

## BIRD COMMUNITIES OF NORTHERN FORESTS: PATTERNS OF DIVERSITY AND ABUNDANCE<sup>1</sup>

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*Abstract.* Diurnal bird communities in Southeast Alaska and adjacent Canada, censused in 1992-1994, sometimes had higher diversity and abundance in deciduous than coniferous forest. However, variation within each broad vegetation type and among years obscured any general pattern. Furthermore, rarefaction curves did not differ between forest types and a wider comparison between the communities of deciduous and coniferous forests in western North America was variable in both magnitude and direction. Thus, there is little evidence for a general trend toward greater diversity in bird communities of western and northern deciduous forests. Both deciduous and coniferous forests of the far north are geologically young, and there was some evidence that deciduous forest, at least, may not be saturated with bird species. Certain species were missing or shifted from conifer habitat elsewhere to deciduous habitat in our area. Coastal islands with coniferous forest and mainland patches of deciduous habitat supported about as many species as expected from the number of individuals present.

A small number of bird species dominated the community at each site, but the dominant species differed considerably among locations. Proportional similarity of coastal and interior forest was low, except for locations at the north end of the Inside Passage, which supported species characteristic of both coastal and interior forests. The similarity of community composition in deciduous and coniferous stands was also low, especially on the coast.

*Key words:* Species diversity; relative abundance; bird community; Alaska, Yukon; British Columbia; habitat breadth; habitat shifts; boreal forest; temperate rainforest; riparian forest.

### INTRODUCTION

The study of avian communities has attracted many ecologists over the past forty years. Many of the initial efforts emphasized patterns and processes on a very local scale. Some of the early work foundered because of a too-narrow perspective and a tendency to focus on single variables. More recent studies have emphasized the necessity of multi-scale, multi-factor approaches and the inclusion of both short-term and long-term (historical) temporal variables. The difficulties of assessing numerous variables and several scales, both temporal and spatial, and the disrepute into which some community ecology fell, seem to have deterred ecologists in recent years from embarking on studies of avian communities. Nevertheless, there is still a need for studying these communities, both for understanding basic ecology and for enlightened land management and conservation. The coastal rainforest of Alaska is subject to increasing anthro-

pogenic disturbance and fragmentation, but almost no studies exist of its avian communities. This paper provides the first intensive study of the bird communities of this north-temperate rainforest.

This study stemmed from an observation, in 1990, that we caught many more birds in understory mist-nets set in deciduous forest, even in very small patches, than in the surrounding extensive coniferous forest in Southeast Alaska. This observation stimulated two follow-up questions: 1) Is this contrast between coniferous and deciduous forests a general one, characteristic of the entire community and found in other regions as well, and 2) What factors might contribute to the observed pattern? We have divided the presentation of results into two papers. The first one (this paper) is a description of diversity and abundance of the entire diurnal avifauna, which sets the stage for an examination of factors that may contribute to patterns of diversity and abundance of understory birds (Willson and Comet 1996) and provides a basis for comparison with other communities of forest birds. The primary goal of this part of the study is to compare the diversity (species richness), relative abundance,

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and community similarity of diurnal birds in deciduous and coniferous forests at three locations in northwestern North America. A secondary goal includes preliminary assessments of the effects of habitat patchiness.

### STUDY AREAS

Our primary study sites were located in coastal rainforest in Southeast Alaska, near Juneau (ca. 58°22'N, 134°35'W). Coastal rainforest vegetation of Southeast Alaska is dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Principal understory plants include blueberry (*Vaccinium* spp.), rusty menziesia (*Menziesia ferruginea*), western skunk cabbage (*Lysichiton americanum*), and devil's club (*Oplopanax horridum*). Small, occasional stands of deciduous trees are scattered through the "sea" of coniferous trees, especially in successional areas exposed by flooding, glacial retreat, or avalanches. Deciduous stands are primarily of alders (*Alnus* spp., esp. *A. sitchensis*) and willows (*Salix* spp.), but cottonwoods (*Populus trichocarpa*) also occur in some areas.

We censused birds in several lowland forested sites near Juneau. All three mainland conifer sites were part of the "sea" of coniferous vegetation in the area. Davies Creek (DACR): Spruce-hemlock forest grew on a slope of varying steepness, bisected by an abandoned logging road and associated small patches of shrubby seral stages. Most of the area was covered by large, mature trees, numerous shrubs, and many fallen logs; the remainder was advanced second-growth with fewer fallen logs and a less complex understory. Herbert River (HERV): Spruce-hemlock forest grew on a level floodplain between two rivers. Occasional small swales a few meters wide lacking conifer trees were occupied by willows and alders. There were many fallen trees and associated root wads, and the lower branches of the conifers were commonly festooned with clumps of moss. Two hiking trails crossed the area. Peterson Creek (PECR) on Douglas Island: Spruce-hemlock forest was bisected by a creek and hiking trail. Topographic relief was small, but some parts of the area were poorly drained, with a more open canopy. Douglas Island is well over 100 km<sup>2</sup>, and separated from the mainland by a narrow tidal channel and wetlands.

