

Bird assemblages in temperate forests of North and South America: a comparison of diversity, dynamics, guild structure, and resource use

Ensamblajes de aves en bosques templados de Norte y Sudamérica: una comparación de diversidad, dinámica, estructura gremial y uso de recursos

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ABSTRACT

Using available data on entire bird assemblages of temperate forests in North and South America, we compare ecological patterns and dynamics between continents and suggest a comprehensive but low-cost research program to fill some of the many conspicuous gaps in the present state of knowledge. The scanty data available for comparison suggest that ecological trends of avifaunas are reasonably similar between grossly similar forest types on the two continents, but that important dissimilarities also occur due to different phylogenies, geologic histories, compositions of vegetation, and climate. For example, fruits apparently provide a steadier resource base in South America than in North America, whereas masting seed-, nut-, and cone-bearing trees, and "masting" insect larvae seem more prevalent in North than in South America. Accordingly, the South American avifaunas studied to date contain substantial proportions of frugivores or frugivore-insectivores, whereas North American avifaunas appear to contain larger numbers of opportunistic species and/or seed-, nut-, and cone-feeding species. We propose that North American temperate forests are more heterogeneous, seasonal, dynamic, and irruptive than their South American counterparts, from a bird's eye view. The consequence could be that South American avifaunas are less opportunistic than their North American counterparts in response to spatiotemporal heterogeneity in resources or community structure; that is, they migrate less over short and long distances. Nevertheless, data are not available to test this assertion. We propose a careful comparative study of avifaunas in evergreen and nearby deciduous forests on both continents.

Key words: Avifauna, avifaunal dynamics, guild structure, resource use, migration, intercontinental comparison, seasonality, United States, Chile, Argentina.

RESUMEN

Usando información disponible sobre ensambles completos de aves en bosques templados de Norte y Sudamérica, comparamos los patrones y su dinámica ecológica entre continentes y sugerimos un programa comprehensivo pero de bajo costo para llenar algunos de los numerosos vacíos en el estado actual del conocimiento. Los pocos datos disponibles para la comparación sugieren que las tendencias ecológicas de las avifaunas son razonablemente similares entre tipos semejantes de bosque en ambos continentes, pero que importantes disimilitudes también existen debido a diferentes filogenias, historias geológicas, composiciones de vegetación y clima. Por ejemplo, los frutos aparentemente proveen una base de recursos más estables en Sudamérica que en Norteamérica, en tanto que los árboles con enorme producción de semillas, nueces, conos, o insectos irruptivos parecen ser más prevalentes en Norteamérica que en Sudamérica. Concordantemente, las avifaunas sudamericanas hasta ahora estudiadas contienen proporciones sustanciales de frugívoros o frugívoro-insectívoros, en tanto que las avifaunas norteamericanas parecen contener mayores números de especies oportunistas y de consumidores de semillas, nueces y conos. Proponemos que, desde el punto de vista de las aves, los bosques templados de Norteamérica son más heterogéneos, estacionales, dinámicos e irruptivos que sus contrapartes sudamericanas. La consecuencia de esto podría ser que las avifaunas sudamericanas sean menos oportunistas que sus contrapartes norteamericanas en respuesta a heterogeneidad espacio-temporal en recursos o en estructura comunitaria, esto es, que ellas migren menos, tanto a distancias cortas como largas. Sin embargo, no hay suficientes datos para poner a prueba esta afirmación. Proponemos un cuidadoso estudio comparativo de avifaunas en bosques siempreverdes y en vecinos deciduos en ambos continentes.

Palabras claves: Avifauna, dinámica avifaunística, estructura gremial, uso de recursos, migración, comparación intercontinental, estacionalidad, Estados Unidos, Chile, Argentina.

INTRODUCTION

For many years, animal ecologists have shown interest in comparing the structure,

dynamics, and function of faunas of distant localities, drawn from different species pools. Such comparisons require a base of thorough descriptive studies such as those common in European and North American ecology during the first half of this century.

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For example, Alee *et al.* (1949) summarized several descriptive studies of vertebrate faunas, and functional relationships among their component species, at particular sites in North America. More recent ecologists have tended to concentrate on particular subsets of vertebrate faunas (e.g., birds) and, at least during the past two decades, have preferred highly analytical or hypothetico-deductive studies to descriptions. With few exceptions (e.g., Karr & James 1975; Landres & MacMahon 1983; Miles *et al.* 1987), recent studies involve examinations of single data sets (e.g., Holmes *et al.* 1979; Sabo & Whittaker 1979; Landres & MacMahon 1980; Sabo 1980; Sabo & Holmes 1983); their unique results, often based on sophisticated multivariate analyses, cannot easily be compared among communities whose avifaunal compositions differ greatly. A common limitation of these studies is that they address guild structure over limited time frames, often the breeding season only. Another is that they focus only on particular subgroups such as passerine birds or other taxonomically restricted units. Even so, the data base for North America is considerably better than in temperate South America, where only a few studies have approached biogeographical or ecological aspects of avifaunas (e.g., Cody 1970; Schlatter 1979; García 1982; Erazo 1984; Ralph 1985; Vuilleumier 1985; Quezada *et al.* 1986). We know of no study on guild structure or seasonal guild dynamics of temperate South American birds.

With limited information, then, we will attempt an overview of the ecological and taxonomic structure of entire avifaunas in temperate forests of North and South America. For North America, we will concentrate on forests in the western (Wyoming) and far western (Sierra Nevada) United States, but will also consider avifaunas from other areas of temperate North America. For South America, we will discuss avifaunas in forests on both the Chilean and Argentine sides of the southern Andes. The scarcity of comparative data has some benefits: it suggests a number of productive areas for future research, and it allows us to speculate shamelessly with relative impunity. Still,

we caution readers that we are committing pseudoreplication on a grand (continental) scale. Data from a very few, geographically close sites on each continent are most likely an extremely biased sample from all possible forest avifaunas on each continent, and some "intercontinental" differences we emphasize here are undoubtedly artifacts of small samples.

METHODS

We examined two types of studies on temperate avifaunas of the Western Hemisphere: studies detailing the ecological structure of entire avifaunas, and studies concentrating on particular subsets of avifaunas or on particular aspects such as seasonal shifts. We found only two North American studies that considered the ecological structure of entire avifaunas (but see Williams 1936 for a pioneering effort); otherwise excellent studies such as those of Winternitz (1976) lack information on food habits. Salt (1953) analyzed three avifaunas in California's Sierra Nevada, describing residence status, habitat use, and food habits over the annual cycles of 1949, 1950, and 1951. All three avifaunas inhabited evergreen forests: xeric pine forest, dominated by *Pinus geofroyi*, in Boca Springs; mixed coniferous forest, dominated by *Pinus ponderosa*, fir, cedar and some black oaks, in Yosemite Valley; and mixed oak forest, dominated by live oaks and sycamores, in Glen Oaks. In a second study, Salt (1957) analyzed six avifaunas near Jackson Hole, Wyoming, describing population density, diet, and habitat use of birds during the summers of 1952 and 1954. The evergreen forests studied were of lodgepole pine (*Pinus contorta*); lodgepole pine-spruce-fir (*P. contorta*, *Picea engelmannii*, *Abies lasiocarpa*); and spruce-fir (*P. engelmannii*, *A. lasiocarpa*, *Pseudotsuga taxifolia*). Salt (1957) also reported on avifaunas of neighboring deciduous willow-sedge (*Salix* sp.), scrub-meadow (short *Populus tremuloides*, with an understory of *Ceanothus*, *Lonicera*, and *Prunus*), and aspen communities (tall *Populus tremuloides*). While these data are not recent nor are the habitats directly

comparable to forests of southern Chile or Argentina, their completeness in terms of ecological structure and their very lack of sophisticated mathematical analysis make them much more appropriate for comparison than later studies. On the other hand, data sets available for rainforests of the Pacific Northwest of the United States (e.g., Brown 1985) lack sufficient spatial resolution and information on ecological structure.

Numerous studies exist on the ecology of particular subsets of North American avifaunas (e.g., the foliage-gleaning or bark-gleaning guilds). We include these studies where they apply to the general comparisons we attempt here.

