

TITS, WARBLERS, AND FINCHES: FOLIAGE-GLEANING BIRDS OF NEARCTIC AND PALEARCTIC BOREAL FORESTS¹

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Abstract. We describe two major patterns of abundance of different types of canopy foliage-gleaning birds at four sites (northwestern Canada, eastern Canada, European Russia, and central Siberia) in boreal forest. First, because of the extreme numerical dominance and breadth of habitat use of the Chaffinch (*Fringilla coelebs*), the European Russian sites stand as outliers to the relationships between the number of species and the abundance of all foliage-gleaning birds, as well as to more detailed patterns of the composition of the foliage-gleaner guild. The Chaffinch is one of the few canopy foliage-gleaning birds in temperate forests that is abundant in agricultural habitats during the nonbreeding season, which probably allowed a rapid expansion of its range and growth in abundance with the advent of farming in Europe. The second pattern emerges when the European Russian sites are excluded from analyses: the proportional abundance and number of species of warblers or warbler-like birds were positively related to overall abundance of foliage gleaners. This suggests that warblers prosper when there is high resource productivity during the breeding season. A possible resolution between the patterns found in European Russia and the other boreal forest sites may be that *Fringilla* are functionally equivalent to warblers and have essentially replaced warblers to achieve their high abundance. The patterns of relative abundance give support to both the Resource Seasonality Hypothesis (warblers versus tits), and the Ecological Replacement Hypothesis (*Fringilla* versus warblers) as explanations for shifts in the numerical dominance of different types of foliage gleaners in different regions.

Key words: boreal forests, community convergence, community structure, continental comparison, foliage-gleaning bird, *Fringilla*, warblers.

INTRODUCTION

The study of similar habitats in different continents is a common approach to testing generalities in the patterns of avian species assemblages. Boreal forests are an attractive focus for these types of studies because they form a continuous band across North America and Eurasia of low diversity forests dominated by a few shared genera of canopy trees. Although one-to-one correspondence between forest types may be elusive, the range of habitats available to birds

is quite comparable. Many of the dominant higher taxa of songbirds, however, are only distantly related between the two continents (Haila and Järvinen 1990). Variation in the taxonomic composition of forest avifaunas has fueled the search for ecological equivalents between regions, as well as for biogeographic and ecological processes that have determined the composition of different assemblages (Morse 1989).

The canopy foliage-gleaner guild is the most abundant and species-rich guild across all boreal forests. Various studies have compared the ecology of specific paired groups of foliage gleaners, particularly the Old World versus New World warblers (Cody 1974, Winkler and Leisler 1994). The problem with this approach is that

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the flush of foliage insects in temperate forests often supports the breeding of a morphologically or ecologically diverse group of species. Species that forage on foliage arthropods are often warbler or warbler-like birds, but also include tits, finches, and flycatchers. The relative importance, both in terms of species richness and abundance, of these different types of foliage gleaners varies considerably between regions. The search for ecological equivalents between sites should, therefore, be expanded beyond specific taxonomic pairings to include all foliage-gleaning species.

Two hypotheses have been put forth to explain intercontinental and regional differences in the dominance of different types of foliage gleaners, particularly with respect to the relative importance of tits versus warblers (Sylviinae or Parulinae). The Ecological Replacement Hypothesis posits that as a result of historical patterns of colonization and diversification, one type of foliage gleaner usurps resources limiting the ecological opportunities for other types. For example, New World assemblages support a large number of species of warbler or warbler-like birds, whereas Old World assemblages (particularly those in southern or western Europe) often have a higher number of tit species (Haila and Järvenin 1990). This has led some (Morse 1989) to speculate that tits replace wood warblers to a large degree in Palearctic forests and to suggest that in southern Europe tits replace Old World warblers (Herrera 1978).

The second hypothesis is more explicitly ecological. The Resource Seasonality Hypothesis posits that certain types of foliage gleaners are specialized on harvesting the bloom of summer arthropods and become more common where the breeding season resource peak is more pronounced. For example, Haila et al. (1987), highlighting the negative correlation between tit and *Phylloscopus* abundance in European census data, suggested that the latter become more numerically dominant in more seasonal habitats. Related to this hypothesis, Wiens (1975) and Rabenold (1978) proposed that the high abundance and diversity of wood warblers in Northeastern coniferous forests of North America is related to the large pulse of food during the breeding season in these forests compared to Western and Southern forests.

This paper is an initial step toward understanding the relative importance of the major

types of foliage gleaners in different boreal forest habitats in light of these hypotheses and with an emphasis on comparing Palearctic and Nearctic sites. Considering survey data gathered from sites in different boreal forest regions, we address the following questions: (1) What is the pattern of variation in relative abundance of different foliage-gleaner types in different regions of the boreal forest? (2) What is the relationship between species richness and abundance of foliage-gleaning birds and different types of foliage-gleaning birds? (3) Is there a predictable relationship between the abundance of different types of foliage-gleaning birds and the overall abundance of foliage-gleaning birds? (4) To what degree do the aforementioned relationships vary between different sites and continents in the boreal forest?