The two deciduous-forest sites near Juneau were contained within the surrounding conifer forest. Sheep Creek (SHCR): Mixed vegetation

was established in a valley, historically disturbed by mining activity, at about 200 m elevation. Most of the valley bottom was densely covered with deciduous vegetation, chiefly alder, willow, elderberry (*Sambucus racemosa*), salmonberry (*Rubus spectabilis*) and viburnum (*Viburnum edule*). Strips of cottonwoods occurred especially along the creek and on talus slopes on the lower valley walls. One ridge was covered with small conifers and scattered groves of large conifers occurred. A few grassy openings were found in the deciduous stands. Recent resumption of mining activities expanded disturbance in the center of the valley. The valley is nearly enclosed by steep, sparsely vegetated walls, but conifer forest approached the valley floor at two points. Back Loop (BKLO): This level wetland is located in the Mendenhall Valley. The dominant vegetation was alder/willow thickets, with the addition of some open meadow with sedges, grasses, blueberry, and labrador tea (*Ledum groenlandicum*), scattered ponds, and tiny isolated stands of conifer trees (usually 1–5 trees). The site was surrounded by conifer forest and suburban development.

In addition, we censused several islands and habitat patches. An array of offshore islands of varying sizes in Auke Bay, 0.8–2.4 km from the mainland, support spruce-hemlock forest. Some islands have been selectively logged in the past, some have steep slopes, and the understory vegetation is similar to other conifer forests with the addition of some *Sorbus*. Four small, isolated deciduous stands (mostly *Alnus* sp.) on the mainland were also censused. These Auke Bay islands and the deciduous habitat patches on the mainland were used for a preliminary examination of the relationship between habitat fragmentation and the avian community.

Additional study sites in Southeast Alaska were located just north of Haines (ca. 59°15'N, 135°26'W), at the northern end of the Inside Passage. The climate in Haines is generally somewhat warmer and drier than in Juneau. Two sites were characterized by spruce-hemlock forest, located near Chilkoot Lake. One site (CHKO) occupied a small bluff above the lower Chilkoot River; large conifer trees grew along the slope of the bluff, but the top of the bluff supported trees of smaller stature. The second site (LASI) was located on a slope on the west side of Chilkoot Lake; it was bisected by a logging road and crossed by numerous small streams. Two study sites

(COFP, KLRI) were placed in the floodplain of the Chilkat River, where extensive stands of large cottonwoods stretch many kilometers north of Haines. Occasional spruce trees were mixed with the cottonwoods, and the understory was composed mostly of viburnum and rose (*Rosa* sp.). A third deciduous site (KLSL, to which we had access in only one year) was located on a slope just above the Chilkat River and had a mixed canopy of cottonwood, birch (*Betula* sp.), and maple (*Acer* sp.), with an understory of rose, snowberry (*Symphoricarpos alba*), gooseberry (*Ribes* sp.), and viburnum. The deciduous sites near Haines were initially included in the study in order to obtain census data from very large stands, which are not available near Juneau; the conifer sites near Haines provided within-location comparisons. Incidental surveys in large riparian stands located in nearby Skagway (about 30 km north of Haines) documented a similar bird community there.

We also conducted censuses near Atlin, B. C. (approx. 59°35'N, 133°45'W), located across the coastal mountain range east of Juneau and Haines. The Atlin sites provided the closest accessible contrast at similar latitude to the study sites in Southeast Alaska on the west side of the mountains and the opportunity to learn if the deciduous/coniferous habitat contrasts seen in the coastal rainforest also obtained where the vegetation was different.

The continental climate of the interior yields a very different flora. Extensive upland areas are characterized by forests of white spruce (*Picea glauca*) with small enclaves of deciduous trees (mostly willow and aspen, *Populus tremuloides*). Other areas are covered by large stands of post-fire successional deciduous trees sometimes mixed with willow and cottonwood, *P. balsamifera* or lodgepole pine (*Pinus contorta*). The understory of the spruce forest is poorly developed; mosses and lichens predominate, with scattered dwarf shrubs and herbs. Upland deciduous stands have an understory of rose (*Rosa acicularis*), viburnum, and soapberry (*Shepherdia canadensis*), plus some herbs. We used four sites on west-facing slopes on the east side of the Atlin Lake drainage, near the B.C./Yukon border about 47 km north of Atlin. One pair of study sites, adjacent stands of spruce (BCSP) and aspen (BCAS), were located at the border; a second pair of sites, again adjacent stands of spruce (YUSP) and aspen (YUAS), were placed about one km north

of the first pair. A fifth site (PCPI) was placed in a lodgepole pine stand, with trees of varying age and occasional willow thickets, on Pine Creek, 6 km east of Atlin. There was little ground cover here except mosses and lichens. A sixth site (PCWI) was located where Pine Creek enters Atlin Lake, almost 3 km south of Atlin, in a floodplain of mixed willow, cottonwood, and alder. There was little ground-cover in early summer, but some herbaceous cover appeared later on. This site was characterized by large amounts of dead wood, both standing and fallen.

#### FIELD METHODS

We used point counts with indefinite radii, recording all diurnal birds seen or heard in each habitat type at each point, excluding birds that merely flew overhead. Counts were timed at 5 min and 8 min, but we used the latter for analyses presented here. Our experience indicated that the longer count gave higher numbers of species in many cases and therefore better represented what was present, and it also allowed us time to confirm counts of individuals. Distance between points was at least 150 m. This distance was insufficient to avoid some overlap of individuals at consecutive points on the transect; therefore censusers made an effort to keep track of individual birds as they moved from point to point. Birds thought to be the same individuals at consecutive points were recorded as repeats and were not included in the assessment of relative abundance. Analysis of the data using only alternate points produced little change in numerical values and no change of conclusions. The use of two censusers on each census allowed confirmation of identifications and counts.