For temperate South America, we located seven investigations of entire avifaunas. Of these, two took place in non-forested habitats: Schlatter (1979) worked in a sclerophyllous scrub community near Santiago, Chile, whereas Quezada *et al.* (1986) worked in an estuarine setting near Concepción, Chile. Cody (1970) made two-month censuses during each of two years in Parque Cerro Nielol, but the site was heavily disturbed by humans, being adjacent to the large city of Temuco. García (1982) and Erazo (1984) conducted monthly bird censuses over a year in evergreen forests of southern Chile, but their estimates of presence and abundance of birds are suspect because they used the unweighted technique of acoustical stations, which is biased toward detecting vocal species (Emlen 1971). Vuilleumier (1985) provided detailed information on the residence status of birds in different vegetation formations of Chilean and Argentine Patagonia, although he did not specify particular sites nor did he report on food and habitat use. Based on our own and our colleagues' field experience in Chile, we modified and amplified Vuilleumier's designations. We deleted some species from his list of forest birds (e.g., Cathartidae and Threskiornithidae), added others (e.g., *Anairetes parulus*, *Phytotoma rara*, *Pygochelidon cyanoleuca*, *Zonotrichia capensis*), and included our assessment of diets or foraging substrates. The southern Chilean forests that we considered were: evergreen

rainforest, or Valdivian broad-leaved forest with *Nothofagus dombeyi* (evergreen); mixed-deciduous forest, or Valdivian broad-leaved forest with *N. obliqua* and *N. procera* (both deciduous). montane evergreen forest, above 1,000 m elevation, dominated by *Araucaria araucana* and *N. dombeyi* (both evergreen). Ralph (1985) reported abundance data for spring 1980 in two cedar forests and four beech forests of southern Argentina. Ralph's (1985) evergreen forest types were "sparse" cedar (*Austrocedrus chilensis*); "dense" cedar; *Nothofagus dombeyi* forest without *Chusquea* understory; and *N. dombeyi* forest with *Chusquea* understory. Deciduous forests were *Nothofagus pumilio* forest with or without *Chusquea* understory. Based on our own and our colleagues' field experience in Chile, we added assessments of diets and foraging substrates.

The only studies dealing with residence status and ecology of particular groups of temperate South American land birds are those on predatory guilds (e.g., Jaksic *et al.* 1981, Jaksic & Jiménez 1986, Jaksic 1988), minor components of forest avifaunas. González (1974) provided rudimentary descriptions of insectivorous guilds in unspecified locations.

We chose one North American study (Salt 1953) and found only one South American study (Vuilleumier 1985) reporting the residence status of the entire avifauna. Using these studies, we categorized birds as residents (the entire population remains on site year-round), partial migrants (a fraction of the population leaves the site for some time), and migrants (the entire population leaves for some time). We used Salt's (1953) data without modification, but based on our own and our colleagues' field experience we modified slightly Vuilleumier's (1985) assessments.

Following Salt (1953, 1957), we classified birds ecologically according to their use of food resources and foraging substrates. We categorized bird species by their primary food or primary substrate, but also noted secondary foods or substrates of substantial importance. Diet categories were: (a) Carnivorous, eaters of vertebrates; (b) Insectivorous, eaters

of arthropods; (c) Granivorous, eaters of seeds but including exploiters of nuts or of seeds in cones; (d) Nectarivorous, eaters of nectar and pollen; (e) Frugivorous, eaters of fleshy fruits; and (g) Herbivorous, eaters of leaves or buds. Foraging substrates were: (a) Ground, involving dwellers of the forest floor, both of litter and soil surface; (b) Air, including fliers or soarers far from perches, and salliers from perches; (c) Foliage, comprising foragers in twigs and attached structures, both in the canopy and understory; (d) Timber, involving dwellers of tree trunks and branches. As before, we categorized bird species by their primary substrate.

For North American birds we follow the nomenclature of American Ornithologists' Union (1983); for southern Chilean and Argentine birds we follow Araya (1985).

RESULTS

COMPARISONS OF DIVERSITY AND TAXONOMY

Avifaunas of California (Salt 1953) and southern Chile (Vuilleumier 1985) display gross similarity in species richness and even in taxonomic composition (Tables 1 and 2). In California (Table 1), species richness ranged from 38 or 39 (the coniferous forests) to 55 (mixed). Salt (1953) attributed this range to different productivities among forests, and to the less seasonal character of the mixed oak. In southern Chile, species richness ranged from 28 in montane forest through 33 in rainforest to 37 in mixed-deciduous forest (Table 2). These differences may likewise reflect forest productivity, or the diversity of substrates and food available. Although bird species richness seemed to be lower in southern Chile than in California, this difference may represent contrasting sampling modes; without replications within regions, we cannot state that such a difference exists. Nevertheless, Vuilleumier (1985) also pointed out the relative impoverishment of the Patagonian avifauna.

Migrant species contributed a higher proportion to Californian avifaunas (69-

85%) than to southern Chilean avifaunas (49-55%; Tables 1 and 2). While this may reflect higher seasonality in California forests, it may also reflect incomplete data on migration for South American birds due to the scarcity of year-round studies. Lists provided in Appendix 8 of Brown (1985) suggest a much lower proportion of migrants (ca. 35%) in temperate forests of Washington and Oregon, but it is not clear whether intra-regional migrations were taken into account.

The temperate forests of California and southern Chile shared several widespread families (Tables 1 and 2), including Accipitridae, Falconidae, Columbidae, Strigidae, Trochilidae, Picidae, Tyrannidae, Hirundinidae, Troglodytidae, Turdidae, Icteridae, and Fringillidae. Other families present in California forests (Phasianidae, Scolopacidae, Caprimulgidae, Mimidae), were absent from southern Chilean forests but occurred in nearby non-forest situations. California families not represented anywhere in southern Chile included not only Holarctic but also Neotropical families: Apodidae, Corvidae, Paridae, Sittidae, Certhiidae, Chamaeidae, Sylviidae, Ptilonotidae, Vireonidae, Parulidae, and Thraupidae. Southern Chilean families absent from California forests included Psittacidae, Furnariidae, Rhinocryptidae, and Phytotomidae.

COMPARISONS OF DENSITY AND BIOMASS

In Salt's (1957) Wyoming study (Table 3), which included data from summer only, the three evergreen forests displayed lower bird densities (38-108/40 hectares), than did the three nearby deciduous sites (442-1,044/40 ha). Insectivores made up 55-75% of bird numbers in evergreen forests, 65-93% in deciduous sites; granivores 25-45%, or 6-27% respectively; and nectarivores 0% or 1-10% respectively. Standing crops of evergreen forests (977-4,556 g/40 ha) also were lower than those in deciduous sites (8,898-11,028 g/40 ha).

Judging by data from Ralph's (1985) short-term studies, evergreen forests in southern Argentina (Table 4) also held

TABLE 1

Diet and foraging substrate for birds in three types of evergreen temperate forest in California (from Salt 1953). Xeric pine = forest dominated by *Pinus jeffreyi*; mixed pine = coniferous forest dominated by *Pinus ponderosa*, fir, cedar, and black oaks; mixed oak = forest dominated by live oaks and sycamores. Codes for status, diet and substrate at the bottom of the table; secondary diet or substrate in parentheses. + = present; - = absent.

Dieta y sustrato de alimentación de aves en tres tipos de bosque templado siempreverde en California (basado en Salt 1953). Xeric pine = bosque dominado por *Pinus jeffreyi*; mixed pine = bosque dominado por *Pinus ponderosa*, abetos, cedros y robles negros; mixed oak = bosque dominado por robles vivos y sicomoros. Códigos para status, dieta y sustrato aparecen a pie de tabla; dieta o sustrato secundario están entre paréntesis. + = presente; - = ausente.