METHODS

STUDY SITES

Fieldwork was conducted in successive summers: central Siberia 1993, northwestern Canada 1994, European Russia 1995, and eastern Canada 1996. We selected four study sites organized into two comparable pairs (Fig. 1). The first pair is "middle taiga" sites with highly continental climates: the southern MacKenzie District of the Northwest Territories (MacKenzie) and the middle section of the Yenisey River between Tunguska and Angara Rivers (Siberia). Both areas were centered on a major river system (Yenisey and Mackenzie are the fourth and seventh longest rivers in the world, respectively) and had a similar range of latitudes (Siberia, 60°10' to 62°15'N; MacKenzie, 60°14' to 61°52'N). Research was conducted at three sites each in Northwest Territories and central Siberia. The Siberian sites (Myrnoe, Vorogova, and Fomka) were a maximum of 295 km apart and the maximum distance was 340 km for the MacKenzie sites (Fort Liard, Fort Simpson, and Fort Providence). The second pair of study areas was located in less continental regions characterized as "South Taiga." Both the European Russian (Europe) and eastern Canadian (Ontario) sites were far more disturbed and developed than the central Siberian and Mackenzie areas. Due to logistical constraints, the Russian fieldwork was conducted primarily within 40 km of the Kostromskaya Taiga Field Station located on the Unja River (58°14'N, 55°25'N). However, 10% of the

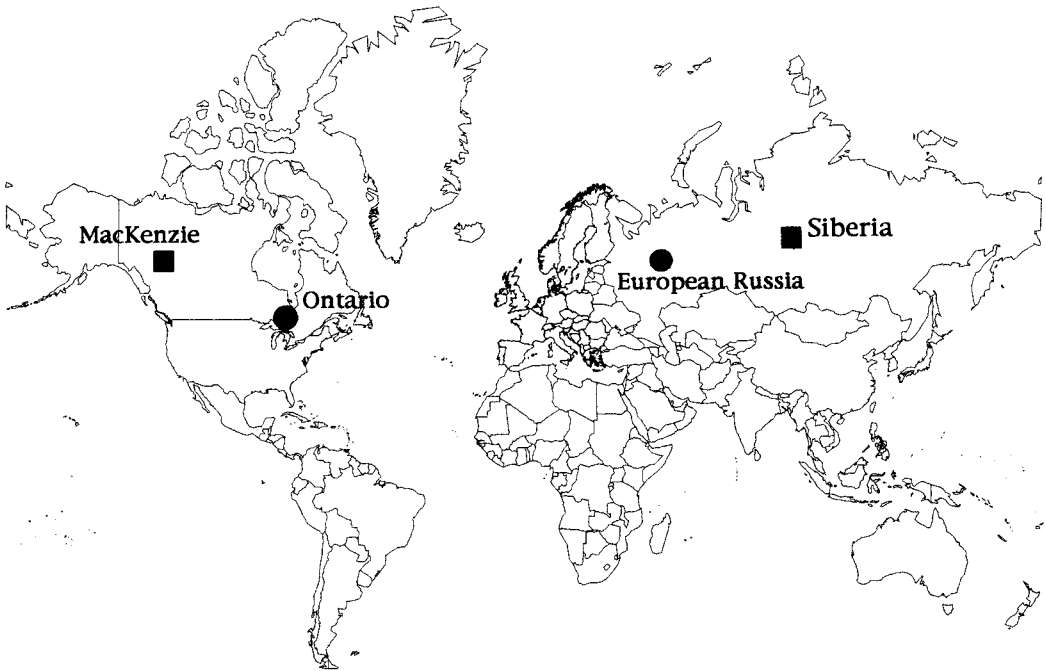


FIGURE 1. Map depicting location of study sites in Canada and Russia. Sites marked with a square are in northern taiga and those with a circle are in southern taiga.

survey points were conducted at the Zvenigorod Research Station 600 km southwest (near Moscow) with the addition of no species. The Ontario sites were primarily in the clay belt between the cities of Gogama, Timmins, Cochran, and Hearst, as well as White River and Marathon with a maximum intersite distance of 490 km and a latitudinal range of 47°51'N to 49°30'N. The lower latitudes of locations in Ontario reflect the overall southern distribution of the boreal forest in this region.

HABITATS SAMPLED

We sampled four types of mature forest habitat in Siberia: (1) riparian alder (*Alnus fruticosus*) and willow (*Salix* spp.), (2) mixed floodplain forest, with spruce-fir (*Picea obovata-Abies sibirica*) and birch (*Betula* spp.), (3) upland birch stands with some aspen (*Populus tremula*), and (4) mixed upland taiga with siberian pine (*Pinus sibirica*), spruce, larch (*Larix sibirica*), fir, and birch. We surveyed five habitat types in MacKenzie: (1) black spruce forest (*Picea mariana*), (2) mixed flood-plain forest, with white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*), (3) riparian, with balsam

poplar, alder (*Alnus tenuifolia*), and willow, (4) trembling aspen stands (*Populus tremuloides*), and (5) jack pine (*Pinus banksiana*) forests. In the European Russian site we sampled (1) mixed, upland second-growth taiga (approximately 60 years old), with spruce (*Picea abies*), aspen, linden (*Tilia cordata*), and birch (*Betula pubescens*), (2) birch-aspen forest, (3) European pine (*Pinus sylvestris*) forest, and (4) riparian elm-alder (*Ulmus-Alnus incana*) woods. In Ontario we sampled (1) aspen stands (aspen, birch [*Betula papyrifera*], and balsam poplar), (2) mixed upland taiga (white spruce, balsam fir [*Abies balsamea*], jack pine, birch, aspen, and poplar), (3) black spruce, and (4) jack pine stands.