We censused points on each transect in different orders on consecutive censuses. Censuses began at dawn (about 02:30 Alaska Standard Time on 1 June), from mid-May (late May in Atlin) to the end of June, 1992–1993. Most of the same sites in Juneau and Atlin (but not Haines) were also censused in 1994. The data were not incorporated in the primary analysis because only some sites were recensused. We do not report these data in detail here but, rather, use this third year of censusing to confirm or challenge some of the patterns seen in the first two years.

We plotted the number of species recorded against the cumulative number of points sampled for each site in each year. In most cases the curve of species accumulation levelled off (or at

least achieved >90% of the maximum number of recorded species) after a small number of points ( $\bar{x} = 5$ , range 3–8) in both Haines and Atlin. In Juneau there was more variability: the species-accumulation curve for most sites reached a plateau at an average of about 5 points (range 2–8), but the curve continued to rise to 12 points in SHCR in 1992 before levelling off, and DACR-1993 and SHCR-1993 curves continued to rise slowly even after 12 points had been sampled. Thus, the number of points sampled at each site (range 8–20) appears to have yielded an adequate representation of the species present in most cases. The rising curve in SHCR may reflect the large structural heterogeneity of the site. There were no consistent differences between vegetation types or among locations in the number of points needed to record a maximum number of species.

When species accumulation was plotted against the number of censuses at each site (six to eight censuses/site, except five at LASI), the curves generally levelled off at an average of four or five censuses (range 3–6). There were no differences between vegetation types in the number of censuses needed to record the maximum number of species. However, the Juneau location was the only one at which six censuses were often needed.

In 1994 we conducted intensive nest searches in marked plots at four sites (SHCR, BKLO, HERV, PECR) near Juneau. The details of these studies will be published elsewhere, but for comparisons of deciduous and coniferous stands we use here the summaries of nest densities on the four sites.

#### ANALYTICAL AND STATISTICAL METHODS

The measures that we compared for different communities follow: a) Site diversity (number of species recorded at a site or species richness per site); b) point diversity (average number of species recorded/point at each site), which would vary independently of site diversity if horizontal habitat heterogeneity were marked; c) spatial heterogeneity (average point diversity/site diversity), an index of variation among points at a site; and d) relative abundance (average number of birds/point). All measures are based on "regular" species, which occurred on >1 census for each site; occasional species that occurred only once were not included. Community similarity was indexed by proportional similarity (PS), following Holmes and Pitelka (1968); this index

combines species occurrence and proportional abundance for each pairwise community comparison.

Three-way ANOVAs were used to examine the effects of location, vegetation type, and year on avian abundance and diversity. We chose to treat all three factors as fixed effects (Model 1). For location and vegetation type, this choice is unambiguous. Year effects could be treated either as random or fixed effects; in this case we restrict the conclusions to the particular years in question, permitting their use as fixed effects (Bennington and Thayne 1994). We commonly discuss main effects even when interaction terms are significant. A significant interaction term can arise when either the magnitude or the direction of the difference for one factor varies with another factor; when the direction of the difference is the principal concern, it is legitimate to test for main effects even when a significant interaction is present (Sokal and Rohlf 1981).

In addition to examining our data in unmodified form, for some comparisons we also examined the outcome of rarefaction, by which we estimated the number of species expected from a random sample of individuals taken from the censuses (James and Rathbun 1981). This is a way of standardizing the samples by the number of individuals. The observed number of species on coastal islands and in mainland habitat patches was compared to the number expected there, given the number of individuals observed. As a basis of comparison, we pooled the censuses, using the same number of randomly selected census points for each site, for mainland conifer sites to compare with islands bearing coniferous vegetation, and for mainland deciduous sites to compare with patches of deciduous vegetation. In addition, we compared the rarefaction curves for each vegetation type in each location.

#### RESULTS

##### PATTERNS OF DIVERSITY AND ABUNDANCE

Relative abundance differed significantly among vegetation types and locations, but not between years (Table 1). Overall, relative abundance was slightly higher in deciduous than coniferous forest, and much lower in Atlin than in Haines or Juneau. However, again there was a significant interaction between vegetation and location, because avian abundance differed little between

TABLE 1. Patterns of diversity (species richness) and relative abundance of forest birds in northern forests. C = coniferous stands, D = deciduous stands. J = Juneau, H = Haines, A = Atlin. Acronyms for sites are spelled out in Methods. Only significant or nearly significant terms of the ANOVA are shown.