Species	Status	Diet	Substrate	Xeric Pine	Mixed Pine	Mixed Oak
ACCIPITRIDAE						
<i>Accipiter striatus</i>	R	C	G	+	-	-
<i>Accipiter cooperii</i>	M	C	G	-	-	+
<i>Buteo jamaicensis</i>	P	C	G	+	-	+
FALCONIDAE						
<i>Falco sparverius</i>	P	I	G	+	+	-
PHASIANIDAE						
<i>Callipepla californica</i>	R	G	G	-	-	+
SCOLOPACIDAE						
<i>Actitis macularia</i>	M	I	G	-	+	-
COLUMBIDAE						
<i>Columba fasciata</i>	P	G	F(G)	-	+	+
<i>Zenaidura macroura</i>	P	G	G	+	-	+
STRIGIDAE						
<i>Otus asio</i>	R	I	G	-	-	+
CAPRIMULGIDAE						
<i>Chordeiles minor</i>	M	I	A	+	-	-
<i>Phalaenoptilus nuttallii</i>	M	I	A	+	-	-
APODIDAE						
<i>Aeronautes saxatalis</i>	M	I	A	-	+	-
TROCHILIDAE						
<i>Archilochus alexandri</i>	M	N	F	-	-	+
<i>Calypte anna</i>	R	N	F	-	-	+
<i>Selasphorus rufus</i>	M	N	F	+	-	-
<i>Stellula calliope</i>	M	N	F	-	+	-
PICIDAE						
<i>Colaptes cafer</i>	P	I	G(T)	+	+	+
<i>Melanerpes formicivorus</i>	R	G(I)	F(T)	-	+	+
<i>Dendrocopos villosus</i>	R	I	T	+	+	-
<i>Dendrocopos pubescens</i>	R	I	T	-	+	-
<i>Dendrocopos nuttallii</i>	R	I	T	-	-	+
<i>Dendrocopos albolarvatus</i>	M	I	T	+	+	-
TYRANNIDAE						
<i>Myiarchus cinerascens</i>	M	I	A	-	-	+
<i>Empidonax traillii</i>	M	I	A	-	+	-
<i>Empidonax wrightii</i>	M	I	A	+	-	-
<i>Empidonax difficilis</i>	M	I	A	-	-	+
<i>Empidonax griseus</i> **	M	I	A	+	-	-
<i>Contopus sordidulus</i>	M	I	A	+	+	+
HIRUNDINIDAE						
<i>Tachycineta thalassina</i>	M	I	A	+	+	-
<i>Petrochelidon pyrrhonota</i>	M	I	A	-	-	+
CORVIDAE						
<i>Cyanocitta stelleri</i>	P	G	F	+	+	+
<i>Aphelocoma coerulescens</i>	R	G	F	-	-	+
<i>Nucifraga columbiana</i>	M	G	F	+	-	-
PARIDAE						
<i>Parus gambeli</i>	R	I	T	+	+	-
<i>Parus inornatus</i>	R	G(I)	F(T)	-	-	+
<i>Psaltiriparus minimus</i>	R	I	F	-	-	+
SITTIDAE						
<i>Sitta carolinensis</i>	M	I	T	+	-	-
<i>Sitta canadensis</i>	P	I	T	+	+	-
<i>Sitta pygmaea</i>	M	I	T	+	-	-
CERTHIIDAE						
<i>Certhia familiaris</i>	R	I	T	+	+	-

Species	Status	Diet	Substrate	Xeric Pine	Mixed Pine	Mixed Oak
CHAMAEIDAE						
<i>Chamaea fasciata</i>	R	I	F	—	—	+
TROGLODYTIDAE						
<i>Troglodytes aedon</i>	M	I	F	—	—	+
<i>Thryomanes bewickii</i>	R	I	F	—	—	+
<i>Catherpes mexicanus</i>	R	I	G	—	+	—
MIMIDAE						
<i>Toxostoma redivivum</i>	R	I	G	—	—	+
TURDIDAE						
<i>Turdus migratorius</i>	P	I	F(G)	+	+	—
<i>Hylocichla guttata</i>	M	I	G	—	—	+
<i>Hylocichla ustulata</i>	M	I	G	—	+	+
<i>Sialia mexicana</i>	M	I(F)	F(G)	—	+	+
<i>Sialia currucoides</i>	M	I	G	+	—	—
<i>Hyadestes townsendi</i>	M	I	F	+	—	—
SYLVIIDAE						
<i>Poliophtila caerulea</i>	R	I	F	—	—	+
<i>Regulus satrapa</i>	R	I	F	—	+	—
<i>Regulus calendula</i>	M	I	F	+	+	+
PTILOGONATIDAE						
<i>Phainopepla nitens</i>	M	I(F)	F	—	—	+
VIREONIDAE						
<i>Vireo huttoni</i>	R	I	F	—	—	+
<i>Vireo bellii</i>	M	I	F	—	—	+
<i>Vireo solitarius</i>	M	I	F	+	+	+
<i>Vireo gilvus</i>	M	I	F	+	+	+
PARULIDAE						
<i>Vermivora celata</i>	M	I	F	+	—	+
<i>Dendroica petechia</i>	M	I	F	—	+	+
<i>Dendroica auduboni</i>	P	I	F	+	+	+
<i>Dendroica nigrescens</i>	M	I	F	—	+	+
<i>Dendroica townsendi</i>	M	I	F	—	—	+
<i>Dendroica occidentalis</i>	M	I	F	+	—	+
<i>Oporornis tolmiei</i>	M	I	F	—	+	—
<i>Wilsonia pusilla</i>	M	I	F	+	—	+
ICTERIDAE						
<i>Agelaius phoeniceus</i>	M	G	G	—	+	—
<i>Icterus cucullatus</i>	M	I	F	—	—	+
<i>Euphagus cyanocephalus</i>	M	I(G)	G	—	+	—
THRAUPIDAE						
<i>Piranga ludoviciana</i>	M	I	F	+	+	+
FRINGILLIDAE						
<i>Pheucticus melanocephalus</i>	M	I(F)	F	—	+	+
<i>Passerina amoena</i>	M	G	G	—	—	+
<i>Hesperiphona vespertina</i>	M	G(I)	F	—	+	—
<i>Carpodacus purpureus</i>	R	G	F(G)	—	+	—
<i>Carpodacus cassinii</i>	R	G	G(F)	+	—	—
<i>Carpodacus mexicanus</i>	R	G	G	—	—	+
<i>Spinus psaltria</i>	R	G	G	—	—	+
<i>Spinus lawrencei</i>	M	G	G	—	—	+
<i>Chlorura chlorura</i>	M	G	G	+	—	—
<i>Pipilo erythrophthalmus</i>	P	G	G	+	+	+
<i>Pipilo fuscus</i>	R	G	G	—	—	+
<i>Junco oreganus</i>	P	G	G	+	+	+
<i>Spizella passerina</i>	M	I(F)	G	+	+	+
<i>Zonotrichia leucophrys</i>	M	G	G	+	—	+
<i>Zonotrichia atricapilla</i>	M	G	G	—	—	+
<i>Passerella iliaca</i>	M	G	G	—	—	+
<i>Melospiza melodia</i>	R	G	G	+	—	+
TOTAL NUMBER OF SPECIES				39	38	55
% MIGRATORY SPECIES				85	79	69

Status: R = Resident; M = Migrant; P = Partial migrant.

Diet: C = Carnivorous; I = Insectivorous; G = Granivorous; N = Nectarivorous; F = Frugivorous.

Substrate: G = Ground; A = Air; F = Foliage; T = Timber.

* Synonymy could not be established.

TABLE 2

Diet and foraging substrate for birds in three types of evergreen temperate forest in southern Chile (modified from Vuilleumier 1985). Rainforest = Valdivian broad-leaved forest with *Nothofagus dombeyi* (evergreen); mixed-deciduous = Valdivian broad-leaved forest with *N. obliqua* and *N. procera* (both deciduous); montane = forest above 1,000 m elevation, dominated by *Araucaria araucana* and *N. dombeyi* (both evergreen). Codes for status, diet and substrate at the bottom of the table; secondary diet or substrate in parentheses. + = present; - = absent.

Dieta y sustrato de alimentación de aves en tres tipos de bosque templado siempreverde en el sur de Chile (basado en Vuilleumier 1985). Rainforest = bosque valdiviano latifolio con *Nothofagus dombeyi* (siempreverde); mixed-deciduous forest = bosque valdiviano latifolio con *N. obliqua* y *N. procera* (ambos deciduos); montane = bosque sobre 1.000 m elevación, dominado por *Araucaria araucana* y *N. dombeyi* (ambos siempreverdes). Códigos para status, dieta y sustrato aparecen a pie de tabla; dieta o sustrato secundario están entre paréntesis. + = presente; - = ausente.