POINT COUNTS

Because bird censusing techniques often differ between studies and regions, it is often difficult to make systematic comparisons. For the purposes of this analysis, we gathered field data employing the same point-count methodology at all sites. Point counts (Hutto et al. 1986, Petit et al. 1995) consisted of a series of up to 15 5-min counts located 200 m apart. Censuses were con-

ducted 30 min after sunrise for approximately 3 hr when wind speeds are less than 12 km hr⁻¹. The number and approximate distance of all birds were recorded as well as the mode of detection (song, call note, strictly visual). As much as possible, all points on a transect were located in a single habitat type at a minimum of 100 m from a habitat edge, which requires large tracts of habitat for surveying. Point counts were conducted from 5–25 June, which corresponds with the peak singing activity of migratory species. Resident species (tits) initiate breeding earlier than migrants and so were probably vocalizing less than migrants during our work. Although this may cause underestimation of tit populations, we regard this as an equivalent bias for all sites. In addition, a comparison of our point count data with published census data from the same region showed a high correlation ($r = 0.95$) between the two data sets with respect to composition of different types of birds and no significant underestimation of tits (see Results). Because of the severe problems of differential detectability between species and habitats, we have relied upon the mean number of birds within 50 m of the point to assess foliage gleaner abundance (Petit et al. 1995). In order to standardize the species list to assess overall species richness, we used the total number of species detected with an abundance greater than 0.02 individuals per point, and standardized effort by randomly subsampling the data from 75 points. The summary of individual species by site is available at the Smithsonian Migratory Bird Center web site (<http://www.si.edu/smbc>).

In MacKenzie, we sampled mixed white spruce near Ft. Liard and Black Mesa (91 point counts, see below), Ft. Simpson (20), and Ft. Providence (27); black spruce near Ft. Liard (60), Ft. Simpson (32), and Trout Creek (17); riparian deciduous near Ft. Liard (55) and Ft. Simpson (35); aspen near Ft. Liard (43) and Ft. Simpson (32). In Siberia, we sampled upland taiga near Myrnoe (177), Volgova (45), and Fomka (58); floodplain taiga near Myrnoe (32), Volgova (64), and Fomka (57); birch near Vorogova (61) and Fomka (48); and riparian near Myrnoe (43), Vorogova (48), and Fomka (57). In Ontario, we sampled upland mixed forest near Marathon (40), Hearst (57), Cochrane (18), White Lake (28), and Timmins (5); aspen-poplar near Timmins (91) and White River (9); and

black spruce near Gogama (12), Timmins (11), Cochrane (53), Marathon (6), and Obatanga (5).

PUBLISHED CENSUS DATA

Point counts provide a standardized rapid assessment, which allows direct comparison between sites. We have examined published censuses based mainly on territorial mapping or more rarely on repeated fixed transects to assess the generality of some of the qualitative results of the analysis from our point count data. The censuses were selected to cover a broad habitat and geographic range, but are by no means exhaustive. The data set (available from first author) includes 21 censuses from eastern North America, 6 from western Canada, 28 from northern Europe (West of Urals), and 20 from Siberia. We calculated the mean value (or in the case of Breeding Bird Censuses from Canada, we used published means following Erskine [1977]) when more than one survey was conducted in the same habitat and site.

CLASSIFICATION OF FOLIAGE-GLEANER TYPE

We subdivided the canopy foliage-gleaning guild into four types, corresponding to differences in morphology or, in the case of flycatchers, large differences in foraging behavior: (1) tits (species of Paridae or *Aegithalos*), (2) finches (*Fringilla*, Emberizids, Carduelinae), (3) warblers (Parulinae, Vireonidae, and the probably polyphyletic [Sheldon and Gill 1996] Sylviinae including *Regulus* and *Sylvia*), and (4) flycatchers (*Empidonax*, *Ficedula*, *Erithacus*, *Phoenicurus*). The last group includes species that forage predominantly from leaves, twigs, and branches with a mean attack distance > 1 m, but not those such as *Muscicapa* and *Contopus* spp. which forage for aerial arthropods. Two uncommon species (Gray Jay *Perisoreus canadensis*, and Golden Oriole *Oriolus oriolus*) that were not easily classified were ignored in the analyses.

We have included some species that are often not considered foliage-gleaning species. Based on our foraging observations at our study sites, these species probably do a substantial amount of their foraging off foliage or twigs. The non-traditional species include some that also forage on the ground (European Robin *Erithacus rubecula*, Dark-eyed Junco *Junco hyemalis*, Chipping Sparrow *Spizella passerina*, and Yellow-breasted Bunting *Emberiza aureola*). These species were commonly found in the canopy. How-

ever, with ground-foraging birds it is often difficult to determine how much of their foraging time is spent on the ground, because there they are more difficult to observe. We also include some Cardueline finches, which are well known to feed on seeds extensively, even when rearing young (Newton 1967). In the forest habitats we studied, siskins and bullfinches forage commonly for foliage arthropods during the height of the breeding season. These species were generally uncommon on our surveys and exclusion of these species does not greatly alter the major conclusions of this paper.

