with a positive relationship (Table 4). It accounted for variation in richness in 1993 only, but with a negative relationship (Table 4). Forest stand attributes that accounted for the greatest variation in mean abundance of bird species included slope, density of trees per hectare by DBH size classes, volume per hectare of downed wood by piece size class, density of snags per hectare by DBH size classes, overstorey canopy height, overstorey and understorey canopy covers, shrub

cover, herb cover, and moss cover (Table 4). Except for elevation, many of the forest structural attributes selected using Model 2 varied for each bird species year to year. Richness and total bird abundance in both 1992 and 1993 were best explained by density of huge snags (≥ 100 cm DBH) in combination with total density of trees over 10 cm DBH, volume of downed wood (≥ 100 cm diameter piece size class), or elevation.

Biogeoclimatic Zones

The MDS scatter plot indicated that stands within the same zones were more similar in bird species and their relative abundances than those between the zones (Figure 1). However, these bird communities in the different zones appeared less isolated in 1993 than 1992 because the CWH stands of the CHa study area (Figure 1, year 1993) marginally overlapped some of the MH stands (study areas CHb, CY, GA). The stands in the CHa study



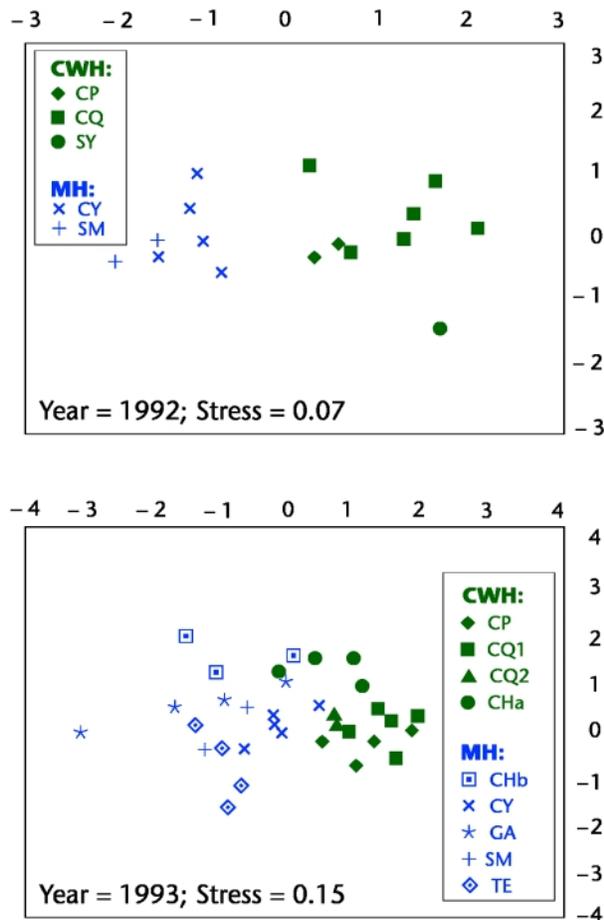


FIGURE 1. Two-dimensional nonmetric MDS ordinations, computed for 1992 and 1993, for stands within the two biogeoclimatic zones, including graphic distribution of the different study areas (represented by abbreviations: see Table 1).

area differed from the others in the CWH by variant (CWHms1 compared to CWHvm 1 or 2) and more northerly latitude; however, low “stress” measures (i.e., differences between plotted and true dissimilarities) indicated classification of bird communities within zones was relatively strong (high *P*-value) for both years (see Van Sickle 1997). The permutation testing confirmed that between-zone similarities were, on average, less than within-zone similarities, and zones were effectively classifying bird species into distinct communities (Table 5).

Our ANOVA models showed that bird species composition differed between the two zones since mean abundance of a number of individuals significantly differed between the zones. In the CWH zone, Swainson’s

TABLE 5. Matrix of mean similarities using Renkonen Percent Similarity. *M* is the ratio of mean between-zone similarity with mean within-zone similarity. A larger *M* usually indicates no difference in class structure; however, for both years a significant difference between similarity measures in the two zones shows that zone effectively classifies bird community.

	1992		1993	
	CWH (<i>n</i> = 9)	MH (<i>n</i> = 7)	CWH (<i>n</i> = 15)	MH (<i>n</i> = 18)
CWH	0.675	0.521	0.630	0.485
MH	0.000	0.729	0.000	0.565
Observed ratio, <i>M</i>	0.746		0.815	
Proportion of <i>M</i> s less than observed <i>M</i> after complete enumeration	<i>P</i> = 8.74 × 10 ⁻⁵		<i>P</i> = 3.09 × 10 ⁻⁸	

thrushes were more abundant in both years (Table 6), while hairy woodpeckers and Pacific-slope flycatchers were more abundant in 1992 (Table 6). In the MH zone, dark-eyed juncos and pine siskins were more abundant in both years; however, gray jays and red crossbills were more abundant in 1992, and red-breasted nuthatches and hermit thrushes were more abundant in 1993 (Table 6). Although species composition of the bird communities differed between zones, neither total bird abundance nor richness between MH and CWH zones differed significantly in either year (Table 6).