Species	Status	Diet	Substrate	Rainforest	Mixed-Deciduous	Montane
ACCIPITRIDAE						
<i>Accipiter bicolor</i>	M	C	G(A)	+	+	+
<i>Buteo polyosoma</i>	P	C	G	-	+	+
<i>Buteo ventralis</i>	R	C	G	+	+	-
<i>Geranoaetus melanoileucus</i>	R	C	G	-	+	+
FALCONIDAE						
<i>Phalcoboenus albogularis</i>	R	C	G	-	+	+
COLUMBIDAE						
<i>Columba araucana</i>	R	F(G)	G	+	+	-
PSITTACIDAE						
<i>Enicognathus ferrugineus</i>	P	F(G)	F(G)	+	+	+
<i>Enicognathus leptorhynchus</i>	R	F(G)	F(G)	+	+	-
STRIGIDAE						
<i>Bubo virginianus</i>	R	C	G	-	+	+
<i>Glaucidium nanum</i>	P	C	G(F)	+	+	+
<i>Strix rufipes</i>	R	C	G	+	+	-
TROCHILIDAE						
<i>Sephanoides galeritus</i>	P	N(I)	F(A)	+	+	+
PICIDAE						
<i>Picoides lignarius</i>	P	I	T	+	+	+
<i>Colaptes pitius</i>	R	I	T(G)	+	+	+
<i>Campephilus magellanicus</i>	R	I	T	+	+	+
FURNARIIDAE						
<i>Sylviothorhynchus desmursii</i>	R	I	F	+	+	-
<i>Aphrastura spinicauda</i>	P	I(F)	T(F)	+	+	+
<i>Pygarrhichas albogularis</i>	R	I	T	+	+	+
RHINOCRYPTIDAE						
<i>Pteroptochos castaneus</i>	R	I(G)	G	+	+	+
<i>Pteroptochos tarnii</i>	R	I(G)	G	+	+	+
<i>Scelorchilus rubecula</i>	R	I(G)	G	+	+	+
<i>Eugralla paradoxa</i>	R	I(G)	G	+	+	-
<i>Scytalopus magellanicus</i>	R	I(G)	G(F)	+	+	+
TYRANNIDAE						
<i>Pyrope pyrope</i>	M	I(F)	A	+	+	+
<i>Elaenia albiceps</i>	M	I(F)	F(A)	+	+	+
<i>Anairetes parulus</i>	P	I(F)	F	+	+	+
<i>Colorhamphus parvirostris</i>	M	I	F(A)	+	+	+
PHYTOTOMIDAE						
<i>Phytotoma rara</i>	P	H	F	+	+	+
HIRUNDINIDAE						
<i>Tachycineta leucopyga</i>	M	I	A	+	+	+
<i>Pygochelidon cyanoleuca</i>	M	I	A	+	+	+
TROGLODYTIDAE						
<i>Troglodytes aedon</i>	M	I	F	+	+	+
TURDIDAE						
<i>Turdus falcklandii</i>	R	F(I)	G(F)	+	+	+
ICTERIDAE						
<i>Curaeus curaues</i>	R	I(H)	G	+	+	+
FRINGILLIDAE						
<i>Phrygilus patagonicus</i>	M	G(H)	G	+	+	+
<i>Phrygilus gayi</i>	M	G(H)	G	+	+	+
<i>Carduelis barbatus</i>	P	G(H)	G	+	+	+
<i>Zonotrichia capensis</i>	M	G(H)	G	+	+	+
TOTAL NUMBER OF SPECIES				33	37	31
% MIGRATORY SPECIES				55	51	61

Status: R = Resident; M = Migrant; P = Partial migrant.

Diet: C = Carnivorous; I = Insectivorous; G = Granivorous; N = Nectarivorous; F = Frugivorous; H = Herbivorous.

Substrate: G = Ground; A = Air; F = Foliage; T = Timber.

TABLE 3

Diet and foraging substrate, as well as density (number/100 acres = number/40 hectares) and standing crop (g/40 hectares), for birds in six habitat types of Wyoming (from Salt 1957). Evergreen forest types are: Lod-Pine = lodgepole pine; Pi-Sp-Fi = lodgepole-spruce-fir; Spru-Fir = spruce-fir.

Deciduous community types are: Wil-Sedg = willow-sedge swamp; Scr-Mead = scrub-meadow; Aspen = aspen flatland. D. = modal diet, S. = modal substrate. See codes at the bottom of the table

Dieta y sustrato de alimentación, así como densidad (número/100 acres = número/40 hectáreas) y cosecha en pie (g/40 há), de aves en seis tipos de hábitat de Wyoming (basado en Salt 1957). Bosques templados siempreverdes son:

Lod-Pine = pino barraca; Pi-Sp-Fi = asociación de pinos, piceas y abetos; Spru-Fir = asociación de piceas y abetos.

Comunidades deciduas son: Wil-Sedg = comunidad de sauce y pastos; Scr-Mead = comunidad de arbustos y pradera;

Aspen = comunidad de álamos. D = dieta modal; S = sustrato modal. Véanse códigos a pie de tabla

Species	D.	S.	Lod-Pine No.	g	Pi-Sp-Fi No.	g	Spru-Fir No.	g	Wil-Sedg No.	g	Scr-Mead No.	g	Aspen No.	g
SCOLOPACIDAE														
<i>C. gallinago</i>	I	G	—	—	—	—	—	—	12	1,170	—	—	—	—
TROCHILIDAE														
<i>S. platycercus</i>	N	F	—	—	—	—	—	—	—	—	45	180	—	—
<i>S. caliope</i>	N	F	—	—	—	—	—	—	43	108	—	—	13	34
PICIDAE														
<i>C. cafer</i>	I	G	—	—	—	—	—	—	—	—	—	—	53	7,743
<i>S. varius</i>	I	T	—	—	—	—	—	—	7	303	—	—	50	2,265
<i>D. villosus</i>	I	T	—	—	2	119	3	195	—	—	—	—	—	—
<i>P. arcticus</i>	I	T	—	—	—	—	1	51	—	—	—	—	—	—
TYRANNIDAE														
<i>E. traillii</i>	I	A	—	—	—	—	—	—	52	657	10	127	43	551
<i>C. sordidulus</i>	I	A	—	—	—	—	—	—	3	46	—	—	17	237
<i>N. borealis</i>	I	A	—	—	—	—	1	44	—	—	—	—	—	—
HIRUNDINIDAE														
<i>I. bicolor</i>	I	A	—	—	—	—	—	—	—	—	—	—	468	9,352
CORVIDAE														
<i>P. canadensis</i>	G	F	3	224	—	—	—	—	—	—	—	—	—	—
<i>N. columbiana</i>	G	F	2	221	12	1,521	20	2,639	—	—	—	—	—	—
PARIDAE														
<i>P. gambeli</i>	I	T	7	80	8	94	7	84	—	—	—	—	—	—
SITTIDAE														
<i>S. canadensis</i>	I	T	—	—	3	33	4	35	—	—	—	—	—	—
CERTHIIDAE														
<i>C. familiaris</i>	I	T	—	—	1	9	4	34	—	—	—	—	—	—
TROGLODYTIDAE														
<i>T. aedon</i>	I	F	—	—	—	—	—	—	—	—	—	—	23	246
TURDIDAE														
<i>T. migratorius</i>	I	G	—	—	2	194	4	308	22	1,910	15	1,320	30	2,649
<i>H. guttata</i>	I	G	—	—	—	—	4	90	—	—	—	—	—	—
<i>H. ustulata</i>	I	G	—	—	—	—	3	84	7	201	50	1,500	—	—
<i>S. currucoides</i>	I	G	—	—	—	—	—	—	—	—	—	—	30	801
SYLVIIDAE														
<i>R. satrapa</i>	I	F	—	—	1	3	12	61	—	—	—	—	—	—
<i>R. calendula</i>	I	F	—	—	9	57	8	51	—	—	—	—	—	—
VIREONIDAE														
<i>V. gilvus</i>	I	F	—	—	—	—	—	—	—	—	60	678	13	151
PARULIDAE														
<i>D. petechia</i>	I	F	—	—	—	—	—	—	102	986	—	—	127	1,231
<i>D. auduboni</i>	I	F	7	88	18	240	8	101	—	—	—	—	—	—
<i>O. tolmiei</i>	I	F	—	—	—	—	—	—	10	114	85	969	30	343
<i>G. trichas</i>	I	F	—	—	—	—	—	—	52	517	5	50	—	—
THRAUPIDAE														
<i>P. ludoviciana</i>	I	F	5	145	18	531	13	386	—	—	—	—	—	—
FRINGILLIDAE														
<i>P. melanoceph.</i>	I	F	—	—	—	—	—	—	2	78	45	2,070	20	920
<i>P. amoena</i>	G	G	—	—	—	—	—	—	—	—	50	750	—	—
<i>C. casinii</i>	G	G	—	—	2	61	1	39	—	—	—	—	—	—
<i>P. enucleator</i>	G	F	—	—	1	31	4	179	—	—	—	—	—	—
<i>S. pinus</i>	G	F	2	21	—	—	1	17	—	—	—	—	—	—
<i>S. tristis</i>	G	G	—	—	—	—	—	—	—	—	—	—	7	80
<i>J. oreganus</i>	G	G	10	177	9	166	7	124	—	—	35	620	7	119
<i>S. passerina</i>	I	G	2	21	11	135	3	34	—	—	30	366	13	163
<i>Z. leucophrys</i>	G	G	—	—	—	—	—	—	15	428	35	998	40	1,143
<i>P. iliaca</i>	I	G	—	—	—	—	—	—	20	612	—	—	—	—
<i>M. lincolnii</i>	I	G	—	—	—	—	—	—	65	1,138	50	875	53	935
<i>M. melodia</i>	G	G	—	—	—	—	—	—	30	630	25	525	7	141
TOTAL BY No./GRAMS			38	977	97	3,194	108	4,556	442	8,898	540	11,028	1,044	29,104
Insectivorous (%)			55	34	75	44	69	34	80	87	65	72	93	95
Granivorous (%)			45	66	25	56	31	66	10	12	27	26	6	5
Nectarivorous (%)			0	0	0	0	0	0	10	1	8	2	1	< 1

Diet: I = Insectivorous; G = Granivorous; N = Nectarivorous.