RESULTS

NUMERICAL DOMINANCE, ABUNDANCE, AND COMPOSITION OF FOLIAGE-GLEANING GUILDS

We found significantly more foliage-gleaning individuals per point in European Russia than other sites, largely a result of the very high abundance of Chaffinches in all habitats (ANOVA based on mean per habitat, overall habitat effect $F_{3,13} = 28.2$, $P = 0.006$, Tukey's post-hoc comparison was significant only for Europe versus other sites). The upland Siberian sites had low densities compared to similar North American sites (Table 1). Jack pine forest on sandy glacial outwash is equivalent to European pine forests of Siberia, which were not surveyed and so were not considered in this comparison. The dominant species varied among habitats in the two North American and Siberian sites (Table 1), with warblers generally dominating the former and tits the latter. However, the Chaffinch was the dominant foliage-gleaner in all four habitats at the European Russian site. The average proportion of Chaffinches across habitats in European Russia was 0.44. The highest values for the other sites were Willow Tit (*Poecile montanus*) in Siberia (0.17), Tennessee Warbler (*Vermivora peregrina*) in MacKenzie (0.19), and Yellow-rumped Warbler (*Dendroica coronata*) in Ontario (0.11).

In terms of numbers of individuals, the relative importance of different types of foliage gleaners varied among the different study sites. The proportion of finches varied significantly (Kruskal-Wallis $H = 11.0$, $P = 0.01$) with the highest proportion (56%, Table 1) in European Russia, also a consequence of the high Chaffinch abundance. Siberia had a moderate (26%), and the New World sites low (15% and 9%), pro-

portions of finches. The New World sites had a significantly greater proportion of warblers (72%; $H = 12.3$, $P = 0.006$). We found no overall significant difference in the proportion of tits and flycatchers across sites. However, except for the riparian vegetation, with its lack of cavities, central Siberia had a strikingly high proportion of tits (33%) compared to other regions.

SPECIES RICHNESS VERSUS ABUNDANCE OF FOLIAGE GLEANERS AND FOLIAGE-GLEANER TYPES

The correlation between species richness and abundance of foliage gleaners across habitats was significant and strong ($r = 0.85$, $P < 0.001$) with European Russia excluded, and somewhat weaker, but still significant, with the Russian habitats included ($r = 0.73$, $P < 0.001$, Fig. 2); the Russian sites are brought into conformity with other sites by removing the Chaffinch numbers ($r^2 = 0.83$, $P < 0.001$).

The relationship between species number and abundance across foliage-gleaner type (warbler, finch, etc.) also was strong for the pooled North American and Siberian sites ($r = 0.96$, $P < 0.001$), but considerably weaker if the European Russian sites are included ($r = 0.72$, $P < 0.001$). Species richness and abundance of type were significantly correlated when considered separately for Siberia ($r = 0.91$), MacKenzie (0.84) and Ontario (0.97) (all P values < 0.01), but not European Russia (0.54).

ABUNDANCE OF FOLIAGE-GLEANER TYPES VERSUS OVERALL FOLIAGE-GLEANER ABUNDANCE

It is likely that the variation in overall abundance of foliage-gleaning birds reflects differences in food resources of different habitats. Based on this assumption, we have plotted the relative abundance of different foliage-gleaner types against total foliage-gleaning bird abundance (birds per point). We conducted ANCOVA using site and the mean total number of foliage gleaners per point as independent variables and the mean number of individuals of different types as the dependent variable. The analysis was first run with the site by abundance interaction term. When there was no significant interaction, the ANCOVA was then run without the interaction term to test for the effect of site and abundance (Wilkinson 1990). Because of the anomalously high abundance of Chaffinches

TABLE 1. Number of species, individuals per point, percentage of individuals and number of species in different types, and numerically dominant species in each habitat surveyed in this study.

