

Richard G. Lawford Paul B. Alaback
Eduardo Fuentes
Editors

High-Latitude Rainforests and Associated Ecosystems of the West Coast of the Americas

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Richard G. Lawford
Office of Global Programs
National Oceanic and Atmospheric
Administration
1100 Wayne Avenue
Silver Spring, MD 20920-5603, USA

Paul B. Alaback
School of Forestry
Montana Forest and Conservation
Experiment Station
University of Montana
Missoula, MT 59812-1063, USA

Eduardo Fuentes
Catholic University
Laboratory of Ecology
Castilla 114-D
Santiago
Chile

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11. Avian Communities in Temperate Rainforests of North and South America

Mary F. Willson, Toni L. De Santo, Carlos Sabag,
and Juan J. Armesto

The climate and topography of the temperate rainforest biomes of North and South America have many similarities (e.g., Alaback, 1991). However, the biogeographic and phylogenetic relationships of the avian inhabitants of these biomes differ greatly, as does the structure of their habitats. There is no particular reason to expect great similarities in avian community structure in the two regions, but a comparison of communities can be instructive by setting the stage for more directly functional and predictive approaches (e.g., Jaksic & Feinsinger, 1991; Meserve & Jaksic, 1991; Willson, 1991). Here we examine first the abundance, diversity, guild structure, and selected biological attributes of bird communities in coastal temperate rainforests of Alaska and Chile. We then broaden the comparison, using previously published information for avian communities of the south temperate forests of Argentina and Chile and the north temperate forests in North America, specifically those in the northwestern part of that continent and those of the midwestern United States, to try to make more general statements. Our goals are: 1) to describe differences and similarities in avian communities in these forests, focusing on diversity, abundance, and selected biological attributes; 2) to assess the similarity of the bird community of the Chilean rainforest to the Alaskan coastal rainforest and to Canadian interior forests; and 3) to begin to examine some sources of the differences in community structure.

Methods

Census information consists of point-counts near Juneau and Haines, Alaska (58°N – 59°N) and on Isla Grande de Chiloé (42°S), Chile. Counting stations, located along transects in the study sites, were separated by $>150\text{ m}$ in Alaska (Willson & Comet, unpublished manuscript) and $>100\text{ m}$ in Chiloé (Willson, De Santo, Sabag, & Armesto, 1994). The counts did not include nocturnal birds, shorebirds, or waterbirds. The data reported here refer to regularly occurring species, meaning those that were recorded on more than one census day; each site was sampled at least four times during the breeding season. All counts were made in 1992 (Alaska: May and June; Chile: November and December), during the morning hours. Each point-count lasted 8 minutes, and most study sites had at least eight points. On average, four points were sufficient to record 85% of the regularly occurring species observed at each site in both Chile and Alaska, and 98% (range 93%–100%) of such species were obtained by six points. *Diversity of species* is defined as species richness, for our purposes in this chapter, and all abundance data are relative abundances, in terms of the number of birds/point/day. All references to “abundance” have to do with the number of birds detected; we did not examine possible regional differences in detectability. Documentation of the Chilean censuses is reported in Willson, De Santo, Sabag, and Armesto (1994), and that of the Alaska censuses is reported in Willson and Comet (unpublished manuscript).

For purposes of comparisons of diversity and abundances in Alaska and Chile for this chapter, we use only study sites that occupied at least 50 ha, and most were much larger. The floristically diverse, broadleaf Chilean forests are dominated by *Nothofagus*, *Drimys*, *Weinmannia*, and myrtaceous trees (Arroyo, Riveros, Peñaloza, Cavieres, & Faggi, this volume). *Picea sitchensis* and *Tsuga heterophylla* dominate the Alaskan coastal conifer forests, and *Populus trichocarpa* comprises the canopy of the Alaskan deciduous forests in which point-counts were done.

We also ask whether the Chilean forest bird communities are notably similar in structure to those of the Alaskan coastal forest, by comparing them to the communities in Canadian forests at similar latitudes. For this purpose, bird censuses in *Picea glauca*, *Pinus contorta*, *Populus tremuloides*, and *Salix/P. trichocarpa/Alnus* stands in British Columbia and Yukon are used.

In addition to point-counts, mist-net censuses of understory birds were conducted in both areas, both in some of the study sites used for point-counts and in other sites. Mist nets were operated in the same kinds of forests as the point-counts, with the addition of some stands of *Alnus* in Alaska. A total of 380 mist-net hours were spread over three sites in Chiloé (8 nets/site). In Alaska, about 680 mist-net hours were accumulated in two deciduous sites and 635 net-hours in a conifer site near Juneau

(at least 10 nets/site); capture rates for an additional conifer site near Ketchikan were obtained from Canterbury. Most of the nets were 30 mm or 36 mm mesh size, and 12 m by 2 m in net size. Mist-net data are used here only to compare capture rates of birds in understory.

The broader comparisons, using data in the literature, included forests with diverse species composition and a variety of stand size. South temperate data were derived from Cody (1970), Ralph (1985), and Vuilleumier (1972), with a latitudinal range of about 38°S–42°S (plus one site at 30°S). Midwestern U.S. data for deciduous forest were obtained for Wisconsin (Bond, 1957; using only stands >100 ha, to ensure that some large tracts were included) and Illinois (Willson, 1974; using each stand only once, to avoid pseudoreplication), and for coniferous forest in Minnesota and Michigan (from Willson, 1986); latitudinal range was about 40°N–49°N. In a general way, the midwestern U.S. data provide a partial control for simple latitudinal effects such as gradients in species diversity, but more importantly, they are a ready source of comparative information that allowed us to attempt these broad contrasts. Data for forests of the north and west in North America came from Spindler and Kessel (1980; coniferous and deciduous), Flack (1976; deciduous), Theberge (1976; coniferous and deciduous), Kessler and Kogut (1985; coniferous), with a latitudinal range of about 49°N–63°N. These studies were used only for comparisons of total species present and of guild structure among regions and forest types. Differences in census methods among these studies mean that all comparisons must be taken as preliminary estimates.