Location	Site	Veg. type	Site diversity		Point diversity		Relative abundance	
			1992	1993	1992	1993	1992	1993
Juneau	DACR	C	18	20	11.2	14.5	7.1	10.4
	HERV	C	15	23	10.8	13.9	11.7	10.9
	PECR	C	20	19	13.0	13.0	8.5	8.4
	Avg.		17.7	20.7	11.7	13.8	9.1	9.9
	BKLO	D	20	19	11.8	11.3	7.4	7.0
	SHCR	D	21	19	12.3	11.3	9.6	10.0
	Avg.		20.5	19.0	12.1	11.3	8.5	8.5
Haines	CHKO	C	13	16	7.5	13.4	5.6	7.5
	LASI	C	—	12	—	9.1	—	9.2
	Avg.		13.0	14.0	7.5	11.3	5.6	8.4
	COFP	D	18	22	14.1	15.2	12.5	11.6
	KLRI	D	20	22	12.1	13.0	11.3	10.6
	KLSL	D	19	—	12.1	—	8.5	—
	Avg.		19.0	22.0	12.8	14.1	14.1	11.1
Atlin	BCSP	C	16	19	10.8	11.9	5.5	5.2
	YUSP	C	15	16	10.3	9.0	4.5	4.0
	PCPI	C	10	9	5.4	5.2	1.8	2.0
	Avg.		13.7	14.7	8.8	8.7	3.9	3.7
	BCAS	D	16	15	9.9	8.6	5.8	2.8
	YUAS	D	17	14	11.0	7.7	5.6	2.9
	PCWI	D	16	18	11.6	13.4	8.3	8.8
	Avg.		16.3	15.7	10.8	9.9	6.5	4.8
ANOVA Summary (Model I, 3-way)	veg F = 10.5, P = 0.005 loc F = 8.0, P = 0.003 veg × loc F = 3.5, P = 0.052 D > C (except Juneau) (18.8 > 15.6) J = H = A, but J > A (19.5 = 17.0 = 15.1)		veg F = 3.6, P = 0.073 loc F = 4.5, P = 0.026 veg × loc F = 3.0, P = 0.073 D > C (except Juneau) 11.8 > 10.3 J = H = A, but J > A (12.1 = 11.4 = 9.6)		veg F = 6.2, P = 0.022 loc F = 14.0, P = 0.000 veg × loc F = 4.0, P = 0.036 D > C (except Juneau) 8.9 > 6.7 J = H > A (8.9 = 9.8 > 4.8)			

vegetation types in Juneau. Although in Haines, and in Atlin 1992, relative abundance was consistently greater in deciduous than in coniferous vegetation, the difference was not evident in Juneau or in Atlin 1993. However, nest searches in Juneau in 1994 revealed that nest density was very high in SHCR (0.12/100 m<sup>2</sup>), much lower in BKLO (0.02/100 m<sup>2</sup>), and very low in two coniferous sites (0.01/100 m<sup>2</sup> for PECR and HERV), suggesting that census data might not reflect an extremely high density of birds in SHCR. In 1994, relative abundance was similar in both vegetation types and greater in Juneau than Atlin.

Site diversity differed significantly between deciduous and coniferous vegetation types and among locations, but not between years (Table 1). Overall, diversity was higher in deciduous than coniferous forest and lower in Atlin than in Juneau, with Haines intermediate and similar to

both. There was a significant interaction between vegetation type and location because the diversity in coniferous and deciduous vegetation types differed little in Juneau. Rarefaction curves for each location except Haines 1992 showed no consistent differences in species accumulation between deciduous and coniferous stands. In 1994, there was little difference of species diversity between vegetation types, however, although Atlin again supported low diversity.

Point diversity differed significantly among locations and marginally significantly between vegetation types, but not between years (Table 1). Point diversity was lower in Atlin than in Juneau, with Haines indistinguishable from both. A marginally significant interaction term occurred because diversity differed little between vegetation types in Juneau. In 1994, point diversity differed little between vegetation types, and point diversity was lower in Atlin than Juneau. Average

TABLE 2. Ranks of community measures for each vegetation type and location. H = Haines, J = Juneau, A = Atlin; D = deciduous, C = coniferous vegetation.

Site diversity	HD	≥	JD	≥	JC	>	AD	>	AC	≥	HC
	20.2		19.8		19.2		16.0		14.2		13.7
Point div.	HD	≥	JC	≥	JD	>	AD	≥	HC	>	AC
	13.3		12.7		11.6		10.4		10.0		8.8
Rel. abund.	HD	>	JC	≥	JD	≥	HC	>	AD	>	AC
	12.9		9.5		8.4		7.4		5.7		3.8

spatial heterogeneity of bird species composition within sites differed relatively little, ranging from 0.59 to 0.72, with no indication of relationship to vegetation type or location.

Average site diversity, point diversity, and relative abundance data for each vegetation type × location showed some consistent trends. Haines-deciduous always ranked highest; Haines-coniferous, Atlin-coniferous and-deciduous were always low; Juneau-deciduous and-coniferous were always similar (Table 2).

Although there were no detectable year effects overall, inspection of the data for each site in each year revealed several marked annual differences between 1992 and 1993 at certain sites. Relative abundance increased by an average of about two birds/point at CHKO and by more than three birds/point at DACR (Table 1). Several species contributed to this trend at both sites, but the biggest change at both sites occurred in Chestnut-backed Chickadees (*Parus rufescens*). In contrast, large decreases (more than 2.5 birds/point) were seen at BCAS and YUAS in 1993; relative abundance in 1994 was also low at these sites. The largest decreases at both aspen sites occurred in Yellow-rumped (Myrtle) Warblers (*Dendroica coronata*, -0.95 birds/point) and Dark-eyed (mostly Slate-colored) Juncos (*Junco hyemalis*, -1.59). Numbers of Yellow-rumps increased at one spruce site (+0.17) and both Pine Creek sites (+0.77). Juncos decreased in both Atlin spruce sites (-0.45) but increased only slightly in PCPI (+0.23). Other species showing some noticeable decrease in 1993 were Hammond's Flycatcher (*Empidonax hammondi*, -0.41) in YUAS, American Robin (*Turdus migratorius*, -0.61) and Warbling Vireo (*Vireo gilvus*, -0.66) at both aspen sites. Hermit Thrushes (*Catharus guttatus*) were absent from Atlin sites in 1992 but present in 1993.