Discussion

Individuals

Forest stand structure is important for birds because it can directly influence availability and quality of breeding and foraging habitat (Hilden 1965; Roth 1976; Cody 1981). Although the amount and type of forest stand attributes change with elevation, other factors associated with elevation, such as temperature and forage productivity (insect or seed), also likely interact and influence the distribution patterns of bird species (Wiens and Nussbaum 1975; Manuwal *et al.* 1987; Janes 1994). Our results were indicative of this. For example, we found that stand attributes alone explained only the variation in abundance of one species along the elevational gradient—the dark-eyed junco (Table 4). The distributions of the other bird species appeared related to stand attributes in combination with



TABLE 6. Least-squares (LS) means and standard errors (SE) for each zone (MH, CWH) using unranked observations and significance. Differences in individual bird species' mean abundance, richness, and total bird abundance using analysis of variance for 1992 (unadjusted degrees of freedom 1, 3) and 1993 (unadjusted degrees of freedom 1, 5).

Species	1992			1993		
	MH LSMean (SE)	CWH LSMean (SE)	F	MH LSMean (SE)	CWH LSMean (SE)	F
Gray jay	0.15 (0.00)	0.00 (0.00)	98.23 ^a	0.23 (0.07)	0.08 (0.06)	6.10 ^b
Hairy woodpecker	0.03 (0.03)	0.13 (0.03)	10.03 ^a	0.02 (0.02)	0.05 (0.20)	1.79
Pacific-slope flycatcher	0.02 (0.06)	1.12 (0.06)	25.48 ^a	0.11 (0.22)	0.74 (0.22)	4.33 ^b
Red crossbill	5.05 (0.75)	1.63 (0.77)	9.37 ^a	0.56 (0.40)	0.00 (0.00)	1.49
Swainson's thrush	0.03 (0.13)	0.88 (0.13)	39.19 ^a	0.04 (0.11)	0.58 (0.11)	15.26 ^a
Dark-eyed junco	0.46 (0.06)	0.07 (0.07)	13.52 ^a	0.90 (0.14)	0.14 (0.13)	33.50 ^a
Pine siskin	4.23 (0.20)	1.18 (0.22)	80.99 ^a	0.87 (0.07)	0.16 (0.07)	104.8 ^a
Red-breasted nuthatch	0.37 (0.05)	0.19 (0.05)	5.51 ^b	0.56 (0.06)	0.18 (0.06)	20.35 ^a
Hermit thrush	0.34 (0.04)	0.10 (0.04)	6.77 ^b	0.55 (0.04)	0.21 (0.04)	21.00 ^a
Steller's jay	0.03 (0.06)	0.12 (0.06)	2.81	0.00 (0.00)	0.07 (0.02)	5.27 ^b
Winter wren	0.48 (0.12)	1.24 (0.12)	7.13 ^b	0.39 (0.18)	0.94 (0.18)	5.13 ^b
American robin	0.25 (0.07)	0.08 (0.07)	0.002	0.02 (0.03)	0.12 (0.03)	4.27 ^b
Golden-crowned kinglet	0.68 (0.12)	0.34 (0.13)	4.33	0.49 (0.17)	0.93 (0.16)	4.23 ^b
Townsend's warbler	0.49 (0.12)	0.35 (0.12)	0.73	0.57 (0.29)	0.47 (0.28)	0.00
Vaux's swift	0.07 (0.03)	0.08 (0.03)	0.01	0.06 (0.04)	0.16 (0.04)	3.05
Chestnut-backed chickadee	0.69 (0.10)	0.91 (0.10)	1.35	0.82 (0.14)	1.09 (0.14)	1.86
Brown creeper	0.18 (0.11)	0.46 (0.11)	3.73	0.20 (0.10)	0.44 (0.10)	2.91
Red-breasted sapsucker	0.19 (0.09)	0.11 (0.9)	0.18	0.32 (0.13)	0.20 (0.13)	0.49
Varied thrush	0.48 (0.21)	0.55 (0.21)	0.07	0.75 (0.09)	0.63 (0.09)	0.14
TOTAL BIRD ABUNDANCE	22.38 (1.40)	18.96 (1.44)	2.58	13.42 (1.36)	14.09 (1.32)	0.20
RICHNESS	11.18 (0.91)	12.19 (0.93)	0.40	9.27 (0.77)	9.75 (0.75)	1.66

^a $P \leq 0.05$

^b $0.05 < P \leq 0.10$

unmeasured elevation-associated factors. Furthermore, we found that some bird species appeared more abundant in one biogeoclimatic zone or the other (Table 6), which also supports the notion that factors associated with elevation, such as climate and plant associations, are influencing bird distributions in coastal southwestern British Columbia.

We suspect that annual differences in bird-habitat relationships (Tables 4 and 6) occurred because environmental conditions can vary annually, affecting the abundance of individuals and their habitat use (Gilbert and Allwine 1991). For example, a later snowpack in 1993 compared to 1992 might have contributed to year-to-year differences in individual bird species abundance (Savard *et al.* in press) and thus differences in habitat use along the

elevational gradient or between zones. In addition, we used some different study areas and survey points (e.g., Cheakamus in 1993) in each of the two years that might have contributed to geographic differences in abundance not detected in our analyses (Manuwal *et al.* 1987).