Guild assignments for each species were based on our observations in Alaska and Chile and on published information (e.g., Harrison, 1975, 1979, for nest locations in North America; Holmes, Bonney, & Pacala, 1979, and Manuwal, 1991, for foraging of some species; Flack, 1976, for aspen forests; Johnson, 1967, for Chilean birds). Root (1967) defined a *guild* as “a group of species that exploit the same class of environmental resources in a similar way.” The guilds used for our comparisons represent broad categorizations of patterns of habitat use; fine tuning of categories (e.g., distinguishing subcanopy from canopy foragers, or ground from understory foragers, or insectivores from various types of omnivores in Chile) is not yet possible. Nevertheless, our guilds capture the major distinctions that emerged from more detailed and quantitative studies elsewhere, in which vertical stratum and proximity to tree trunks provided the major distinctions among guilds (Holmes, Bonney, & Pacala, 1979; Holmes & Recher, 1986).

Although Holmes and colleagues dealt with foraging guilds, here we include nest-sites as well, given that nesting biology has been shown to have important consequences for community structure (Martin, 1988a, 1988b). The guilds include the following broad categories: 1) big-tree users, nesting or foraging on trunks and large branches; 2) users of

covered nests, including those nesting in tree cavities as well as in other holes or building dome nests; 3) understory users, including those that nest or forage principally in the understory (<3 m or so); some birds were assigned to an "understory" guild on the basis of common foraging and/or nesting locations, but males of these species often sing from the canopy (e.g., *Passerina cyanea*, *Ixoreus varius*, *Turdus migratorius*, and *Catharus guttatus*, to name a few in North America, and *Turdus falklandii* in Chile); 4) aerial feeders, including species that often feed on the wing, either hawking or hover-gleaning insects; 5) canopy seed predators, including species known to extract seeds from fruits or cones for a major portion of their diet; 6) leaf-gleaners, including insectivorous species that feed while moving along or between branches. These categories are a first approximation, pending an increased information base, especially for Chile. Many of the guilds used in this chapter are based on the location of a particular resource, because of our interest in what might happen if the availability of such resources were altered (Willson, De Santo, Sabag, & Armesto, 1994). Number 2 above is a clear exception, in that it depends in part on particular types of constructed nests, rather than a resource. Nevertheless, we include it, because nesting habits can have a profound effect on patterns of reproductive success, which in turn can influence species presence and abundance.

In this preliminary assessment, a given species can belong to more than one of these guilds, and the sum of all the guilds need not be 100% of the community. The guild assignment of most midwestern species can be obtained from Willson (1974), and those for Alaska and adjacent Canada are from Flack (1976) and Willson (unpublished). For Chiloé, some guild assignments are shown in Willson, De Santo, Sabag, and Armesto (1994); in addition, the canopy seed predators are *Enicognathus leptorhynchus*, *Columba araucana*, and *Phrygilus patagonicus*; aerial feeders include *Elaenia albiceps*, *Pyrope pyrope*, *Colorhamphus parvirostris*, and *Tachycineta leucopyga* (both *Elaenia* and *Pyrope* also consume much fruit); and leaf-gleaners include *Anairetes parulus*, *Colorhamphus parvirostris*, *Eugralla paradoxa*, *Scytalopus magellanicus*, and *Sylviorhynchus desmursii*.

Statistical Methods

Direct comparisons of diversity, abundance, and guild structure for our 1992 data for Chile and Alaska are made with one-way parametric ANOVAs, Kruskal-Wallis nonparametric one-way ANOVAs, and Mann-Whitney U tests. In these comparisons, as in those described in the following paragraph, we analyze the data first by the proportion of regular species in each guild and then by the proportion of individuals that belong to each guild. We use the terms *speciose*, *diverse*, and *species rich* interchangeably in referring to proportionate or relative guild structure by species, and the term *abundance* to mean proportions of individuals.

For the broader comparison among regions, we divided both northern and southern forests into two types (conifer and broadleaf), because experience in Alaska has suggested important biological differences between them and because other studies (e.g., James & Rathbun, 1981) have found differences in avian community structure between the two kinds of forest. We search for patterns, using a Model I two-way parametric ANOVA (with arcsin-transformation of percents) or region (south, midwest, northwest) \times forest type (broadleaf, conifer). This approach allows us to detect interactions between the chosen factors and the effects of each factor. In some cases, directional differences are apparent despite a significant interaction term, and these can be treated, properly, along with the results of ANOVAs that lack significant interaction terms (Sokal & Rohlf, 1981). In addition, we can make predictions, based on what is known or believed about the basic biology of each kind of forest, about the direction of differences between communities of these forests. Post-hoc tests following the ANOVA permit a ranking of all the regional forest types, which is then examined for trends. The predictive approach is stronger in some ways, because it permits the negation of some possible explanations. However, it has the obvious frailty that the prediction is only as good as the information on which it is based; negation can occur because the background logic and information—and hence the prediction—are faulty. Nevertheless, it can be a useful tool in this preliminary phase as a means of examining some possible sources of differences among the communities.

