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Divergence in foraging behavior of foliage-gleaning birds of Canadian and Russian boreal forests

Abstract We compared foraging behavior of foliage-gleaning birds of the boreal forest of two Palaearctic (central Siberia and European Russia) and two Nearctic (Mackenzie and Ontario, Canada) sites. Using discriminant function analysis on paired sites we were able to distinguish foliage-gleaning species from the Nearctic and Palaearctic with few misclassifications. The two variables that most consistently distinguished species of the two avifaunas were the percentage use of conifer foliage and the percentage use of all foliage. Nearctic foliage-gleaner assemblages had more species that foraged predominantly from coniferous foliage and displayed a greater tendency to forage from foliage, both coniferous and broad-leafed, rather than twigs, branches, or other substrates. The greater specialization on foliage and, in particular, conifer foliage by New World canopy foliage insectivores is consistent with previously proposed hypotheses regarding the role of Pleistocene vegetation history on ecological generalization of Eurasian species. Boreal forest, composed primarily of spruce and pine, was widespread in eastern North America, whereas pockets of forest were scattered in Eurasia (mostly the mountains of southern Europe and Asia). This may have affected the populations of birds directly or indirectly through reduction in the diversity and abundance of defoliating outbreak insects. Loss of habitat and resources may have selected against ecological specialization on these habitats and resources.

Introduction

Of all the major biomes, boreal forest (or taiga) – comprising 11% of the world's forest in a 10–23° circumpolar belt (Bonan and Shugart 1989) – arguably has the most similar vegetation between the continents. Yet, the Palaearctic and Nearctic boreal forests support bird assemblages with largely independent evolutionary histories. The disparity between the similarity of vegetation and the lack of evolutionary relationship of birds provides an opportunity to test whether ecologically similar faunas develop in response to similar habitats. Similarities in patterns in the face of the different evolutionary histories can result from differential filtering of species colonizing the habitat or actual convergent evolution (Schluter 1986), but in either case argue for the importance of similar extant ecological conditions in shaping bird assemblages.

Avian ecologists have used such intercontinental studies to search for evidence of trophic convergence, based primarily upon morphological similarity (Karr and James 1975; Ricklefs and Travis 1980; Blondel et al. 1984; Niemi 1985; Wiens 1991). Fewer studies have compared foraging behavior or diet based on data gathered in the field (Cody 1974; Remsen 1985; Terborgh and Robinson 1985; Holmes and Recher 1986; Wiens 1991). With respect to boreal forest assemblages, Haila and Järvinen (1990) provided an analysis of species richness, faunal similarities and ecological structure of boreal forest avifaunas. However, we know of no studies that have directly compared the foraging ecology of avian species of New World and Old World sites.

The strongest evidence for ecological convergence is the presence of species-to-species matching between the

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comparable assemblages (Cody 1974; Schluter 1986; Wiens 1991; Ricklefs and Miles 1994). Although comparable assemblages often have examples of ecologically similar species, overall pairing of species has rarely been demonstrated. Given this finding, an examination of the overall patterns of dissimilarity, as opposed to convergence, might be more instructive (Wiens 1989). For example, a basic question is whether the foraging characteristics of the species assemblages show an overall pattern of divergence. If systematic divergence is detected, then the species-matching hypothesis cannot be supported and the search must shift to the underlying explanations for the overall divergence. Therefore, it is the overall divergence hypothesis we address for boreal forest bird communities in this paper.

We compare patterns of foraging ecology of birds of Old World and New World boreal forest, because foraging ecology is relatively easily quantified and is generally assumed to play a central role in habitat use as well (MacArthur 1958). To provide further focus, we restricted our study to canopy foliage gleaners – the most species rich foraging guild of temperate zone forests. We analyze these data to address the following question: do foliage-gleaning species in Eurasian and North American boreal forests have emergent differences in their constituent foraging strategies?

Materials and methods

Study sites

Overview

Boreal forest shows similarity in both floristics and structure. The dominant trees are of the same genera worldwide (such as *Pinus*, *Picea*, *Abies*, *Larix*, *Betula*, and *Populus*) and the understory plant species often have circumpolar distribution. The basic structure of the forest is also simple and similar (Erskine 1977). Most boreal forests have a single-layered canopy with a subcanopy of saplings, shrub, and ground layers of herbs or a spongy bed of mosses and lichens. Boreal forests also have similar landscape patterns. Rather than vast tracts of unbroken coniferous forest, boreal forests are generally a complex mosaic of conifer and broad-leafed elements, sensitive to variation in soil moisture and disturbance regimes (Bonan and Shugart 1989). Coniferous or mixed forest dominates undisturbed upland sites. Broad-leafed vegetation grows on flood plains of rivers (alder, willow, and poplar) or in upland areas disturbed naturally by fire and anthropogenically by logging and fire.

In contrast to the plants that comprise the boreal flora, the birds that breed in these woods are often unrelated between the continents (Haila and Järvinen 1990; Helle and Mönkkönen 1990). Although certain groups have circumpolar species (wrens) or congeners (*Parus*, *Regulus*, *Sitta*, and *Carpodacus*), many taxa, particularly those composed of tropical migrants have no taxonomic counterparts, and boreal forest species are part of largely independent radiations of insectivorous birds. These include wood warblers, tanagers and tyrant flycatcher in the New World and sylvioid warblers and muscicapine thrushes and flycatchers in the Old World.