Furthermore, site diversity increased markedly between years at Haines-COFP (four spp.)

and Juneau-HERV (eight spp.). In general, the additional species recorded were observed in very low numbers or are known to exhibit large annual variations in local abundance. These species included Red-breasted Nuthatch (*Sitta canadensis*), Red Crossbill (*Loxia curvirostra*), and Pine Siskin (*Carduelis pinus*).

Wood warblers (Emberizidae: Parulinae) were consistently better represented in deciduous forest communities than in conifer stands at all locations. Sparrows (Emberizinae) were more diverse in deciduous than coniferous stands in coastal forest, and thrushes (Muscicapidae: Turdinae) were usually more diverse in deciduous forests. Woodpeckers (Picidae) were slightly more diverse in deciduous stands in Haines and Atlin, but in Juneau they were recorded only in conifer stands, and then in low abundance.

#### COMMUNITY SIMILARITY

Overall, the avifaunas of Juneau and Atlin were least similar (proportional similarity [PS] = 28%). The avifauna of Haines held many species in common with both other locations, but was somewhat more similar to Juneau (PS = 58%) than to Atlin (43%).

The pooled avian communities of deciduous and coniferous stands were quite different in the coastal forests of both Juneau and Haines (PSs = 22%; Table 3), although the communities of the two vegetation types were less different in Atlin (PS = 43%). Comparisons within vegetation type showed a narrow range of average PS values from 68–77% in most cases; thus, even apparently similar habitats commonly supported moderately different bird communities. Comparisons between the communities of the aspen and willow sites and of the spruce and pine sites in Atlin (that is, within broad vegetation type, but between vegetation of differing structure and composition) yielded lower PS values (57%, 53%, respectively). The two deciduous sites in Juneau

TABLE 3. Proportional similarity among avian communities in different vegetation types.  $n$  = number of comparisons included in the average. When more than two sites are compared at any location, all possible pairwise comparisons are included. For Atlin, the first comparisons are between aspen stands (Deciduous) and between spruce stands (Coniferous); the second comparisons are between aspen and willow or spruce and pine, as indicated.

Location		Vegetation type		
		Deciduous	Coniferous	Decid × Conif
Juneau	Avg.	36%	68%	22%
	Range	(33–40%) $n = 2$ (2 sites, 2 yr)	(60–75%) $n = 6$ (3 sites, 2 yr)	(21–22%) $n = 2$ (2 yr)
Haines	Avg.	76%	69%	22%
	Range	(73–78%) $n = 4$ (3 s, 1 yr; 2 s, 1 yr)	— $n = 1$ (2 s, 1 yr)	(19–26%) $n = 2$ (2 yr)
Atlin (1)	Avg.	76%	77%	
	Range	(65–87%) $n = 2$ (2 aspen sites, 2 yr)	(72–83%) $n = 2$ (2 spruce sites, 2 yr)	
Atlin (2)	Avg.	57%	53%	43%
	Range	(55–59%) $n = 2$ (aspen × willow, 2 yr)	(52–53%) $n = 2$ (spruce × pine, 2 yr)	(37–53%) $n = 4$ (spruce × aspen, 2 yr; pine × willow, 2 yr)

were still less similar (36%); in fact, these two sites differed more than the two vegetation types in Atlin (see above).

When the species of each community (vegetation type × location) were ranked in decreasing order of abundance, the number of species comprising the top 50% of the total for each community was similar (five to seven) in all locations. At each site, this number varied from two to five, but no general patterns were evident between vegetation types or among locations in either year.

The dominant species (indexed as proportion of the bird community) differed markedly among locations. Pooled samples for each location showed that, in both years, Varied Thrushes (*Ixoreus naevius*) and Winter Wrens (*Troglodytes troglodytes*) dominated (comprised  $\geq 10\%$  of the avifauna) in Juneau, Wilson's Warblers (*Wilsonia pusilla*) dominated in Haines, and Yellow-rumped Warblers and Swainson's Thrushes (*C. ustulatus*) were predominant in Atlin.

Within vegetation types at each location, there was some variation in dominant species. However, some consistent patterns were that Yellow-rumped Warblers and Swainson's Thrushes were usually in the top three most abundant species at all Atlin sites and always at least in the top six species. Varied Thrushes and Winter Wrens were in the top four at all Juneau conifer sites,

and Townsend's Warblers (*D. townsendi*) in Haines-coniferous vegetation. Wilson's Warblers predominated at all Haines deciduous sites, and Hammond's Flycatchers in most Haines deciduous sites.

At all three locations, the proportion of long-distance migrants was greater in deciduous than coniferous forests. On average, 69% of the species (range 65–73%) and 89% of the individuals (range 81–93%) of deciduous forests were long-distance migrants, compared to 49% (range 40–55%) of species and 60% of individuals (range 53–67%) in coniferous forest.

#### HABITAT SELECTION

Some species were notable for the breadth of habitats occupied. If the relative abundance of a species exceeded about 0.3 birds/point/day in a range of habitats, we considered the species a habitat generalist. Notable generalists in the interior forests in Atlin included Yellow-rumped Warbler, Dark-eyed Junco, and Swainson's Thrush, which were common on all Atlin sites, both deciduous and coniferous. However, on the coast, the junco was scarce and patchily distributed in a variety of vegetation types, and Yellow-rumps and Swainson's Thrushes were moderately common only in some deciduous sites. American Robins occupied both deciduous and

TABLE 4. Numbers of species observed and expected (by rarefaction) on islands and in habitat patches. Size of smallest islands and patches given to nearest 0.1 ha.