Comparison of Alaskan and Chilean Rainforests: Results

Diversity and Abundance

Site diversity (the number of regularly occurring species at each site) differed with marginal significance among the three forest types (refer to Table 11.1; one-way ANOVA, $F = 3.64$, $p = 0.065$). However, point diversity (the average number of regularly occurring species per point) differed significantly among forest types: point diversity was highest in Alaskan deciduous forest and lowest in Alaskan conifer stands; Chiloé was intermediate and not significantly different from either (see Table 11.1; one-way ANOVA, $F = 4.0$, $p = 0.05$; Tukey post-hoc test). On average, point diversity in Chiloé accounted for a similar proportion of site diversity (68%) as in the other sites (74%, 80%), probably indicating similar spatial heterogeneity in avian distributions within sites in all three kinds of forest.

The greatest average number of birds per census point per day was found in Chilean forests, and the lowest, in Alaskan coniferous forests; Alaskan deciduous forests were intermediate (Table 11.1; one-way

Table 11.1. Avian Species Diversity and Abundance in Temperate Rainforests of Southeast Alaska and Chile, Using Regularly Occurring Species (Defined as Those Recorded on at Least 2 Census Days at a Site). Some species are migratory in the interior but not on the coast of Alaska (e.g., *Troglodytes troglodytes*, *Regulus satrapa*), and are here counted as nonmigratory.

Location, forest type	Site Diversity (Spp./site)	Point Diversity (Mean No. spp./point)	Abundance (Mean No. birds/point/day)	Percentage Long- distance Migrants
Southeast Alaska				
Deciduous	18, 18, 18	15.9, 13.3, 14.1	13.0, 11.7, 9.3	83, 83, 72
Average	18.0	14.4	11.3	79
Conifer	14, 16, 15, 20, 12, 18	7.9, 11.6, 10.8, 13.2 10.4, 13.0	5.9, 7.0, 11.9, 8.7, 7.5, 7.3	38, 50, 67, 53, 55, 41
Average	15.8	11.2	8.1	50.1
Chiloé, Chile				
Broadleaf, Mature	19, 20, 16	14.8, 13.2, 11.7	15.8, 11.8, 16.4	16 (21), ¹ 20 (25), ¹ 17 (17)
Broadleaf, Secondary	22	12.0	14.3	14 (18)
Average	19.3	12.9	14.6	16.8 (20.3)

¹ Including *Columba araucana*.

ANOVA, $F = 12.44$, $p = 0.002$; Tukey post-hoc test showed that the significant difference was found between Chiloé and Alaskan coniferous forest). Mist-net samples from the understory, however, suggest either that the denser populations of Chiloé occur chiefly in the upper strata of the forest, or that the understory birds are more difficult to capture in mist nets. The catch rate of birds in understory in Chiloé (0.13–0.22 birds per mist-net hour) was uniformly lower than that for Alaskan deciduous stands (0.36–1.05); the samples for Alaska coniferous stands (0.06–0.15) were extremely low (one-way anova, $F = 6.81$, $p = 0.037$).

Composition

A number of taxonomic families are shared by the avifaunas of Alaska and Chiloé forests, and both regions hold species of families and sub-families not shared with the other region (e.g., Chiloé: Psittacidae, Furnariidae, Rhinocryptidae; Alaska: Paridae, Sittidae, Certhiidae, Bombycillidae, Vireonidae, Emberizidae—Parulinae, Muscicapidae—Sylviinae). More interesting are genera shared by these widely separated regions: *Picoides*, *Colaptes*, *Turdus*, *Zonotrichia*, *Carduelis*, *Tachycineta*, and *Troglodytes*. Chile even has one species that occurs in much of North America, although not in Alaskan coastal forests (*Troglodytes aedon*).

The most common species in the Alaskan deciduous stands were *Wilsonia pusilla*, *Vermivora celata*, and *Dendroica coronata*, ranking in the top three for abundance in the majority of sites. In Alaska coniferous stands, the most common species (top three at most sites) were *Ixoreus varius*, *Troglodytes troglodytes*, and *Dendroica townsendii*. Five of these six most common species are summer residents (and long-distance migrants) in Alaska, and four belong to a single subfamily (Emberizidae—Parulinae).

The most common species at all sites on Chiloé was the tyrannid *Elaenia albiceps*, a summer resident and long-distance migrant (Johnson, 1967; Sabag, 1993). The chucao (*Scelorchilus rubecula*; Rhinocryptidae) ranked in the top three at three sites but was probably overestimated because of its loud, ringing call. Also commonly ranked in the top three were the only lowland hummingbird in the region (*Sephanoides galertitus*) and a furnariiid (*Aphrastura spinicauda*).

Notable Biological Differences

One major difference between the avifaunas of southeast Alaska and Chiloé is the high proportion of southeast Alaskan species that are long-distance migrants (see Table 11.1). Migrants comprise 38% to 67% of the regularly occurring species in Alaskan coastal conifer forest and as much as 72% to 83% of the species in deciduous forest. In contrast, long-distance migrants constitute less than 20% of the regularly occurring

Chilote forest-bird community (or <25% if *Columba araucana* is included as a long-distance migrant; we lack information on the migratory patterns of Chilote populations of *C. araucana*). Several additional species in both southeast Alaska and Chiloé make local seasonal movements.

A second major difference between North American and Chilean rainforests is found in the clutch sizes of many species of birds. Many species of breeding birds in Chiloé usually lay clutches of two to three eggs, and only a few regularly lay at least four eggs (Johnson, 1967). In contrast, many North American birds commonly lay clutches of at least four eggs; most of the data derive from studies below the 49th parallel (Ehrlich, Dobkin, & Wheye, 1988; Harrison, 1979), and clutches at high northern latitudes are often even larger than those at lower latitudes (Lack, 1968; Morton, 1974). The geographic differences in clutch size are found in birds of various taxonomic and biogeographic affiliations, habitats, and nesting habits. Even closely related species commonly, but not invariably, exhibit the difference in clutch size: *Turdus migratorius* (3–4) versus *T. falklandii* (2–3); *Colaptes auratus* (5–8) versus *C. pitius* (4–6); *Troglodytes aedon* (6–7) and *T. troglodytes* (5–6) versus *T. aedon* (4–7); *Tachycineta bicolor* (5–7) versus *T. leucopyga* (4–6); *Zonotrichia leucophrys* (3–5) versus *Z. capensis* (3–4); *Picoides pubescens* (4–5) versus *P. lignarius* (3–5). In addition, several genera not found in our censuses also show this pattern (e.g., *Mimus*, *Agelaius*, *Sturnella*, and *Cistothorus*).