Substrate: G = Ground; A = Air; F = Foliage; T = Timber.

TABLE 4

Diet and foraging substrate, as well as density (number/40 hectares) and standing crop (g/40 hectares), for birds in six types of temperate forest in southern Argentina (from Ralph 1985). Evergreen forest types are: Sp-Cedar = sparse cedar (*Austrocedrus chilensis*); De-Cedar = dense cedar; Dom-Chus = *Nothofagus dombeyi* without *Chusquea* understory; Dom+Chus = *N. dombeyi* with *Chusquea* understory. Deciduous forest types are: Pum-Chus = *Nothofagus pumilio* without *Chusquea* understory; Pum+Chus = *N. pumilio* with *Chusquea* understory. D. = modal diet, S. = modal substrate, tr = trace, less than 0.5%. See codes at the bottom of the table.

Dieta y sustrato de alimentación, así como densidad (número/40 hectáreas) y cosecha en pie (g/40 há), de aves en seis tipos de hábitat del sur de Argentina (basado en Ralph 1985). Bosques templados siempreverdes son: Sp-Cedar = cedro ralo (*Austrocedrus chilensis*); De-Cedar = cedro denso; Dom-Chus = *Nothofagus dombeyi* sin sotobosque de *Chusquea*; dom+Chus = *N. dombeyi* con sotobosque de *Chusquea*. Bosques templados deciduos son: Pum-Chus = *Nothofagus pumilio* sin sotobosque de *Chusquea*; Pum+Chus = *N. pumilio* con sotobosque de *Chusquea*. D = dieta modal; S = sustrato modal. Véanse códigos a pie de tabla

Species	D.	S.	Sp-Cedar No.	g	De-Cedar No.	g	Pum-Chus No.	g	Pum+Chus No.	g	Dom-Chus No.	g	Dom+Chus No.	g
ANATIDAE														
<i>C. poliocephala</i>	H	G	—	—	—	—	—	—	—	—	—	—	1	2,500
ACCIPITRIDAE														
<i>B. polyosoma</i>	C	G	1	975	1	975	4	3,900	—	—	—	—	—	—
PHASIANIDAE														
<i>C. californica</i>	G	G	4	800	20	4,000	—	—	—	—	—	—	—	—
PSITTACIDAE														
<i>E. ferrugineus</i>	F	F	—	—	—	—	—	—	4	800	—	—	1	200
TROCHILIDAE														
<i>S. galeritus</i>	N	F	—	—	16	80	32	160	140	700	—	—	164	820
PICIDAE														
<i>P. lignarius</i>	I	T	—	—	—	—	4	156	1	39	—	—	—	—
<i>C. pitius</i>	I	T	—	—	—	—	1	150	—	—	—	—	1	150
<i>C. magellanicus</i>	I	T	—	—	—	—	4	800	—	—	—	—	1	200
FURNARIIDAE														
<i>A. spinicauda</i>	I	T	—	—	12	120	120	1,200	116	1,160	60	600	140	1,400
<i>T. pyrrholeuca</i>	I	G	68	1,768	44	1,144	—	—	—	—	—	—	—	—
<i>T. anthoides</i>	I	G	28	672	36	864	—	—	—	—	—	—	—	—
<i>P. albogularis</i>	I	T	—	—	—	—	12	156	16	208	4	52	12	156
RHINOCRYPTIDAE														
<i>P. tarnii</i>	I	G	—	—	—	—	8	960	16	1,920	4	480	24	2,880
<i>S. rubecula</i>	I	G	1	45	—	—	4	180	8	360	—	—	8	360
<i>S. magellanicus</i>	I	G	1	15	—	—	1	15	1	15	—	—	1	15
TYRANNIDAE														
<i>P. pyrope</i>	I	A	—	—	1	22	4	88	28	616	—	—	—	—
<i>E. albiceps</i>	I	F	124	2,108	52	884	336	5,712	288	4,896	164	2,788	280	4,760
<i>A. parulus</i>	I	F	108	1,188	52	572	—	—	—	—	—	—	—	—
PHYTOMIDAE														
<i>P. rara</i>	H	F	—	—	1	60	—	—	—	—	—	—	—	—
HIRUNDINIDAE														
<i>P. cyanoleuca</i>	I	A	—	—	—	—	8	112	8	112	—	—	—	—
TROGLODYTIDAE														
<i>T. aedon</i>	I	F	108	1,080	144	1,440	196	1,960	200	2,000	80	800	104	1,040
TURDIDAE														
<i>T. falcklandii</i>	F	G	4	376	16	1,504	12	1,128	—	—	8	752	1	94
ICTERIDAE														
<i>C. curaeus</i>	I	G	4	360	—	—	—	—	8	720	—	—	—	—
FRINGILLIDAE														
<i>P. patagonicus</i>	G	G	8	160	20	400	60	1,200	48	960	28	560	40	800
<i>P. unicolor</i>	G	G	—	—	4	112	—	—	—	—	8	224	—	—
<i>C. barbatus</i>	G	G	40	1,400	36	1,260	44	1,540	4	140	4	140	1	35
TOTAL BY No./GRAMS			499	10,947	455	13,437	850	19,417	886	14,646	360	6,396	779	15,410
Insectivorous (%)			89	66	75	38	82	59	78	83	87	74	74	72
Granivorous (%)			10	22	17	43	13	14	6	7	11	14	5	5
Nectarivorous (%)			0	0	4	1	4	1	16	5	0	0	21	5
Carnivorous (%)			tr	9	tr	7	tr	20	0	0	0	0	0	0
Frugivorous (%)			1	3	4	11	1	6	tr	5	2	12	tr	2
Herbivorous (%)			0	0	tr	tr	0	0	0	0	0	0	tr	16

Diet: C = Carnivorous; I = Insectivorous; G = Granivorous; N = Nectarivorous; F = Frugivorous; H = Herbivorous.
Substrate: G = Ground; A = Air; F = Foliage; T = Timber.

fewer birds (360-779/40 ha) and lower avian biomass (6,396-15,410 g/40 ha) than nearby deciduous forests (850-886 birds/40 ha and 14,646-19,417 g/40), but differences were less than among the Wyoming avifaunas (Table 3). Insectivores made up 74-89% of the avifauna by number in evergreen forests and 78-82% in deciduous forests; granivores 5-17% and 6-13% respectively. Nectarivores contributed few individuals (0-4%), except at the site with a bamboo understory, where they contributed 16%. Together, carnivores, frugivores, and herbivores made up at most 20% of bird biomass in evergreen forests, and up to 26% in deciduous forests. Nectarivores are apparently much more abundant in the rainforests of Chiloé Island (P. Feinsinger, pers. obs.), making up over 30% of the avifauna by number of individuals captured in mist nests (J.J. Armesto, pers., comm.).

To summarize, the Wyoming sites studied by Salt (1957) held on the average 378 birds/40 ha, whereas the Argentine forests studied by Ralph (1985) held 638 birds/40 ha. This 69% increase north-south, if not a sampling artifact, might reflect productivity differences between the forests. On the average, insectivores contributed 73% of bird numbers in Wyoming, granivores 24%, and nectarivores 3%. Comparable figures for southern Argentina are 81%, 10%, and 8%, respectively (carnivores, frugivores, and herbivores together contributed the remaining 1%). The differences might reflect a relatively greater productivity of insects and nectar than of seeds in southern Argentina, as compared to Wyoming. Biomass figures agree with the north-south trend: on average, the Wyoming sites supported 9,626 g/40 ha whereas the Argentine sites supported 13,375 g/40 ha. This is a comparatively 39% higher standing crop. On the average, insectivores contributed 61%, granivores 39%, and nectarivores < 1% to avian biomass in Wyoming; comparable figures for southern Argentina were 65%, 18%, and 2%, with the remaining 15% in carnivores, frugivores, and herbivores. The major differences between sites sampled in these studies, then, are the relatively low stand-

ing crop of granivores in southern Argentina and the relatively high biomass of carnivores, frugivores, and herbivores combined. That granivory reaches overall lower levels in South America than in North America has also been reported by Mares & Rosenzweig (1978), Morton (1985), and Brown & Ojeda (1987).