Habitat	£ No. indivi- duals/Pt	n Species	% Individuals in Types (n species)				Dominant species	%
			warbler	finch	tit	flycatcher		
European Russia								
Mixed Taiga	3.44	17	33 (7)	49 (3)	4 (4)	13 (3)	Chaffinch	42
Alder-Elm Riparian	4.20	16	38 (7)	52 (4)	4 (3)	6 (2)	Chaffinch	34
Birch-Aspen	3.47	14	26 (6)	58 (3)	4 (2)	12 (3)	Chaffinch	52
Pine	3.38	14	22 (5)	56 (3)	17 (3)	6 (3)	Chaffinch	47
Mean	3.62	15.3	30 (6.3)	54 (4.3)	7 (3)	9 (3.3)		
Central Siberia								
Upland Taiga	0.74	6	37 (2)	14 (2)	47 (2)	2 (0)	Willow Tit	27
Flood plain Taiga	1.22	11	49 (6)	23 (3)	27 (2)	2 (0)	Willow Tit	22
Alder Riparian	1.77	12	63 (6)	36 (5)	4 (1)	1 (0)	Blythe's Reed Warbler	31
Birch-Aspen	0.73	6	23 (1)	32 (2)	26 (2)	14 (1)	Brambling	22
Mean	1.11	9	43 (3.75)	26 (3)	26 (2.75)	5 (0.25)		
Mackenzie								
White Spruce	1.83	12	76 (7)	13 (2)	5 (1)	4 (1)	Tennessee Warbler	29
Black Spruce	1.18	7	68 (3)	14 (2)	5 (1)	2 (0)	Tennessee Warbler	34
Riparian	1.44	11	64 (6)	5 (2)	2 (1)	31 (2)	Least Flycatcher	25
Aspen	1.26	8	60 (7)	2 (0)	1 (0)	30 (1)	Least Flycatcher	30
Jack Pine	0.61	6	43 (2)	41 (3)	7 (1)	0 (0)	Yellow-rumped Warbler	19
Mean	1.26	10.8	62 (5.0)	15 (1.8)	4 (0.8)	13 (0.8)		
Ontario								
Mixed Taiga	1.85	17	91 (13)	5 (2)	1 (0)	3 (2)	Bay-breasted Warbler	26
Black Spruce	1.44	13	78 (8)	8 (2)	4 (2)	10 (1)	Yellow-rumped Warbler	18
Aspen	1.92	13	82 (10)	3 (1)	2 (1)	12 (1)	Red-eyed Vireo	17
Pine	0.93	8	70 (5)	20 (2)	8 (1)	2 (1)	Yellow-rumped Warbler	18
Mean	1.54	12.7	80 (9.0)	9 (1.75)	4 (1)	6 (1.25)		

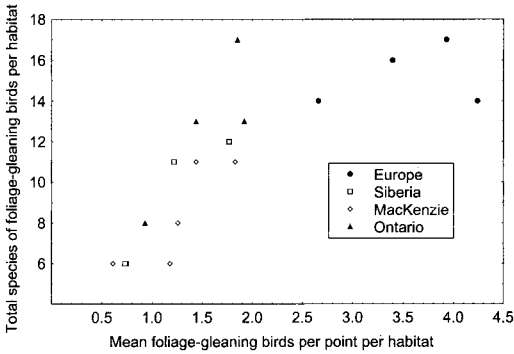


FIGURE 2. The mean number of foliage gleaners per type per habitat versus the number of species per type of foliage-gleaners in 75 points in each habitat with abundance > 0.02 per point.

at the European Russian site, we analyzed the data with all sites and with the European Russian data excluded. When we eliminated the European Russian habitats from the analysis, with their overriding dominance of Chaffinches, we found a strong relationship between the abundance of warbler-like birds and foliage-gleaner abundance (Fig. 3A). The ANCOVA (overall $r = 0.96$) showed a large effect of bird abundance ($F_{1,9} = 336.8$, $P < 0.001$) and a smaller effect of site ($F_{2,9} = 17.6$, $P < 0.001$). When European Russia was included, the correlation between warbler abundance and overall foliage-gleaner abundance was considerably weaker, but still significant ($r = 0.69$, $P = 0.001$).

We found a weak or nonexistent relationship between the abundance of other types and overall foliage-gleaner abundance (Fig. 3A). In terms of relative abundance (the proportion of foliage-gleaners of a given type) and with European Russia excluded, warblers showed a significant increase with increasing foliage-gleaner abundance ($r = 0.81$, $P = 0.001$) and tits showed a weaker, but significant, negative relationship ($r = -0.58$, $P < 0.01$). With European Russia included, only finches showed a significant correlation with abundance ($r = 0.64$, $P = 0.006$).

When the relationship between warbler abundance and overall bird abundance (Fig. 3A) for all sites is examined, the high abundance of Chaffinches and the lower than expected abundance of warblers at the European sites suggest a possible functional relationship. Summing the abundance of *Fringilla* and warblers produces an extremely tight relationship between their

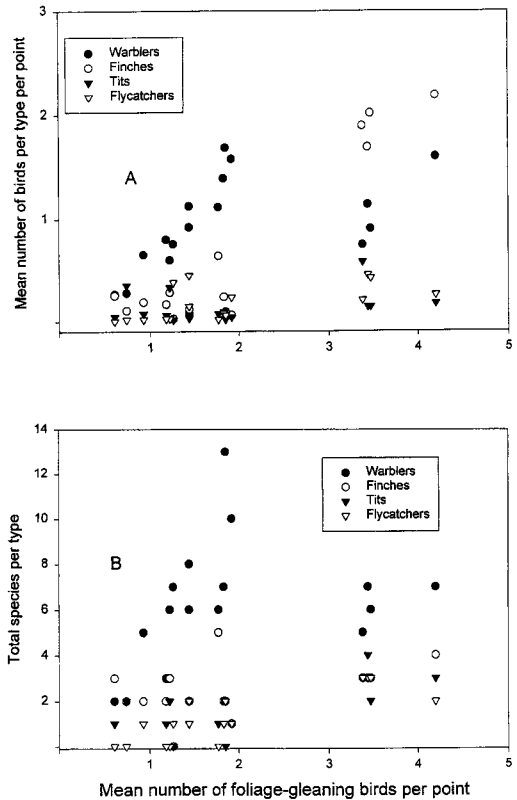


FIGURE 3. A. The mean number of total foliage gleaners per point versus the mean number of foliage-gleaning birds per point for each habitat surveyed. Note that the four points at the far right of the graph for each type are European showing the reversal of the position of finches and warblers from the relationship of other sites. B. The total number of foliage-gleaner species per type per habitat versus the mean number of foliage-gleaning birds per habitat.