Guild Structure

Big-tree users comprised equivalent proportions of the avifauna, by species (refer to part A in Table 11.2) and by abundance of individuals (part B, Table 11.2), in Chiloé and Alaska conifer stands, and a significantly lower proportion in Alaska deciduous stands. Species using covered nests were most frequent in Chiloé, and least frequent in Alaska deciduous forest (part A, Table 11.2). The relative abundance of covered-nesting species was lowest in Alaska deciduous forest and slightly higher in Chiloé than Alaska coniferous forest (part B, Table 11.2). Thus, although the diversity of covered nesters in Chiloé was much higher than in Alaska coniferous forest, their relative abundance was less different, reflecting the commonness of *Troglodytes troglodytes* in conifer forests and the relative rarity of some Chilean covered-nesting species.

Understory birds comprised a greater proportion of the avifauna, by both species richness (part A, Table 11.2) and abundances (part B, Table 11.2) in Alaska deciduous stands, followed by Alaska conifer stands. Chilote forests held the fewest species and individuals of this guild (parts A and B, Table 11.2). Leaf-gleaners were least speciose and least abundant in Chiloé (parts A and B, Table 11.2). In contrast, aerial feeders were most diverse and most abundant in Chiloé.

Table 11.2. Guild Structure of Forest Avifauna of Southeast Alaska and Chiloé

Part A) Average proportion of regular species in each guild in each region (range in parentheses). An * between two values in the same row marks the likely source of significant differences, i.e., no overlap or a Mann-Whitney U pairwise test between adjacent entries in the table would be significant.

Guild	Alaska		Chiloé Broadleaf (n = 4)	Kruskal-Wallis	p
	Deciduous (n = 3)	Coniferous (n = 6)			
Big-Tree Users	11% (—)	*	17% (14%–20%)	18% (13%–26%)	6.54
Covered Nesters	17 (—)	*	23 (20–27)	47 (38–53)	10.53
Understory Birds	70 (67–72)	*	48 (36–60)	39 (32–44)	8.68
Aerial Feeders	6 (6–7)		5 (0–8)	12 (10–14)	8.03
Canopy Seed Predators	0 (—)		2 (0–7)	13 (6–16)	8.68
Leaf-Gleaners	39 (28–44)		27 (20–33)	17 (13–19)	8.93

Part B) Proportion of individuals in each guild in each region. * As in A, an * indicates marginal significance.

Guild	Alaska		Chiloé Broadleaf (n = 4)	Kruskal-Wallis	p
	Deciduous (n = 3)	Coniferous (n = 6)			
Big-Tree Users	4% (3%–4%)	*	9% (6%–21%)	15% (6%–21%)	7.11
Covered Nesters	4 (<1–6)	*	23 (11–37)	40 (30–50)	9.51
Understory Birds	74 (69–78)	*	60 (42–75)	(*) 36 (26–50)	7.81
Aerial Feeders	9 (5–13)		7 (<1–14)	* 30 (22–38)	7.94
Canopy Seed Predators	1 (<1–3)		1 (0–3)	* 8 (5–11)	7.83
Leaf-Gleaners	32 (29–36)		28 (14–45)	(*) 12 (7–17)	5.27

The results for canopy seed predators, indicating a higher frequency of species and individuals in Chiloé than Alaska (parts A and B, Table 11.2), is at least partly an artifact. Many of the seed predators of the North American conifer forest are sporadic and even nomadic in occurrence and often do not breed during the season used by most birds for nesting (Benkman; personal communication). Therefore, they are not often recorded in spring "breeding-bird" censuses and are certainly underestimated in this study (especially *Loxia* species).

We compared guild structure of the Chilean bird community to that of Alaskan coastal forests and that of Canadian interior forests to the east of the coastal range of mountains near Juneau to determine if the bird communities of the two rainforests (Alaska coastal, Chiloé) are convergent in structure. The guild structure of Chilote forest birds is no more similar to that of Alaskan coastal forests than it is to that of Canadian forests. The proportionate frequency of species in Chiloé is most similar to Alaskan forests (specifically conifer forests) for three guilds (big-tree users, understory birds, leaf-gleaners), and most similar to Canadian forests of the remaining three guilds (covered nesters, aerial feeders, canopy seed predators), as shown in Table 11.3. This result suggests that guild structure of the Chilote forest birds is not particularly similar to that of Alaskan coastal forest birds.

Comparison of Guild Structure in North and South Temperate Forests

Patterns

Data from our censuses were combined with data extracted from published studies, and classified by location (northwest North America, midwest North America, south temperate) and forest type (broadleaf, conifer). The resulting six categories were subjected to two-way ANOVA, in a search for general patterns. Because we already know that there is some heterogeneity within the northwest region (i.e., between Alaskan coastal and Canadian interior forests), this exercise serves chiefly to look for patterns on a continental scale. Where direct comparisons of these results with those of the preceding section yield different results, that difference may reflect the difference in scale and perhaps point to interesting exceptions to generalizations.