COMPARISONS OF DIET AND SUBSTRATE

The modal diet of birds in the forests studied in both North and South America was insectivorous, with granivorous diets the next most common (Table 5). These two diet categories, however, included a larger proportion of North American than South American avifaunas. The latter included larger numbers of carnivores, strict frugivores, and strict herbivores (these two latter categories were absent from the North American sites studied). Nectarivores provided similarly small but constant contributions to avifaunas on both continents (although unpublished data from Chiloé Island suggest that hummingbirds may be more abundant at least in that particular area; J.J. Armesto, pers. comm.). Again, we emphasize that apparent intercontinental differences may be artifacts of the sites studied, or even the particular sampling techniques used. For example, some North American forests have reasonable carnivore densities as well as strict frugivores (waxwings: *Bombycilla* spp., Bombycillidae).

The modal substrate of birds in the forests studied in North America was foliage, followed by ground, whereas in South America these positions were reversed (Table 6). The presence of Rhinocryptidae, all ground-dwellers, may have contributed to the observed reversal. Air and timber were similarly well represented among substrates of avifaunas on both continents.

COMPARISONS OF AVIFAUNAL AND GUILD STRUCTURE

Several studies of North American avifaunas deal with functional organization in terms of feeding, or guild structure

TABLE 5

Percent frequency by number of bird species with different diets in temperate forest types of California, Wyoming, southern Chile, and southern Argentina.

EG = Evergreen forest, DE = Deciduous forest or scrub.

Frecuencia numérica porcentual de especies de aves con distintas dietas en bosques templados de California, Wyoming, sur de Chile y sur de Argentina.

EG = bosque siempreverde, DE = bosque o matorral deciduo

Forest type	Carnivorous	Insectivorous	Frugivorous	Granivorous	Nectarivorous	Herbivorous	No. spp.
CALIFORNIA (mean):	(3)	(68)	(0)	(26)	(3)	(0)	(44)
Xeric pine EG	5	69	0	23	3	0	39
Mixed conifer EG	0	76	0	21	3	0	38
Mixed oak EG	4	60	0	32	4	0	55
WYOMING (mean):	(0)	(69)	(0)	(28)	(3)	(0)	(15)
Lodgepole pine EG	0	50	0	50	0	0	8
Pine-spruce-fir EG	0	71	0	29	0	0	14
Spruce-fir EG	0	74	0	26	0	0	19
Willow-sedge DE	0	80	0	13	7	0	15
Scrub-meadow DE	0	64	0	29	7	0	14
Aspen flatland DE	0	74	0	21	5	0	19
CHILE (mean):	(17)	(55)	(10)	(12)	(3)	(3)	(34)
Rainforest EG	12	58	12	12	3	3	33
Mixed-deciduous EG	21	51	11	11	3	3	37
Montane forest EG	19	56	6	13	3	3	31
ARGENTINA (mean):	(4)	(61)	(9)	(20)	(4)	(2)	(14)
Sparse cedar EG	8	62	8	22	0	0	13
Dense cedar EG	7	46	7	26	7	7	15
<i>N. dombeyi</i> - <i>Chusquea</i> EG	0	56	11	33	0	0	9
<i>N. dombeyi</i> + <i>Chusquea</i> EG	0	60	13	13	7	7	15
<i>N. pumilio</i> - <i>Chusquea</i> DE	6	70	6	12	6	0	17
<i>N. pumilio</i> + <i>Chusquea</i> DE	0	73	7	13	7	0	15

(e.g., Salt 1953, 1957; Wilson 1974; Stiles 1978, 1980; DesGranges 1980; Landres & MacMahon 1980; Beedy 1981). With few exceptions (Salt 1953, 1957), however, these studies tend to ignore large birds such as raptors, game birds, and sometimes even corvids. None examines changes in an entire avifauna's guild structure over an entire annual cycle, particularly in forests of different seasonalities. The closest to an ideal study would be a combination of Wilson (1974), Wagner (1981), and Holmes *et al.* (1986). On the other hand, of the many studies that focus on guilds *per se*, with exceptions noted in the next sections most consider only one or a few guilds over one season of the year (e.g., Eckhardt 1979; Morrison 1981; Noon 1981; Rusterholz 1981). Some compare particular guilds among sites (e.g., Karr 1971; DesGranges 1980; Stiles 1980; Beedy 1981; Landres & MacMahon 1983). A few calculate the consumer biomass per guild (Salt 1957; Karr 1968, 1971;

Kricher 1973; Holmes & Sturges 1975; Beedy 1981; Smith & MacMahon 1981; Landres and MacMahon 1983). Others detail avian responses to vegetation succession (e.g., Karr 1968; Willson 1974; Smith & MacMahon 1981), although only Willson's (1974) study deals specifically with successional changes in guild structure.

With these limitations in mind, we propose that by far the most commonly employed foraging mode within North American forest avifaunas, in terms of numbers of species involved, is foliage-gleaning for arthropod prey. This foraging mode characterizes a diverse group of species that exhibit marked population fluctuations in response to cycles of abundance of their food resources. Most tend to be migrants. In contrast, timber dwellers such as bark-drillers and bark-probers tend to be much less diverse, to exhibit populations lower in density, and to be non-migratory.

TABLE 6

Percent frequency by number of bird species with different foraging substrates in temperate forest types of California, Wyoming, southern Chile, and southern Argentina.

EG = Evergreen forest, DE = Deciduous forest or scrub

Frecuencia numérica porcentual de especies de aves con distintos sustratos de alimentación en bosques templados de California, Wyoming, sur de Chile y sur de Argentina.

EG = bosque siempreverde, DE = bosque o matorral deciduo

Forest type	Ground	Air	Foliage	Timber	No. spp.
CALIFORNIA (mean):	(33)	(11)	(44)	(12)	(44)
Xeric pine EG	36	15	31	18	39
Mixed conifer EG	26	11	47	16	38
Mixed oak EG	38	7	53	2	55
WYOMING (mean):	(40)	(6)	(41)	(13)	(15)
Lodgepole pine EG	25	0	63	12	8
Pine-spruce-fir EG	29	0	42	29	14
Spruce-fir EG	32	5	37	26	19
Willow-sedge DE	47	13	33	7	15
Scrub-meadow DE	57	7	36	0	14
Aspen flatland DE	47	16	32	5	19
CHILE (mean):	(51)	(9)	(25)	(15)	(34)
Rainforest EG	49	9	27	15	33
Mixed-deciduous EG	54	8	24	14	37
Montane forest EG	51	10	23	16	31
ARGENTINA (mean):	(52)	(5)	(25)	(18)	(14)
Sparse cedar EG	77	0	23	0	13
Dense cedar EG	53	7	33	7	15
<i>N. dombeyi</i> - <i>Chusquea</i> EG	56	0	22	22	9
<i>N. dombeyi</i> + <i>Chusquea</i> EG	46	0	27	27	15
<i>N. pumilio</i> - <i>Chusquea</i> DE	41	12	18	29	17
<i>N. pumilio</i> + <i>Chusquea</i> DE	40	13	27	20	15

Except for work on frugivorous birds of Chiloé Island, Chile (Armesto *et al.* 1987), South American temperate forests lack studies of even a single avian guild. Limited qualitative evidence indicates that temperate South American birds engage in much more frugivory, involving both fruits on or near the ground and those in higher foliage, than do their North American counterparts (Armesto *et al.* 1987; Armesto & Rozzi 1989).

Both North and South American temperate forests contain insectivorous ground-foraging birds (Turdidae and Icteridae). Conspicuously missing from the North American avifauna, though, are the Rhinocryptidae, abundant ground- and understory-foraging birds in many South American temperate forests. In contrast, the guild concentrating on the abundant nuts and cones produced by North American temperate forests (primarily Corvidae), including temperate rainforests (Brown

1985), is conspicuously absent from temperate South America. Corvids, with their Holarctic origin, could be absent for purely biogeographical reasons (although they penetrate well into subtropical Argentina). Are their south temperate counterparts the parakeets (Psittacidae) that wander widely and consume, among other foods, seeds from *Araucaria* cones (J.E. Jiménez, pers. comm.)? *Araucaria* cones are less hard than north temperate pine cones and need not be cracked to reach their seeds. Thus, parakeets of South American temperate forests are better counterparts to North American crossbills (*Loxia* spp., Fringillidae) than to corvids.