Communities

Forests at higher elevations in coastal British Columbia support few bird species and individuals during the winter months (Campbell *et al.* 1990, 1997). Instead, higher-elevation forests are more important seasonally for residents, altitudinal migrants, and neotropical migrants that exploit resources as the snowpack recedes and temperatures increase (Rice *et al.* 1980). We found that few bird species dominated the coastal old-growth



forests we investigated; this is consistent with other studies for the South Coast (e.g., Wetmore and Booth 1986; Manning 2000). Incidental, rare, low-density, and uncommon bird species bolstered richness at our higher and lower elevation survey points (Table 2). Other than rare or uncommon species, which occurred in both zones, we did not identify zone-dependent bird species (Manuwal *et al.* 1987; Finch 1989). Our results (Table 4) for 1993 weakly support the reported general trend of declining richness with elevation (Rahbek 1995; for range 0–3500 m). However, we are cautious in our interpretation of this trend because we only used a portion of the available gradient (400–1500 m instead of 0–2700 m). Furthermore, our comparisons between the biogeoclimatic zones (Table 6) also suggest richness and total bird abundance do not differ for the portions of the elevational gradient that they represent.

Yet our comparisons of the two zones, as demonstrated with the MDS and permutation testing for both 1992 and 1993, indicate that community composition differed between these zones (Table 5, Figure 1). Compared to the CWH zone, the MH zone generally had more species that flock (e.g., red crossbills, gray jays, and pine siskins) or forage on seed solely or in addition to insects, berries, or other foods (e.g., red crossbills, gray jays, pine siskins, red-breasted nuthatches, and dark-eyed juncos) (Table 6). Seedeaters have also been reported as numerically dominant in sub-alpine areas of the Cascade Mountains in Washington State (Manuwal *et al.* 1987). We may have detected differences in bird species composition between the zones (Table 5, Figure 1) and not in richness and total bird abundance (Table 6) because we only sampled heterogeneous old-growth forests (Franklin and Spies 1991; Lertzman and Krebs 1991). Therefore, if the numbers or variety of niches available for birds to exploit did not change along the elevational gradient within these heterogeneous old forests, the numbers of bird species and individuals along the gradient or between zones would remain similar. This idea is also supported by our finding that the variation in richness and total bird abundance was best explained, regardless of elevation, by the stand attributes characteristic of old-growth forest, including the occurrence of huge snags (≥ 100 cm DBH) (Table 3). Thus, factors that change along the elevational gradient within old-growth forests, such as amount and types of stand attributes and forage productivity, more likely influence bird species composition and dominance within those forests.

To maintain the observed distribution of bird species in coastal forests, old-growth forest should be represented over the entire elevational gradient.

Management Implications

We compared bird communities of old-growth forests (251+ years) over a range of elevations (400–1500 m) because forest harvesting in coastal British Columbia had, until recently, been concentrated at lower elevations (MacKinnon and Vold 1998). Thus, more old-growth forest was likely to be conserved as habitat for birds at higher elevations, although less land area existed overall. For example, about 54% of the forested area (3.9 million ha) in the CWH is currently classified as old growth compared to 71% of the forested area (1.2 million ha) in the MH (MacKinnon and Vold 1998). Our research findings support the idea that retention of old-growth forest in both biogeoclimatic zones is important in managing for bird diversity; however, if the objective is to maintain the observed distributions of bird species and their habitats, then consideration should be given to retaining old-growth forest that represents different types of stand structure and is distributed over the elevational gradient.

We suggest stand structure is important because our research showed that stand attributes of old-growth forest, particularly huge snags (≥ 100 cm DBH), are related to richness and total number of individuals in the associated bird communities regardless of elevation. Larger snags are important to some birds for foraging and nesting, or for the associated patches of high-quality habitat (Lundquist and Mariani 1991). Yet within the bird community the abundance of some species declined with huge snags (e.g., pine siskin in 1993). Therefore, retention of various types of old-growth forest within the different biogeoclimatic zones (B.C. Ministry of Forests and B.C. Ministry of Environment 1999) would generally help manage for different bird habitats and bird diversity.

Our results suggest that retention of old growth in the different biogeoclimatic zones will partially maintain observed species distributions because the classification



criteria used to define zones appears to effectively correspond with differences between community composition and breeding habitats selected by some species. However, abundance of most bird species also varied along the elevational gradient that crossed both zones, although the abundance of some of these same bird species did not differ by zones (e.g., chestnut-backed chickadee). Hence, some bird species may respond to changes in factors along the elevational gradient that are not adequately described using the more general classification for zones. Therefore, we recommend that to maintain the observed distribution of bird species in coastal forests, old-growth forest should be represented over the entire elevational gradient rather than just retaining reserves within broad elevational zones such as biogeoclimatic zones.

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