Broadleaf forests consistently held more species of big-tree users than did conifer forests, although the ANOVA showed a significant interaction of location and forest type (see part A in Table 11.4). Location had no detectable effect on species diversity of big-tree users. Birds in this guild were less abundant in northwestern forests and marginally less abundant in conifer than in broadleaf forests (especially in midwest and south temperate; refer to part B in Table 11.4).

Table 11.3. Comparison of Guild Structures of Forest Birds in Coastal Southeast Alaska, Adjacent Interior Canada, and Chiloé

Guild					Kruskal-Wallis	<i>p</i>	
Big-Tree Users	CC (16.5)	CD (15.2)	AD (12.3)	AC (8.0)	Ch (2.5)	12.86	0.012
Covered Nesters	CC (17.5)	Ch (14.3)	CD (9.3)	AC (6.3)	AD (4.5)	12.54	0.014
Understory Birds	AD (14.7)	CD (14.0)	CC (12.3)	AC (8.3)	Ch (4.3)	8.01	0.066
Aerial Feeders	CD (18.0)	Ch (14.5)	CC (10.0)	AD (5.5)	AC (5.3)	15.01	0.005
Canopy Seed Predators	CC (17.5)	Ch (14.3)	CD (9.3)	AC (6.5)	AD (4.5)	14.01	0.007
Leaf-Gleaners	CC (16.5)	CD (15.2)	AD (12.3)	AC (8.0)	Ch (2.5)	14.94	0.005

The frequency of species in each guild for each regional forest type is compared by Kruskal-Wallis test, ranked in descending order (average ranks in parentheses), and the position of Chiloé birds in this rank-order is determined by inspection. Codes are as follows: AD = Alaska deciduous; AC = Alaska coniferous; Ch = Chiloé; CD = Canada deciduous; CC = Canada coniferous. By region, Chiloé is closest to Alaska for three guilds, and to Canada for the other three guilds. By forest type, Chiloé is closest to northern conifer forests for five guilds and about equidistant between conifer and deciduous for one guild (aerial).

Diversity of species using covered nests was higher in broadleaf than in conifer forest, but their abundance was similar (parts A and B, Table 11.4). South temperate forests held more species of covered-nesters than the other forests, and this guild was least abundant in northwestern forests. Thus, midwestern forest birds of this guild had relatively fewer species but equal proportions of individuals, as compared to south temperate forests, and equal proportions of species but more individuals, as compared to northwestern forests. This indicates that there was a greater average density per species in the midwestern users of covered nests.

Understory species diversity showed no significant trends with location or forest type (part A, Table 11.4). Abundance was least in northwestern forests, and greater in conifer than in broadleaf forests (part B, Table 11.4). Aerial feeders were least speciose and least abundant in northwestern forests, and more diverse and more abundant in broadleaf than coniferous forests (parts A and B, Table 11.4).

Canopy seed predators were most diverse in south temperate forests, followed by northwestern and midwestern forests (part A, Table 11.4). Abundance patterns followed the same ranking (part B, Table 11.4). However, the value for northwestern forests is underestimated, as discussed earlier. Furthermore, the low values for midwestern forests reflect the extinction of two major canopy seed predators in the last century (*Ectopistes migratorius* and *Conuropsis carolinensis*). Therefore, this trend is spurious but serves to emphasize the point that canopy seed-eaters in the Chilote forests are a noteworthy component of the avifauna.

Leaf-gleaners were least speciose and least abundant in south temperate forests (parts A and B, Table 11.4). They were consistently (but not significantly) more diverse in conifer than broadleaf forests, and significantly more abundant in conifer forests.

Predictions About Comparative Guild Structure

First, the architectural form of most broadleaf trees produces many large branches, whereas that of conifers is commonly a set of relatively small branches off the main trunk. If the difference in branching pattern is associated with a parallel difference in availability of foraging surfaces and cavity nest-sites, then one might predict a greater diversity or abundance of big-tree users in broadleaf forests. The linear array of the six categories of forest (3 locations \times 2 types) showed that, indeed, broadleaf forests tend to host more species of big-tree users than conifer forests (part A, Table 11.4), although the Tukey post-hoc test did not detect significant differences at the predicted point in the array. In contrast, corresponding differences in abundances were not apparent between broadleaf and conifer forests (part B, Table 11.4). Large broadleaf trees may offer more avenues for exploitation, but not necessarily more resources.

Table 11.4. Regional Comparison of Guild Structure of Forest Birds, for South Temperate Rainforest in Chile and Argentina, North Temperate Forests in the Midwest of North America, and Northwestern Forests of Alaska and Canada (Codes: S = south temperate; M = midwest; N = northwestern; B = broadleaf; C = conifer; D = deciduous; for comparison of broadleaf forests with conifer forests, B includes D. Sample sizes are N_D (19), N_C (17), M_D (20), M_C (3), S_B (14), S_C (2). Significant differences in pattern, and interactions were determined by two-way ANOVA (see text); an * indicates significant interaction. Data are shown when the direction of difference is consistent (even when the interaction is significant or the overall ANOVA is not significant); data are not shown when the interaction is significant and the direction of difference is not consistent. Nonsignificant differences in linear ranks, determined by Tukey post-hoc test, are underlined; the numbers accompanying the rankings are the average percents for each regional forest type.)

Part A) By species.