abundance and overall bird abundance ($r = 0.99$) similar to that found for warblers in the three non-European communities alone. The ANCOVA produced a strong effect of overall foliage-gleaner abundance ($F_{1,12} = 394.3$, $P < 0.001$) and a weaker effect of site ($F_{3,12} = 15.5$, $P < 0.01$).

The number of species of warblers also was highly correlated with the abundance of foliage-gleaning birds ($r^2 = 0.85$, $P < 0.001$) when the European site was excluded (Fig. 3B) and not significantly correlated when these data were included (Fig. 4, $r = 0.39$, $P = 0.16$). An ANCOVA on warbler species number (European Russia excluded) produced no significant interaction between site and overall abundance. The

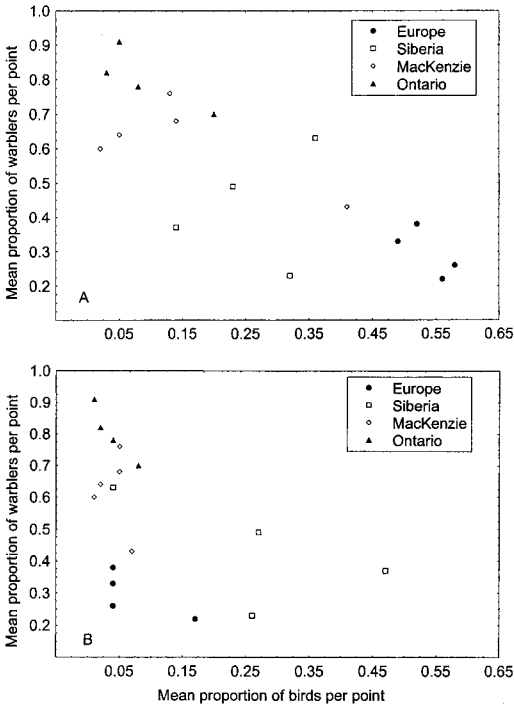


FIGURE 4. A. Proportion of finches versus warblers for each habitat surveyed with point counts. B. Proportion of tits versus warblers for each habitat surveyed with point counts.

ANCOVA without interactions produced a significant model ($r = 0.89, P < 0.001$) with only foliage-gleaner abundance entering as a significant variable ($F_{1,9} = 20.8, P < 0.01$). The diversity of other types was not significantly related to bird abundance or site.

COMPLEMENTARITY OF ABUNDANCE OF DIFFERENT FOLIAGE-GLEANER TYPES

A strong negative correlation ($r = -0.79, P = 0.001$, Fig. 4A) was found between the proportion of finches and warbler-like birds across different habitats. New World communities are mostly represented at the high warbler/low finch portion of the graph, and European communities on the opposite end. Siberian communities show the greatest scatter because these habitats support the greatest number of tits, which is not reflected in this relationship. On the other hand, the correlation between the proportion of warbler-like birds and tits was suggestive, but not significant ($r = -0.48, P = 0.08$, Fig. 4B). The suggestion of a relationship occurs primarily be-

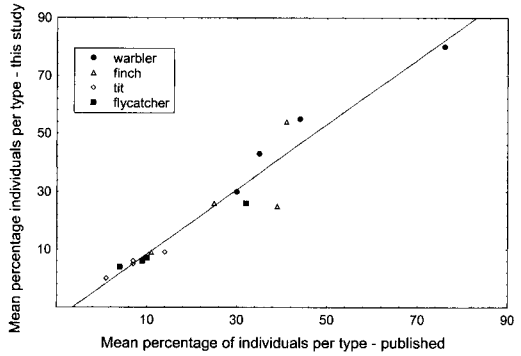


FIGURE 5. Mean percentage of individuals in different foliage-gleaner types for census plots from a region (e.g., eastern North America, northern Europe, etc.) versus the mean percentage of individuals in different foliage-gleaner types for point counts from the same region (this study).

cause of the three Siberian habitats with high tit and low warbler abundance. When European Russian sites were excluded, the dominant negative correlation was between warblers and tits ($r = -0.73, P = 0.005$) with a somewhat weaker, yet significant negative correlation between warblers and finches ($r = -0.61, P = 0.03$). In the case of the analyses with and without European Russia, we found no significant relationship between tits and finches ($r = 0.10$ and 0.28 , respectively), nor did we find any significant relationships between the proportion of flycatchers and any other type.