COMPARISONS OF SEASONAL CHANGES IN GUILD STRUCTURE

Thorough analyses of single guilds of insectivorous birds in North American

temperate forests (e.g., Root 1967; Williamson 1971; Wagner 1981) have documented seasonal changes in guild composition with the arrival and departure of migrants, often long-distance latitudinal migrants. The impact of migrants on guild structure (who forages on what where, using which behaviors), however, can not be distinguished from changes caused by seasonal shifts in the resource base or in breeding status. Rabenold (1978, 1979) studied arboreal insectivorous birds in spruce-fir forests of the eastern United States, comparing forests with similar structure but different latitudes. He found that less seasonal (lower latitude) forests held more avian residents and fewer migrants than higher latitude sites, yet the latter had a more complex guild structure during the summer. Rabenold (1978, 1979) attributed these differences to seasonality in resources: lower latitude forests presumably experience relatively less of a spring-summer pulse in arthropod production than do higher-latitude counterparts. Residents in the latter may be unable to track these seasonal resource highs and lows, leaving abundant "resource space" for summer immigrants. In lower latitude forests, year-round residents may be able to track better the less drastic fluctuations in food resources, leaving fewer "spring-summer vacancies" for migrants.

No hard data exist on the dynamics of guild structure in South American temperate forests. Several Accipitridae, Psittacidae, Strigidae, Trochilidae, Picidae, Furnariidae, Tyrannidae, Phytotomidae, Hirundinidae, Troglodytidae, and Fringillidae are known to be partial or complete seasonal migrants (Table 2; see also Schaltter 1979; Vuilleumier 1985; Armesto *et al.* 1986). Thus, seasonal changes in guild structure, albeit undocumented to date, undoubtedly occur in South American temperate forests.

COMPARISONS OF THE FOOD RESOURCE BASE

The most likely cause of the major contrasts suggested in the last two sections is food availability (see Holmes & Recher 1986 for the same conclusion). In this section we discuss all classes of food

resources potentially exploitable by birds in the temperate forests of North and South America, making educated guesses where no hard evidence is available.

Seeds

Seeds, small energy packets requiring little processing time, occur in temperate forests of both hemispheres. Seed production by forest shrubs and herbs must be considerably lower than production in more open habitats supporting high densities of grasses and other herbs, accounting for the relatively low species richness of true granivores in forests (cf. Willson 1974). In contrast, trees may sometimes produce high quantities of seeds. Trees of cool north temperate forests often display marked inter-annual fluctuations in seed production (Silvertown 1980). Few comparable data exist for South American forests, but inter-annual fluctuations have been reported for three tree species (González *et al.* 1989).

Nuts, and seeds in cones

Cones (considered as units) and nuts may be considered large energy packets requiring at least moderately long processing times. In North America, such packets occur abundantly on pines (*Pinus*) and other conifers, oaks (*Quercus*), hickories (*Carya*), and other trees or large shrubs. Many birds depend entirely (crossbills = *Loxia* spp., Fringillidae) or at least partially (e.g., some Corvidae) on this food. Production of nuts and cones exhibits clear inter-annual variation even in warm temperate forests of the southeastern United States (P. Feinsinger, pers. obs.), more so in cool temperate forests, and especially in boreal forests mostly made up of conifers (Bock & Lepthien 1976; Silvertown 1980; Larson & Bock 1986). Consequently, dependent birds at any one site vary widely in population abundance as opportunistic species wander during lulls in seed production and irrupt during mast years (Bock & Lepthien 1976; Larson & Bock 1986).

As yet we cannot say if South American cone-bearers (e.g., *Araucaria*, *Fitzroya*,

Pilgerodendron, *Podocarpus*, *Saxegothaea*) or nut-producers (e.g., *Gevuina*) mast like their North American counterparts, or produce predictable crops annually. On the other hand, *Podocarpus* and *Saxegothaea* do not produce typical cones; rather, their seeds have fleshy arils that may attract frugivorous birds. Nor is it clear whether many animals depend heavily on such food resources, although parakeets (Psittacidae) certainly exploit nuts and cones at times. In any event, at least the cone-bearing forests display a great geographic contrast between the two continents. *Araucaria* stands in South America exist as relatively small, isolated islands in a sea of mixed or broad-leaved forest, whereas coniferous forests blanket large areas of North America from low to high latitudes. Nut- and seed-bearers capable of masting dominate broad-leaved North American forests as well, whereas broad-leaved deciduous or evergreen (rain) forests, at least in Chile, contain relatively fewer nut-bearing species and more berry-bearing species than counterparts in North America (Armesto 1987; Armesto & Rozzi 1989).

Fleshy fruits

Fleshy fruits such as berries and drupes seem to be less available and more seasonal in cool North American temperate forests (Thompson & Willson 1979) than in their South American counterparts (Armesto 1987; Armesto *et al.* 1987; Armesto and Rozzi 1989), whose nearly year-round production of fruit resources better resembles the pattern in warm temperate forests of the southeastern United States (Skeate 1987).

Nectar

Nectar available to hummingbirds also appears to be less seasonal in South than in North America. Outside of coastal southern and central California (Stiles 1973), natural nectar supplies in temperate North American forests usually last for 4-5 months at most (P. Feinsinger, pers. obs.). At least on the temperate Chilean

Island of Chiloé, hummingbirds have access to some nectar supplies year-round (C.C. Smith, pers. comm.).

Fungi

Although exploited by some mammals (Cork & Kenagy 1989; Meserve & Jaksic 1991), fungi do not appear to serve as major food resources for any birds in either continent. Almost no data exist about fungal availability. Presumably, fungi occur sporadically in less humid, more seasonal forests, but nearly continuously in west forests such as in the Pacific Northwest of the United States, or the beech forests of southern Chile and Argentina.

Flying insects and land vertebrates

We have no reason to suspect any major differences between continents in the availability or seasonality of these two very different food categories, except that flying insects may be more continuously available in south temperate than in north temperate forest (cf. Hodkinson & Hughes 1982; Goward *et al.* 1987).

Foliage and its arthropods

Although foliage serves as a direct food resource for very few birds (in this comparison, only for the Phytotomidae of South America), it serves as an indirect resource by determining the availability and seasonality of birds' most intensely utilized foods. Foliage also provides shelter from predators (Martin 1988). In North America, the most widespread evergreen forests are composed of conifers, whereas deciduous forests are broad-leaved. Therefore, phylogeny, leaf shape, phytochemistry, forest structure, substrate structure, and seasonality all change simultaneously with a shift from evergreen to deciduous. From the perspective of a north temperate bird, then, tremendous and synergistic differences exist between evergreen and seasonally deciduous forests. A south temperate bird might perceive a much less acute difference between these two forest types in South America. Here, most forests

of both types are broad-leaved, often dominated by trees of the same genus (*Nothofagus*). Conifers are few in species and limited in geographical extent. Undoubtedly, the two forest types in South America differ somewhat in phytochemistry and structure, but these differences must be minor compared to those between coniferous evergreen and broad-leaved deciduous forest of North America. The major feature differing between the two South American forest types, from a bird's viewpoint, is likely to be seasonality.

Some life-history stages of foliage arthropods tend always to be available on functioning leaves or needles of north temperate forest trees and in dead leaves as well. Availability of these prey is highest during spring leaf flushing. Presumably, these features also characterize south temperate forests. The relative seasonality, and peak availability, of foliage insects must be greater in deciduous than in evergreen forests even when closely related species are concerned. We wish to draw particular attention to one group of foliage insects of tremendous importance to North American forest avifaunas: larvae of Lepidoptera and Hymenoptera (cf., Holmes *et al.* 1986; Holmes in press). Lepidopteran larvae in particular provide a crucial resource base for breeding birds. Sporadic irruptions of a few species of lepidopterans, sawflies, and hornworms characterize many North American forests, both coniferous and broad-leaved. These irruptions apparently play crucial short- and long-term roles in the population and community dynamics of insectivorous birds (Holmes *et al.* 1986; Holmes in press). Although lepidopteran larvae of *Ormiscodea* sp. are known to irrupt sporadically (R. Murúa, R.P. Schlatter, T.T. Veblen, pers. comm.), no adequate documentation exists for irruptions in South American temperate forests, nor even for the average density of these larvae or their importance to birds.

The general picture

The overall impression provided by the admittedly speculative comparisons above

is that North American temperate forests, from a bird's viewpoint, are more heterogeneous (both phylogenetically and structurally), seasonal, dynamic, and irruptive than their South American counterparts. The latter appear to be more productive (net primary productivity) and with a longer growing season (Goward *et al.* 1987), perhaps higher in secondary (insect) productivity (Hodkinson & Hughes 1982), and likely with less temporal variation overall. We caution readers that this generalization involves the widespread North American forests that experience highly seasonal, continental climates. Avifaunas of maritime forests of northwestern North America, much more limited in extent but physiognomically and climatically more directly comparable to the temperate South American forests, may also be less dynamic, migratory, and irruptive than the better studied avifaunas to the east and south (Brown 1985). For example, seed or cone masting and insect outbreaks occur infrequently in Pacific Northwest forests, if at all (J. Franklin, pers. comm.). Because directly comparable data bases are not available, however, at this time we cannot evaluate this possibility.