Guild	Interaction	Pattern		Rankings					
		Leaf type	Location	<u>S_B</u>	<u>M_D</u>	<u>N_D</u>	<u>M_C</u>	<u>N_C</u>	<u>S_C</u>
Big-Tree Users	* ^a	B > C (25% > 15%)	M = S = N (25% = 21% = 20%)	27	26	<u>22</u>	<u>18</u>	<u>18</u>	0%
Covered Nesters	no	B > C (32% > 22%)	S > M = N (47% > 28% = 23%)	<u>50</u>	<u>29</u>	<u>29</u>	<u>25</u>	<u>24</u>	22%
Understory Birds	*	—	—	<u>S_C</u>	<u>N_D</u>	<u>N_C</u>	<u>M_C</u>	<u>S_B</u>	<u>M_D</u>
Aerial Feeders	no	B > C (15% > 6%)	S = M > N (16% = 15% > 8%)	55	53	48	39	30	27%
Canopy Seed Predators	no	C > B (5% > 2%)	S > N > M (11% > 3% > 0.4%)	19	15	12	11	7	6%
Leaf-Gleaners	no	C > B (28% > 23%) ^b	M = N > S (33% = 29% > 9%)	12	11	5	<u>2</u>	<u>2</u>	0%
				42	31	28	26	13	9%

^a Interaction significant, but direction of difference consistent.

^b ANOVA not significant, but direction of difference consistent.

Table 11.4.

Part B) By abundance.

Guild	Interaction	Pattern		Rankings				
		Leaf type	Location	<u>M_D</u>	<u>S_B</u>	<u>M_C</u>	<u>N_C</u>	<u>N_D</u>
Big-Tree Users	*	B > C ^a (14% > 7%)	M = S > N 18% = 14% > 7%	21	18	9	8	6 0.7%
Covered Nesters	no	B = C (24% = 19%)	S = M > N 29% = 28% > 16%	30	21	19	19	15%
Understory Birds	*	C > B (51% > 32%) ^a	—	31	52	47	41	27 26%
Aerial Feeders	no	B > C (22% > 5%)	S = M > N (29% = 19% > 10%)	66	22	18	16	4 3%
Canopy Seed Predators	no	C = B (2% = 1%;)	S > N > M (6% > 1% > 0.3%)	32	4	2	1	0.9 0%
Leaf-Gleaners	no	C > B (37% > 26%)	N = M > S (36% = 36% > 5%)	47	40	34	33	11 4%

^a $p = 0.06$.^bDirection of difference consistent.

Second, covered nests might be thought to be adaptations to protect the eggs and young from weather, nest predators, or brood parasites (although covered nests do not necessarily prevent brood parasitism by cowbirds; Cruz & Wiley, 1989). If the advantage of a covered nest lies in a protective microlimate, then one might predict that covered nests would be most frequent in the northwest, where birds often nest early, when snow is still on the ground. Alternatively, one could argue that the rainy climates select for protected nests and predict that covered nests would be more frequent in northwestern and southern forests than in the midwest. On the other hand, if the advantage of a covered nest lies in protection from nest predators and brood parasites, one might predict them to be most common in the midwest, where cowbirds, snakes, and avian and mammalian predators abound, or least common in the south temperate forests, which host relatively few species of nest robbers. None of these patterns is seen in the array of six categories of forest, suggesting that neither factor, taken alone, accounts for the observed pattern.

Third, some of these forests are largely evergreen, and some are largely deciduous. One might argue that evergreenness is associated with long-lived leaves, which are allocated higher levels of chemical and morphological protection than deciduous leaves, and that insect herbivores are consequently less abundant on evergreen leaves. If this were true, and if the diversity and abundance of birds is associated with the size of the potential prey population, then leaf-gleaners should be most abundant or diverse in deciduous stands. This is not the case, however: Although southern forests have low levels of leaf gleaners, North American coniferous forests tend to have proportionately more abundant (though no more diverse) populations of leaf gleaners than deciduous forests (although the Tukey test does not detect significant differences at the predicted points in the array). Thus, the hypothesized relationship between evergreenness and insect abundance seems not to explain much of the observed pattern.

Fourth, conifer and broadleaf forests differ in leaf shape and in branching patterns of branchlets and twigs, and they might offer differing availability and diversity of noncavity nest-sites or foraging surfaces. One might predict that nest-sites and diversity of foraging surfaces would be greater in broadleaf forests than in conifers and that the birds using these forests would be more diverse and abundant there. However, there tend to be relatively more species of open-nesters and proportionately more leaf-gleaners in conifer forests (refer to Table 11.4).

Conclusions

Comparisons of Alaskan and Chilean Coastal Rainforests

Site diversity was somewhat higher in Chilean forest and Alaskan deciduous forest than in Alaskan conifer forests. Point-diversity was highest for

Alaskan deciduous forests, intermediate for Chiloé, and lowest for Alaskan coniferous forests. However, the average number of individual birds censused was markedly higher at each census point in Chilean forests, as suggested by Jaksic and Feinsinger (1991), and lowest for Alaskan coniferous forest. The forests of Chiloé, therefore, support an avifauna within the range of diversity of Alaskan coastal forests but substantially denser.

Covered nests are much better represented in the Chilean forest avifauna than in Alaska or the rest of North America. This difference is not apparently associated with adaptation to microclimate or probable risk of nest destruction by vertebrates (although measurements of rates of nest failure are needed to examine this more closely). Instead, there seems to be a taxonomic association: Psittacids, furnariids, and rhinocryptids typically nest in holes or build dome nests and constitute a notable proportion of the Chilean avifauna. Other covered-nesters occur in both regions: Troglodytids and *Tachycineta* always use covered nests, and one species of each occurs in the censused forests of each region. Picidae always nest in cavities, and occur in both regions, but are not common. However, a taxonomic association begs the questions of the origin of the habit. In addition, one reviewer suggested the possibility that long-distance migrants lack time to build covered nests, but the only Neotropical migrant in the Chiloé forests is *Elaenia albiceps*, which builds an open nest.