Veg. type	Island/patch	Size	1992		1993	
			Expected	Observed	Expected	Observed
Conifer	Coghlan	67	13.5	12	17.9	18
	Spuhn	73	15.5	18	18.5	18
	Suedla	11	10.2	10	12.2	10
	Suedla Annex	3.2	4.7	4	5.6	4
	Battleship	1.3	5.3	5	6.8	5
Deciduous	Brotherhood Bridge	1.5	4.2	5	5.5	7
	Herbert River	1.1	3.5	3	4.2	4
	Tee Harbor	0.5	4.2	4	2.7	3
	Lena Loop	0.8	6.0	6	3.5	3

coniferous sites in Atlin but were common only in deciduous sites in Juneau and Haines. Ruby-crowned Kinglets (*Regulus calendula*) were common only in coniferous forest in Atlin but usually occurred in both vegetation types in coastal forests. Red-breasted Sapsuckers (*Sphyrapicus ruber*), never in high numbers, were found in coniferous forest in Juneau but deciduous forest in Haines.

In contrast, some species such as Hammond's Flycatcher and Warbling Vireo consistently favored deciduous sites at all locations where they were present. Records of Orange-crowned Warblers (*Vermivora celata*) and Wilson's Warblers at coniferous sites reflect their occurrence in small openings with deciduous cover. Yellow Warblers and Fox Sparrows (*Passerella iliaca*) were usually found only in certain deciduous sites. Other species, when present, consistently occurred in conifer sites. These included Golden-crowned Kinglet (*R. satrapa*) Chestnut-backed Chickadee, and Pacific-slope Flycatcher (*E. difficilis*).

#### ISLANDS AND HABITAT PATCHES

Most of the conifer-clad islands in Auke Bay supported about as many species as expected based on rarefaction of pooled mainland conifer censuses and the number of individuals recorded. In five of ten comparisons, the difference between the observed and expected number of species was  $<1$ , and in eight of ten comparisons, the difference was  $<2$ ; the observed sometimes even exceeded the expected (Table 4). Two species, Bald Eagle (*Haliaeetus leucocephalus*) and Northwestern Crow (*Corvus caurinus*), are strongly associated with shorelines and therefore occurred commonly in the island censuses but seldom in the mainland censuses. However,

omission of these two shoreline species did not change the basic similarity of species diversity on islands and mainland. Several mainland forest species never appeared in our island censuses (e.g., American Robin, Swainson's Thrush, Yellow-rumped Warbler). In addition, several species occurred irregularly on different islands in different years.

Four small deciduous patches surrounded by conifer forest on the mainland each held about as many species as expected by rarefaction of pooled deciduous censuses on the principal sites and the number of individuals recorded (Table 4). For this comparison, we used only species that are typical of deciduous forest that probably would not have occurred in these patches without the presence of that vegetation. These included Fox Sparrow, Orange-crowned Warbler, Wilson's Warbler, American Redstart (*Setophaga ruticilla*), Yellow-rumped Warbler, and American Robin. We excluded species whose territories were centered in conifer forest but whose foraging range sometimes happened to encompass the some portion of the deciduous patches as well, such as Steller's Jay (*Cyanocitta stelleri*), Pacific-slope Flycatcher, Winter Wren, Golden-crowned Kinglet, and Varied Thrush. Species occurrence in the small deciduous patches sometimes varied annually, as was true for the Auke Bay islands.

#### DISCUSSION

##### PATTERNS OF DIVERSITY AND ABUNDANCE

The diversity of birds tended to be higher in deciduous than coniferous forest of the north, but the direction or magnitude of the trend var-



ied annually, with specific vegetation composition, and location. Likewise, relative abundance tended to be slightly greater in deciduous than coniferous stands in our study; Juneau appeared to be an exception, but censuses probably underestimated avian abundances in one of the deciduous sites. Judging from the number of unmarked birds caught in mist nests and the high density of nests, relative abundances at SHCR may be underestimated, perhaps because very close packing of territories made it difficult to distinguish individuals. In contrast to James and Wamer (1982), we found no difference between rarefaction curves in deciduous and coniferous forests. However, while the diversity in deciduous stands sometimes exceeds that in conifer stands, the reverse seems to be less frequent.

A sample of published reports comparing the bird communities of deciduous and coniferous stands in western North America showed that the contrast in species diversity varies greatly. Some studies report little consistent difference, although others report more species in deciduous than coniferous stands (Salt 1957; Anderson 1972; Theberge 1976; Erskine 1977; Spindler and Kessel 1980; Smith and MacMahon 1981; James and Wamer 1982; Kessler and Kogut 1985; Knopf 1985; Hopkins et al. 1986; Finch and Reynolds 1988; Scott and Crouch 1988a, 1988b). The contrast in diversity accompanied a parallel contrast in avian abundance in some of these studies but not in others, such that differences in diversity, when they occurred, could not be attributed simply to differences in abundance. Most of the far-northern studies show overlapping distributions of species richness in the two vegetation types. Contrasts between forest types tend to decrease with increasing latitude (Haila and Järvinen 1990). Keast (1990) also noted little distinction between the avifaunas of coniferous and deciduous stands, remarking that birds are versatile in their habitat choices. As in the present study, the proportion of the community comprised of long-distance migrants is commonly higher in deciduous than coniferous forest in the north-temperate zone (Nilsson 1979, Tomiałojć and Wesołowski 1990, Rabenold 1993).