PATTERNS IN PUBLISHED CENSUS DATA

Based on the comparison with the census plots or transects, the patterns of the point count data are robust (Fig. 5), particularly considering that the geographic and ecological range of the published data were greater than for our study. The proportion of finches was highest (41.2%) in northern European and western Canadian (39.3%) communities and lowest in eastern North America (11.0%). Warblers were proportionately most common in eastern North America (75.7%) and western Canada (43.5%) and comparably low in the Palearctic regions (36%). Tits were relatively common in Siberia (33.8%) and uncommon in northern Europe and North America (4.1–10%). Flycatchers were relatively common in Europe (14%) and rare elsewhere (0.8–6.9%). The overall patterns of foliage-gleaning guild composition were surprisingly similar when plot and point count data were

compared. The correlation between mean proportion of type in a point count region and plots from the comparable region (e.g., eastern North America vs. Ontario; northern Europe vs. Kostroma, etc., with only spruce and pine habitats included for western Canada) had an r of 0.95 with a slope of 1.10 (Fig. 5).

As in the boreal point-count data set, the proportion of warblers was related to the proportion of both finches ($r = -0.61$, $P < 0.001$) and tits ($r = -0.58$, $P < 0.001$), values which are more similar to each other than those for the point count data (-0.79 and -0.48, respectively). When only Siberia and North America data were included, we found the major negative correlation between tits and warblers ($r = -0.74$, $P < 0.001$), with a weaker relationship between finches and warblers ($r = -0.57$, $P < 0.001$). As in the point count data, the relationship between tit and finch abundance was weak ($r = 0.11$ and 0.10 for analysis with and without northern Europe, respectively). None of the correlations between proportion of flycatchers and other types were significant.

Chaffinch was the most common foliage-gleaning species in 19/25 of the northern European communities, occurring commonly in broad-leaved and coniferous habitats alike, accounting for an average of 30% in northern Europe (range 2–57%). Chaffinches were scarce only in montane sites in Norway, and far north sites (northern Finland and Pechora region of Russia). Probably the most consistently dominant New World species is Red-eyed Vireo (*Vireo olivaceus*). This species was the dominant species in only 5 of 20 censuses in eastern North America, comprising 13.6% of the foliage-gleaners in those habitats, and was almost absent from coniferous forests.

DISCUSSION

Given the clear overdominance of Chaffinches in most European communities, we separate discussion of the distribution of foliage gleaning types into three issues: (1) what were the patterns of abundance of foliage-gleaner types in the non-European communities? (2) what explains the numerical importance of Chaffinches in European forest bird communities? and (3) can the discrepancies between the European habitats and other regions be explained by the hypothesis that *Fringilla* functionally replace warblers?

PATTERNS ACROSS NON-EUROPEAN SITES

When the European site was excluded, the abundance and number of species of warblers showed a highly significant relationship with overall foliage gleaner abundance with only a small effect of site, whereas the abundance of finches and tits was unrelated to overall abundance of foliage gleaners. This observation supports the Resource Seasonality Hypothesis for the importance of warblers in different boreal forest habitats. According to this hypothesis, the high proportion of tits in many Siberia habitats is primarily a result of the reduced summer resources and reduced warbler abundance. Tit populations are generally higher in Siberia, but the absolute number (overall, 0.26 per point) comprises a small portion of breeding foliage-gleaner assemblages (Fig. 4), and variation in the proportion of tits and warblers is largely determined by a large increase in abundance of warblers with increasing foliage-gleaner density. In contrast, the high proportion of tits in southern Europe (Herrera 1978, Haila and Järvinen 1990) is associated with high absolute abundances and may be driven more by mild winter climates and greater winter food resources.

We stress the Resource Seasonality Hypothesis for explaining variation in the proportion of warblers and tits in boreal forest. However, the consistently higher abundance of tits in Palearctic habitats is related to their higher regional species richness and may have a historical explanation. Still, tit abundance in Siberia is high even where only one common species of tit (Willow Tit) was found, which suggests that an ecological explanation is required as well.

OVERDOMINANCE OF CHAFFINCHES IN EUROPEAN ASSEMBLAGES

Many of the patterns discerned in the North American and Siberian data disappeared or were actually reversed when the European data were included. For example, the relationship between foraging-type abundance and species richness diverges strongly from those of the other sites. The proportion of warblers actually declines with foliage-gleaner abundance when the European points were included in the analysis. All of these deviations can be attributed to the strong overdominance of Chaffinches in all four habitats surveyed in European Russia.

Except where it is replaced by the Brambling (*Fringilla montifringilla*) in the far north, the

Chaffinch is a dominant foliage gleaner in all European forests. It comprises from 15–45% of the individual foliage gleaners, with the highest proportions found in northern European forests—both coniferous and broad-leaved. No North American bird approaches this level of abundance in such a wide geographic range or variety of forest types. Within regions as diverse as southern France (Blondel et al. 1990) and northwest Russia (Morozov 1992), the Chaffinch has the broadest habitat amplitude of all forest birds.