The frequency of covered-nesting species on Chiloé contrasts also with that of New Zealand, where the forest trees have many taxonomic similarities, the climate is similarly wet, and the latitude is comparable, but the phylogenetic history of many indigenous bird species is very different from that of Chile. About 20% to 25% of the native species of *Nothofagus* forest sites in New Zealand use covered nests (census data from Kikkawa, 1966; nest information from Anonymous, 1985; Falla, Sibson, & Turbott, 1981). The contrast between the frequency of covered-nesters in New Zealand and Chile seems to reinforce a taxonomic interpretation of the high frequency of covered-nesters in Chilean forest birds. However, a taxonomic correlation in Chile does not provide an explanation that is generalizable to New Zealand, because there is within-family variation in nest type for New Zealand birds (Anonymous, 1985; Falla, Sibson, & Turbott, 1981).

Ecological correlates of small clutches in the northern hemisphere may include high risk of nest predation, low adult survival, or the existence of multiple breeding opportunities during the season (Bennett & Harvey, 1988; Martin, 1993a, 1993b, 1995; Martin & Li, 1992; Saether, 1988). However, such correlations often seem to break down when comparing temperate and tropical regions (Karr, Nichols, Klimkiewicz, & Brawn, 1990), and preliminary evidence from Chile also suggest that at least some of these correlations may not hold there. Similarly, most native passerines in New Zealand produce small clutches (fewer than four eggs),

and correlations of clutch sizes and number of broods per year with nesting habits are not clear (data from Anonymous, 1985; Falla, Sibson, & Turbott 1981; but see Yom-Tov, Christie, & Iglesias, 1994). Regional comparisons offer the opportunity to test the ecological hypotheses about the evolution of clutch size on a larger scale.

Some of the Chilean species may have small clutches for historical or phylogenetic reasons (as opposed to ecological reasons). Some belong to taxa that characteristically produce small clutches everywhere (e.g., pigeons and hummingbirds). Clutch size of others might be constrained if they were geologically recent immigrants to southern forests from the lowland tropics, where small clutches are common. Such an hypothesis leaves unexplained the relatively large clutch sizes of several Chilean species, unless they immigrated from other source faunas or did so earlier. The high level of endemism in the Chilean avifauna (Vuilleumier, 1985) suggests that there has been time for the evolution of significant morphological and behavioral differences in many taxa, and there is no apparent reason why clutch size should be more constrained than morphology and behavior.

The avifaunas of coastal rainforests in Chiloé and southeast Alaska differed somewhat in guild structure. Guild structure of Chilote forest avifaunas was not more similar to Alaskan coastal forest than to Canadian forest avifaunas in the same general region. Long-distance migrants are more often among the common birds in Alaska (and to a slightly lesser degree in Washington and Oregon; Carey, Hardt, Horton, & Biswell, 1991; Gilbert & Allwine, 1991; Manuwal, 1991) than in Chiloé and comprise a much larger proportion of the avifauna. Thus, biogeographical differences and biological interactions (or other factors) appear to override the climatic and topographic similarities in structuring the bird community in these forests.

Guild Structure of North and South Temperate Forests

Broad regional comparisons documented the high richness of covered nesters in south temperate forests. South temperate forests appeared to have relatively few species and birds that forage principally by leaf gleaning, and northwestern forests supported relatively few species and individuals of aerial feeders. Big-tree users were proportionately more speciose and often more abundant in broadleaf forests than in conifer forests, and covered nesters were more diverse in broadleaf forests. Aerial feeders were proportionately more diverse and abundant in broadleaf forests. In contrast, leaf-gleaners were relatively more diverse and abundant in conifer forests, and understory birds were relatively more abundant there.

We did not analyze another interesting guild—that of frugivores that disperse the seeds of fleshy fruits. Fleshy fruits and frugivory are common in both Chiloé and Alaska in late summer (our observations; Armesto,

Smith-Ramírez, Sabag, this volume). However, very few birds in coastal Alaska eat fruits during the breeding season, in contrast to several species in Chiloé. Perhaps the most interesting questions to ask of this guild concern the effect of fruits on the breeding ecology of Chilean birds and the comparisons of foraging ecology in the nonbreeding season in the two regions.

As is common with first efforts to build and understand comparisons, this study raises more questions than it answers. This preliminary study documents some contrasting patterns and identifies some related questions that require more detailed examination both of the patterns themselves and of the processes that form them.

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References

- Alaback, P. 1991. Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients. *Rev Chil Hist Nat*, 64, 399–412.
- Anonymous. 1985. *Complete Book of New Zealand Birds*. Sydney: Readers Digest Services.
- Bennett, P.M., and Harvey, P.H. 1988. How fecundity balances mortality in birds. *Nature*, 333, 216.
- Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecol Monog*, 27, 351–384.
- Carey, A.B., Hardt, M.M., Horton, S.P., and Biswell, B.L. 1991. Spring bird communities in the Oregon Coast Range. *U.S.D.A. Forest Service General Technical Report* 285 (pp. 123–142).
- Cody, M.L. 1970. Chilean bird distribution. *Ecology*, 51, 455–464.
- Cruz, A., and Wiley, J.W. 1989. The decline of an adaptation in the absence of a presumed selection pressure. *Evolution*, 43, 55–62.
- Ehrlich, P.R., Dobkin, D.S., and Wheye, D. 1988. *The Birder's Handbook*. New York: Simon and Schuster.
- Falla, R.A., Sibson, R.B., and Turbott, E.G. 1981. *Collins Guide to the Birds of New Zealand*. Auckland: Collins.
- Flack, J.A.D. 1976. Bird populations for aspen forests of western North America. *Ornithol Monog*, 19, 1–97.
- Gilbert, F.F., and Allwine, R. 1991. Spring bird communities in the Oregon Cascade Range. In L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff (eds.), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests* (pp. 145–158). Portland, OR: U.S.D.A., Forest Service, Pacific Northwest Research Station, Technical Report PNW-GTR-285.
- Harrison, H.H. 1975. *A Field Guide to Bird's Nests*. Boston: Houghton Mifflin.