Annual variations in bird populations are expected. However, the marked yearly differences in avian abundance in our Atlin aspen stands are particularly striking and occurred in species that differed in their distance and time of migration, nest sites, foraging ecology, and proximity to range

limits. We could not link the annual differences to severe spring or summer weather or to potential prey abundance. Whatever the causes of the annual differences, the result altered the contrast between deciduous and coniferous stands.

The three study locations represent a gradient of moisture, and perhaps other factors, with high rainfall in the coastal forest near Juneau, intermediate rainfall near Haines in the rain shadow of the Chilkat Mountains, and low rainfall in the interior near Atlin. In Juneau, species diversities were high and similar in conifer and deciduous forests and similar to deciduous forest in Haines. At the other end of the spectrum, species diversities were low and only moderately different in conifer and deciduous forests in Atlin and similar to conifer forest in Haines. This pattern suggests the possibility that the bird communities of conifer forests may be more sensitive to the gradient of increasing dryness than the communities of deciduous forest—or, conversely, that the bird communities of deciduous forest are more sensitive to a gradient of increasing moisture.

Many northern bird communities may be unsaturated (Flack 1976, Enemar et al. 1984, Virkкала 1991), probably including our northern cottonwood stands. Riparian cottonwood stands in Southeast Alaska are notable for the lack of birds characteristic of this habitat farther south: species such as orioles, kingbirds, grosbeaks, and buntings are missing. A few robins and vireos nest in the canopy, Yellow-rumped and occasional Townsend's Warblers may be found there, and some of the habitat shifts described below may be related to this ecological void, but the cottonwood canopies in this region are not the lively places familiar to bird-watchers farther south.

The boreal forest or taiga is a relatively recent vegetation formation in most of its present locations, coming to occupy its present-day high-latitude range in geologically recent times, about 10,000–15,000 years ago (Blondel 1990, Keast 1990, Haila and Järvinen 1990). Furthermore, climatic changes in much of western North America resulted in the loss of much deciduous forest from the Miocene to the Quaternary (Keast 1990). Deciduous trees in the west are mostly seral, becoming dominant ahead of the conifers on deglaciated, eroded, or burned lands; because glacial retreat, braided rivers, landslides, and fires are frequent in boreal landscapes, deciduous stands are often extensive and common. Many

of the birds of western deciduous forests arrived by colonization, often from the east, rather than by in-situ speciation (Flack 1976, Keast 1990). The ranges of many North American birds are no doubt still expanding northwestward, and colonization by forest birds from Asia should also increase as forests expand to the north and west in Alaska, although spring weather may limit the expansion of some species (Väisänen and Järvinen 1977, Heggberget 1987). Indeed, 24–33% of the species at our study locations are very close to their present northern range limits (Anonymous 1987, Peterson 1990).

Because bird species diversity was similar in conifer and deciduous forests near Juneau and to a lesser degree near Atlin, but the understory avifauna was richer in deciduous forests (Willson and Comet 1996), it appears that more species of birds use the forest canopy in the conifer forest in these two locations. The greater number of canopy species is not due to birds, such as crossbills and siskins, that specialize on conifer seeds because such species appeared infrequently in our censuses. Instead, the canopy birds are mostly insectivorous, probably exploiting the large surface area of leaves and bark that are available in these conifer canopies. Juneau rainforests may support a relatively high diversity of canopy-users because the tree-crowns in spruce-hemlock forest offer both extensive foraging surfaces and a variety of nest sites including not only the dense, leafy branches, but also numerous moss wads and mistletoe clumps. Also, as discussed earlier, the canopy of the relatively small cottonwood stands near Juneau was not heavily occupied. In Atlin, the contrast in canopy structure between aspen and white-spruce forests is marked: aspen crowns are very open, with relatively little cover or surface area, while the spruce forest, although more open than that in Juneau, offers denser foliage. Haines offers an opportunity to examine these suggestions further: our impression is that the conifer stands there have smaller trees, less windthrow, and fewer moss wads than in Juneau.

#### COMMUNITY COMPOSITION

Species dominance appeared to be greater in northern than midwestern forests (Wisconsin and Illinois). The number of species (two to five) comprising the top 50% of the community was lower in northern forests (this study, Theberge 1976, Erskine 1977, Spindler and Kessel 1980, Enemar et al. 1984, Haila and Järvinen 1990) than in many midwestern forests (Mann-Whit-

ney U,  $P < 0.001$ ). In deciduous forest stands in the midwest, four to nine species usually constituted the top 50% of the community (Bond 1957, Willson 1974), although the total number of species recorded from the midwestern forests differed little from most of our coastal forests. Furthermore, the single most common species in our study comprised 15–30% of the total census. This range is similar to that for many other northern forests (Theberge 1976, Erskine 1977, Nilsson 1979, Spindler and Kessel 1980, Westworth and Telfer 1993) and North American conifer forests in general (Wiens 1975). The frequency of our most common species was intermediate between some Alaska interior conifer forests (Spindler and Kessel 1980) and many midwestern forests (11–22%, data from Bond 1957, Willson 1974; Mann-Whitney U,  $p = 0.001$ ). Similar contrasts between our northern forests and midwestern forests are found when comparing the combined frequencies of the top two species/site.