DISCUSSION

The foregoing—a few hard data from specific sites, a number of generalizations based to a lesser or greater extent on data, and generalizations based on little more than reasoning—generate a number of questions that may serve to provoke thought and channel future research. Next we highlight a few specific questions derived from these, questions that could be tested with intensive field work. We conclude with a specific proposal for comprehensive research projects.

GENERAL QUESTIONS AND SPECULATIONS

1) Do history, distinct phylogenies, and different geographies override basic ecological similarities between continents in determining the structure and dynamics of avifaunas? The avifauna of the two

continents' cool temperate forests is phylogenetically quite close. Most ecological categories are filled in similar ways: finches and thrushes, among others, occur on both continents, whereas ecological equivalents to North American warblers, vireos, and chickadees, among others, occur in South America. Nevertheless, if one's working hypothesis is the existence of intercontinental convergence it is always possible to make subjective matches of species or guilds. Thus, approaches to this questions must involve careful research rather than casual observations or data-stuffing into preconceived pigeonholes, as has previously occurred in such intercontinental comparisons (Cody 1974).

2) What role does apparent intercontinental contrast in the abundance of cone- and nut-bearing trees play in determining the abundance and diversity of birds that depend partially or completely on such resources?

3) Given that true nuts are scarce in South American temperate forests, and that nut-caching by birds seems not to occur (e.g., that behavior shown by acorn woodpeckers in the United States), what role does the presence (North America) or absence (South America) of nut caching have on forest dynamics and on population dynamics of other species that in North America exploit those caches (e.g., some rodents, insects, and fungi)?

4) What is the role of primary (vegetation) and secondary (insect larvae) masts in determining avian social organization on either continent?

5) Is consistent fruit availability a stabilizing influence on some temperate South American avifaunas, in contrast to the destabilizing influence of nuts, cones, and insect larvae on North American avifaunas?

6) Considering the proposed greater seasonality and irruptiveness of food resources in North American as opposed to South American temperate forests, is the North American forest avifauna more opportunistic, resilient, and labile than the South American avifauna? Is the latter less responsive to small-scale secondary succession? Is the South American tem-

perate avifauna more sedentary, more "finely tuned", and less opportunistic than its North American counterpart? If so, major perturbations ("catastrophes" sensu Harper 1977) of South American forest landscapes might extinguish resident avifaunas completely, allowing their replacement by entirely new assemblages.

7) Is the apparent low incidence of latitudinal migrants in South American temperate forests, relative to North American forests, the consequence of: (a) the small land mass to the south? (b) the major desert and mountain barriers, for Chilean birds at least, interfering with migration to and from the tropics? or (c) less seasonality in food resources, so that residents can track these better than in North America, leaving relatively little for potential migratory opportunists?

8) What roles do different disturbance regimes play in the ecological radiation of avifaunas? Veblen (1989) has shown that *Nothofagus* forests experience perturbations on many spatial and temporal scales, but in general perturbations are of larger dimension than in North American broad-leaved forests.

9) Has the scale of human disturbance in forests over the past 100-300 years also been distinct enough to cause intercontinental differences in avifaunal responses? In many North American forests, human disturbance, while extensive, has been small-scale. Regenerating sites occur alongside recently cleared sites or woodlots, resulting in a successional patchwork. In temperate South American forests, human disturbance often involves an "advancing front" of large-scale burning and clearing.

10) What role did intercontinental differences in Pleistocene events play in the evolution of latitudinal migration, indeed in the development of the regional avifauna (Vuilleumier 1985)?

SPECIFIC QUESTIONS

1) Are seasonal and supra-annual changes in resources and in avifaunal community structure less pronounced in South than in North American temperate forests?

2) Are there differences between hemispheres in the frequency, roles, and impacts of latitudinal and altitudinal migrants? What proportions of avifaunas are migratory, and what foods do migrants eat? Do migrants have effects on food use by year-round residents, or do migrants concentrate on resources that residents cannot track?

3) Are the differences in avian dynamics between evergreen and deciduous South American forests similar to those between less and more seasonal forests in North America, as shown by Rabenold (1978)?

4) How does the South American forest avifauna respond (a) to anthropogenic secondary succession, (b) to natural disturbance regimes such as treefall-generated gap phase moasics? Does this response differ qualitatively from responses of North American avifaunas (which responses also beg additional studies)?

5) How do guild structure and membership change through the seasons in both continents?

6) What are the long-term (supra-annual) dynamics of South American forest birds and their resources? What is the ecological impact, if any, of masting by forest trees?

A PROPOSAL FOR COMPREHENSIVE RESEARCH

Obviously, very little knowledge is available on which to base a comparison of bird ecology in North and South American temperate forests. Gaps in knowledge exist even for the comparatively well-studied North American forests alone. We suggest that a careful, comprehensive, comparative study of the ecological structure and dynamics of avifaunas on both continents is in order. Such a study would not only be highly valuable from the purely scientific standpoint (in terms of the data generated by the study as well as the unanticipated questions and spin-off studies generated). Careful comparisons of seasonal dynamics, migration patterns, responses to autochthonous and anthropogenic disturbance, and spatiotemporal patterns of habitat use in general would also be crucial

to formulating conservation priorities on continental and local scales.

We propose that an intercontinental comparison begin with an intensive 2-year study and continue thereafter with long-term, less intensive monitoring. The study should involve an absolute minimum of four sites. In South America, these would be a temperate deciduous forest and a nearby evergreen forest. Comparable sites (but of course with the evergreen forest dominated by gymnosperms rather than angiosperms) would be chosen in North America, perhaps in or near the Hubbard Brook Experimental Forest so well studied by Holmes and colleagues (Holmes in press), or near the Cary Arboretum, New York State. The Pacific Northwest forests, although ideally situated, are dominated by conifers and do not adequately lend themselves to comparison with South American temperate forests. Although the threat of intercontinental pseudoreplication would continue to lurk in the background, many findings could be ascribed legitimately to overall intercontinental differences. Alternatively, 15-30 pairs of sites on each continent could be monitored less intensively, with a loss of resolution balanced by a great gain in generalization.

In an unreplicated-but-intense study or, insofar as possible, in the highly replicated approach, for two years the complete avifauna of each site would be subjected year-round to an intensive Salt-type study (Salt 1953, 1957). Researchers would monitor guild membership and its seasonal shifts, more specifically, which bird eats which food items from which substrates when; arrival and departure of migrants; origin and destination of migrants, where possible (of course this information is already available for North American birds); and obvious changes in the resource base. If necessary, detail would be sacrificed in order to obtain a continuous, comprehensive overview of the entire avifauna's ecological structure. One experienced full-time researcher per site might suffice.

Following the intensive 2-year period, the comparative study would continue indefinitely but at a much reduced level. Special watch should be kept for unusual

climatic events or major changes (such as irruptions) in food resources, and any accompanying responses of the avifauna. At the same time (but only after the 2-year initial phase), interested researchers might begin careful and detailed comparative studies on the most dynamic and interesting guilds. Examples might be ground-feeding insectivores (see Noon 1981), among which North American forests have no counterpart for the abundant and conspicuous South American Rhinocryptidae; or frugivore-insectivore guilds (Karr 1968; Willson 1974; Armesto *et al.* 1987). Other guilds might also lend themselves to testing specific hypotheses generated by the initial intensive study. At this stage, comparative ecomorphological studies (cf. Ricklefs & Miles 1984; Landres & MacMahon 1980, 1983) might also be of interest. We suspect, though, that the most important data in the long range will be the carefully designed, carefully collected, purely observational data on community structure and dynamics to be gathered in the basic study.

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APPENDIX 1

Weights (g) of birds used in the computation of standing species' crops in southern Argentina. Data come from field notes (Jaksic, unpubl). *Chloephaga poliocephala* (2,500), *Buteo polyosoma* (975), *Callipepla californica* (200), *Enicognathus ferrugineus* (200), *Sephanoides galeritus* (5), *Picoides lignarius* (39), *Colaptes pitius* (150), *Campophilus magellanicus* (200), *Aphrastura spinicauda* (10), *Thripophaga pyrrholeuca* (26), *Thripophaga anthoides* (24), *Pygarrhichas albogularis* (13), *Pteroptochos tarnii* (120), *Scelorchilus rubecula* (45), *Scytalopus magellanicus* (15), *Pyrope pyrope* (22), *Elaenia albiceps* (17), *Anairetes parulus* (11), *Phytotoma rara* (60), *Pygochelidon cyanoleuca* (14), *Troglodytes aedon* (10), *Turdus falcklandii* (94), *Curaeus curaeus* (90), *Phrygilus patagonicus* (20), *Phrygilus unicolor* (28), *Carduelis barbatus* (35).