- Harrison, H.H. 1979. *A Field Guide to Western Bird's Nests*. Boston: Houghton Mifflin.
- Holmes, R.T., Bonney, Jr., R.E., and Pacala, S.W. 1979. Guild structure of the Hubbard Brook community: A multivariate approach. *Ecology*, 60, 512–520.
- Holmes, R.T., and Recher, H.F. 1986. Determinants of guild structure in forest bird communities: An intercontinental comparison. *Condor*, 88, 427–439.
- Jaksic, F.M., and Feinsinger, P. 1991. Bird assemblages in temperate forests of North and South America: A comparison of diversity, dynamics, guild structure, and resource use. *Rev Chil Hist Nat*, 64, 491–510.
- James, F.C., and Rathbun, S. 1981. Rarefaction, relative abundance, and diversity of avian communities. *Auk*, 98, 785–800.
- Johnson, A.W. 1967. The birds of Chile and adjacent regions of Argentina, Bolivia and Peru. Vol. 2. Buenos Aires: Platt Establecimientos Gráficos.
- Karr, J.R., Nichols, J.D., Klimkiewicz, M.K., and Brawn, J.D. 1990. Survival rates of birds of tropical and temperate forests: Will the dogma survive? *Am Nat*, 136, 277–291.
- Kessler, W.B., and Kogut, T.E. 1985. Habitat orientation of forest birds in southeastern Alaska. *NW Sci*, 59, 58–65.
- Kikkawa, J. 1966. Population distribution of land birds in temperate rainforest of southern New Zealand. *Transactions Royal Society New Zealand, Zoology*, 17, 215–277.
- Lack, D. 1968. Ecological adaptations for breeding in birds. London: Methuen.
- Manuwal, D.A. 1991. Spring bird communities in the southern Washington Cascade Range. In L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff (eds.), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests* (pp. 161–174). Portland, OR: U.S.D.A., Forest Service, Pacific Northwest Research Station, Technical Report PNW-GTR-285.
- Martin, T.E. 1988a. On the advantages of being different: Nest predation and the coexistence of bird species. *Proceedings of the National Academy of Sciences (USA)*, 85, 2196–2199.
- Martin, T.E. 1988b. Processes organizing open-nesting bird assemblages: Competition or nest predation? *Evol Ecol*, 2, 37–50.
- Martin, T.E. 1993a. Evolutionary determinants of clutch size in cavity-nesting birds: Nest predation or limited breeding opportunities? *Am Nat*, 142, 937–946.
- Martin, T.E. 1993b. Nest predation among vegetation layers and habitat types: Revising the dogmas. *Am Nat*, 141, 897–913.
- Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monog*, 65, 101–127.
- Martin, T.E., and Li, P. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology*, 73, 579–592.
- Meserve, P.L., and Jaksic, F.M. 1991. Comparisons of terrestrial vertebrate assemblages in temperate rainforests of North and South America. *Rev Chil Hist Nat*, 64, 511–535.
- Morton, M.L. 1974. Adaptive strategies of *Zonotrichia* breeding at high latitude or high altitude. *Proceedings of the International Ornithological Congress*, 16, 322–336.
- Ralph, C.J. 1985. Habitat association patterns of forest and steppe birds on northern Patagonia, Argentina. *Condor*, 87, 471–483.
- Root, R.B. 1967. The niche exploitation pattern of the blue-gray gnatchatcher. *Ecol Monog*, 37, 317–350.
- Sabag, C. 1993. *El rol de las aves en la dispersión de semillas en un bosque templado secundario de Chiloé (42°S)*. Unpublished masters thesis, Facultad de Ciencias, Universidad de Chile.

- Sæther, B.-E. 1988. Pattern of covariation between life-history traits of European birds. *Nature*, 331, 616–617.
- Sokal, R.R., and Rohlf, F.J. 1981. *Biometry* 2nd ed. San Francisco: Freeman.
- Spindler, M.A., and Kessel, B. 1980. Avian populations and habitat use in interior Alaska taiga. *Sysis*, 13, 61–104.
- Theberge, J.B. 1976. Bird populations in the Kluane Mountains, southwest Yukon, with special reference to vegetation and fire. *Can J Zool*, 54, 1346–1356.
- Vuilleumier, F. 1972. Bird species diversity in Patagonia (temperate South America). *Am Nat*, 106, 266–271.
- Vuilleumier, F. 1985. Forest birds of Patagonia: Ecological geography, speciation, endemism, and faunal history. *Ornithol Monog*, 36, 255–305.
- Willson, M.F. 1974. Avian community organization and habitat structure. *Ecology*, 55, 1017–1029.
- Willson, M.F. 1986. Avian frugivory and seed dispersal in eastern North America. *Curr Ornithol*, 3, 223–279.
- Willson, M.F. 1991. Dispersal of seeds by frugivorous animals in temperate forests. *Rev Chil Hist Nat*, 63, 537–554.
- Willson, M.F., and Comet, T.A. Bird communities of northern forests: Patterns of diversity and abundance. Unpublished manuscript.
- Willson, M.F., De Santo, T.L., Sabag, C., and Armesto, J.J. 1994. Avian communities of fragmented south-temperate rainforests in Chile. *Conserv Biol*, 8, 508–520.
- Yom-Tov, Y., Christie, M.I., and Iglesias, G.J. 1994. Clutch size in passerines of southern South America. *Condor*, 96, 170–177.