Based on MtDNA evidence, Chaffinches probably colonized Europe in the late Pleistocene, as recently as 50,000–95,000 years ago (Marshall and Baker, in press). The species continues to spread into Siberia (Rogacheva 1992). Given the current abundance of this species in European farmlands during the nonbreeding season (O'Conner and Shrubbs 1986, Cramp and Perrins 1994), its spread into the largely forested areas of northern Europe was probably accelerated by the spread of agriculture. Such a recent spread into European farmlands has been suggested for the Dunnock (*Prunella modularis*; Murton 1971) and House Sparrow (*Passer domesticus*; Johnston and Klitz 1977).

Thus far, we have presented a close relationship between both warbler abundance and richness and overall foliage-gleaner abundance in non-European boreal forest, along with an anomalous pattern in the European habitats. These divergent observations can perhaps be resolved if we consider that *Fringilla* are functionally similar to warblers in their resource use and that the expansion of Chaffinch in Europe has occurred at the expense of warbler abundance which would be consistent with the Ecological Replacement Hypothesis. This idea has some support: when we clustered foliage-gleaning species based on foraging behavior and site, Chaffinches clustered tightly with certain *Phylloscopus* warblers, vireos, and Parulinae (Greenberg et al., unpubl. data). With this in mind, it is striking how close the relationship was between warbler abundance and biomass and overall foliage-gleaner abundance across all study sites if *Fringilla* are pooled with warblers (Fig. 3A).

HISTORICAL DYNAMICS OF BOREAL FOREST ASSEMBLAGES

A high abundance of *Fringilla* and a low abundance and diversity of warblers characterize Eu-

ropean boreal forests. To a large degree, this pattern can be explained by historical factors. The center of origin of *Phylloscopus*, the most forest-adapted of the Old World warblers, was probably in Asia. In European forests, *Phylloscopus* are represented by two clades that probably invaded in the Tertiary and have shown little ecological or morphological divergence (Richman 1996). It is likely that through selection or extinction, the high loss of continuous forest cover during the Pleistocene and since human habitation has resulted in a depauperate forest-adapted warbler fauna (Mönkkönen and Welsh 1994). For whatever reason, the presence of a depauperate assemblage of migratory forest insectivores may have set the stage for the more recently expanding populations of Chaffinch to find suitable resources in European forests.

POSSIBLE INTERACTIONS BETWEEN WARBLERS AND CHAFFINCHES

If we are correct in our hypothesis that the Chaffinch was a relatively recent invader of European forests, then it suggests an interesting question: How did European forests support such a large increase in the density of foliage-gleaning birds? Two possibilities are that (1) assemblages were not close to a food-based carrying capacity and that increases in winter resources supplied by agriculture is a sufficient explanation for the expansion of Chaffinches, and/or (2) at least some of the increase occurred at the expense of the breeding population densities of warblers and other foliage-gleaning birds.

Although competition is no longer generally accepted as important in structuring boreal forest communities (Mönkkönen et al. 1997), the possibility that competitive interactions may mediate the distribution and abundance of *Fringilla* and warblers should at least be considered. *Fringilla* tend to arrive earlier than warblers, being able to withstand periods of cold weather by shifting to foraging for seeds (Preobrazhenskaya, pers. comm.), and hence may be able to dominate sites through prior access. In addition to prior residency, *Fringilla* are considerably larger than warblers (20–22 g vs. 7–11 g), which also would contribute to their behavioral dominance. Hogstad (1975) presented evidence for the competitive interaction of another *Fringilla*, the Brambling, and Willow Warblers (*Phylloscopus trochilus*). Interestingly, he found that the Willow Warbler was dominant to the Brambling.

However, other studies have not found evidence of such an interaction (Angell-Jacobsen 1980, Fonstad 1984). Given the biogeographic patterns described here, a close examination of Chaffinch-warbler interactions seems warranted.

CONCLUSIONS

Abundance of foliage-gleaning birds is largely determined by abundance of migratory species of warblers or finches (predominantly *Fringilla*), and these groups increase in their importance with increasing abundance as well. Our results suggest that the warblers and finches are responding to the relative amplitude of summer productivity and resource availability. Tits are generally more diverse and abundant in Palearctic communities, suggesting a role for a historically longer association of this dominant group of resident insectivores in Old World forests. However, the variation in absolute abundance is small and contributes little to the decrease in proportion of migrant foliage-gleaning birds between sites. Furthermore, the abundance of tits was highest in Palearctic communities with only one common tit (upland taiga in Siberia), which suggests that an ecological explanation may be required to explain high tit abundance in Old World sites as well.

The northern boreal forests have developed recently (Haila and Järvinen 1990), and the constantly changing mixes of trees provide highly variable habitat through the Pleistocene. However, for the most part, recent phylogenetic analyses have shown considerable depth to the relationships in such groups as *Dendroica* (Bermingham et al. 1992), *Phylloscopus* and *Regulus* (Richman 1996), and *Parus* (Gill et al 1993). This suggests that current species or closely related ancestral species have interacted in temperate forest since at least the late Tertiary. In this context, the apparent recent invasion of temperate and boreal forests by the Chaffinch stands out. The factors that allowed a less specialized insectivorous bird to achieve numerical abundance are unclear. Perhaps the high productivity of European forests coupled with a depauperate fauna of more specialized insectivores caused by high levels of forest loss during the Pleistocene (Mönkkönen 1994, Mönkkönen and Welsh 1994) set the stage for this invasion.

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