Broad habitat niches may be common for many northern birds (Erskine 1977, Haila and Järvinen 1990, Virkkala 1991, Rabenold 1993). Other studies have noted that certain species such as Swainson's Thrush, Dark-eyed Junco, Yellow-rumped Warbler, American Robin, and the less common Gray Jay (*Perisoreus canadensis*) quite consistently behave as habitat generalists (Carbyn 1971, Theberge 1976, Erskine 1977, Spindler and Kessel 1980, Weisbrod 1980). These observations match ours in Atlin, but in the coastal forests these species were either less common or more restricted in habitat use. Swainson's Thrush occupied a wider range of habitats in Maine in the absence of congeners (Morse 1972), but we found no relationship between the presence or abundance of Swainson's and Hermit Thrushes.

Of particular interest are species that appear to shift habitat type, either among locations in northern forests or between northern forests and those elsewhere. For example, Hammond's Flycatcher is commonly described as nesting in coniferous forests (Robbins et al. 1983, Sakai and Noon 1991), although Ehrlich et al. (1988) noted that it is found occasionally in aspen. In our northern forests, this species is regularly recorded in deciduous forest (this study, Spindler and Kessel 1980, Armstrong 1995) and only rarely in coniferous forest (Willson, unpubl.). Habitat changes by birds more typical of coniferous forest has been reported for southwestern United

States as well (Flack 1976). Other species appeared to occupy a narrower range of habitats in some locations than in others. The Yellow-rumped Warbler is reported to occur in both coniferous and deciduous forest (Robbins et al. 1983, Ehrlich et al. 1988). Although it occurred in both forest types in Atlin, we recorded it only from deciduous forests on the coast. Blackpoll Warblers (*D. striata*), which commonly breed in coniferous forest (Gabrielson and Lincoln 1959, Robbins et al. 1983, Ehrlich et al. 1988, Armstrong 1995), or both coniferous and deciduous forests (Theberge 1976, Willson unpubl. data for Atlin), were censused only in deciduous stands in Juneau.

Absence or rarity of several species appeared to be related to habitat conditions. The large cottonwood stands in Haines and Skagway supported breeding populations of several species including Hammond's Flycatcher and Warbling Vireo found only rarely in the smaller stands near Juneau. Also, certain species were not recorded from the islands in Auke Bay. However, because so many forest species reached the islands including Blue Grouse (*Dendragapus obscurus*) and Brown Creeper (*Certhia americana*), the absence of these species is likely to be related not to lack of access, but rather to lack of appropriate habitat (Martin et al. 1995). Woodpeckers in Juneau and Atlin forests were scarce (see also Bailey 1927, Theberge 1976, Erskine 1977, Spindler and Kessel 1980). However, area naturalists (Noble 1977) occasionally report locally high abundances of Red-breasted Sapsuckers and Hairy Woodpeckers (*Picoides villosus*), especially where there is a high density of severely stressed trees (sapsucker) or a spruce bark-beetle outbreak (Hairy Woodpecker). Our observations in Juneau forests contrasted markedly with the diversity and abundance of woodpeckers in midwestern forests (Bond 1957, Willson 1974).

## GENERAL DISCUSSION

All of the study sites were, to some extent, habitat mosaics. Most of the conifer sites contained a few small (<150 m<sup>2</sup>) enclaves of primarily deciduous vegetation, and the canopy of all the deciduous sites contained occasional large conifer trees. As a result, some species more characteristic of deciduous stands were recorded on conifer sites, and vice versa. This is important to recognize for two reasons: 1) the diversity and possibly abundance values were increased over what would occur in a completely uniform stand;

2) the birds were successful in finding these tiny patches and using them. One or two spruce trees in a deciduous stand appeared to be enough for a Ruby-crowned Kinglet or a Hermit Thrush to hold a territory, and the adults then often foraged in the surrounding deciduous vegetation. In species such as Steller's Jay, Red-breasted Nuthatch, Northern Flicker (*Colaptes auratus*), Boreal Chickadee (*Parus hudsonicus*), territories were probably located across habitat boundaries. Our censuses therefore represented the habitats as they occurred on the ground, and not some idealized pure vegetation type.

Our results have several obvious implications for land management that includes a goal of maintaining avian biodiversity. 1) Habitat-suitability models derived from one location, used to estimate potential populations supported by a given tract of land, cannot necessarily be applied to another location, because at least some birds change habitats in certain areas. Some birds also shift microhabitats (Willson and Comet 1996). Some field information must be derived from each location to ascertain, at minimum, that the species in question actually uses the habitat in the way presumed by the habitat-suitability model. 2) When field censuses are used to monitor species of special interest, they should be conducted in a range of sites that offer a variety of vegetation characteristics and over enough years to encompass a range of annual variation in abundance. Otherwise, there is a considerable risk of obtaining an inadequate representation of the species in question. 3) Because distinctive plant communities often support quite different bird communities, the maintenance of regional biodiversity depends on maintaining a variety of plant communities. In Southeast Alaska, for example, deciduous stands support a markedly different bird community than conifer stands, and deciduous stands themselves vary greatly. It is therefore important for regional biodiversity to maintain both kinds of stands; the richest deciduous stands in Southeast Alaska are the relatively uncommon riparian cottonwood stands, which thus acquire regional significance for biodiversity.

In addition, we emphasize that census information alone, however detailed and thorough, is not enough. Density or relative abundance do not necessarily represent reproductive success (Vickery et al. 1992) and the contribution to population recruitment necessary for population viability. Thus, forward-looking land-manage-

ment plans require information on reproductive success in addition to density. We expect that the majority of avian ecologists are aware of these simple observations, but they have yet to be fully incorporated in most land-management plans.

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