Regions

We conducted fieldwork in central Siberia in 1993–1995, northwestern Canada in 1994, European Russia in 1995, and in eastern

Canada 1996. We selected four study sites in two comparable pairs. The first comparative pair comprises "middle taiga" sites (Hämet-Ahti 1981) with highly continental climates: the southern Mackenzie District of the Northwest Territories (Mackenzie) and the middle section of the Yenissey River between the Tunguska and Angara Rivers (Siberia). Both areas were centered on a major river system (Yenissey and Mackenzie are the fourth- and seventh-longest rivers in the world, respectively) and had a similar range of latitudes (Siberia 60°10′–62°15′ N and Mackenzie 60°14′–61°52′ N). We conducted research at three localities each in Northwest Territories and central Siberia. The Siberian locations (Myrnoe, Vorogovo, and Fomka) were a maximum of 295 km apart and the maximum distance was 340 km for the Mackenzie locations (Fort Liard, Fort Simpson, and Fort Providence). We established the second pair of study areas in less continental regions characterized as "south taiga." Both the European Russian and eastern Canadian sites were far more disturbed and developed than the central Siberian and Mackenzie areas. Due to logistical constraints, the Russian field work was conducted primarily within 40 km of the Kostromskaya Taiga Field Station located in the clay belt along the Unja River (58°14′, 55°25′ N). The Ontario localities were primarily in the clay belt, as well, between 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′–49°30′ N. The lower latitudes of locations in Ontario reflect the overall southern distribution of the boreal forest in this region (Hämet-Ahti 1981).

Habitats sampled

We sampled four types of mature forest habitat in Siberia: riparian alder (*Alnaster fruticosus*) and willow (*Salix* spp.); mixed floodplain forest, with spruce-fir (*Picea obovata-Abies sibirica*) and birch (*Betula* spp.); upland birch stands with some aspen (*Populus tremula*); and mixed upland taiga with Siberian pine (*Pinus sibirica*), spruce, larch (*Larix sibirica*), fir, and birch. We surveyed five habitat types in Mackenzie: black spruce forest (*Picea mariana*); mixed floodplain forest, with white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*); riparian, with balsam poplar, alder (*Alnus tenuifolia*) and willow; trembling aspen stands (*Populus tremuloides*); black spruce (*P. mariana*); and jack pine (*Pinus banksiana*) forests. In the European Russian site we sampled mixed upland second-growth taiga, (approximately 60 years old) with spruce (*Picea abiea*), aspen, and linden (*Tillia cordata*); and birch (*Betula pubescens*); birch-aspen forest; European pine (*Pinus sylvestris*) forest; and riparian elm-alder (*Ulmus-Alnus incana*) woods. In Ontario we sampled aspen stands [aspen, birch (*B. papyrifera*) and balsam poplar]; mixed upland taiga [white spruce, balsam fir (*Abies balsamea*), jack pine, birch, aspen, and poplar]; black spruce; and jack pine stands. Characteristics of these habitats, based on estimates recorded at point count survey circles (Greenberg et al. 1999), are summarized in Table 1.

Methods

Target species

Target species included all foliage-gleaning birds above the herb and low-shrub level: species that feed predominantly on arthropods of foliage and twigs above the herb and low shrub level. However, we include in the analysis only species occurring with an abundance of > 0.02 individuals per point on fixed-diameter (50 m) point counts from the region (Greenberg et al. 1999). Because guild classification is based on foraging location and substrate, we have included birds that are as taxonomically diverse and morphologically distinct as finches, jays, warblers, tits, and flycatchers. We included some species that are often not considered in analyses of foliage-gleaning species, but based on our foraging observations feed substantially on arthropods of foliage and fine twigs. The non-traditional species include some that also forage on the ground

Table 1 Descriptive statistics for the habitats searched for foraging birds in this study. Based on vegetation estimates from 75–250 50-m-radius point count circles per habitat (Greenberg et al. 1999). Cover and height refer to canopy cover and height

Habitat	Height (m)	Percent cover	Percent conifer	Percent spruce[a]	Percent pine	Percent poplar	Percent birch	Percent alder	Percent willow	Percent shrub	Percent herbs	Percent moss
Europe												
Mixed upland	23	74	45	34	11	20	31	0	0	26	26	24
Birch	22	66	3	3	0	36	60	0	0	35	20	4
Pine	18	65	91	9	82	2	3	0	0	22	10	60
Riparian	19	56	15	10	14	3	4	25	45	30	20	0
Mean	20.5	65.3	38.5	13.5	26.8	15.3	24.5	6.3	11.3	28.3	19	22
Siberia												
Mixed upland	25	63	62	31	23	7	27	0	0	20	12	29
Mixed flood	23	67	53	48	4	9	19	11	0	9	27	10
Birch	22	78	10	8	1	23	64	1	0	0	16	6
Riparian	11	63	13	3	0	6	7	50	22	8	30	0
Mean	20.3	67.8	34.5	22.5	7.0	11.3	29.3	15.5	4.4	9.2	21.3	11.3
Ontario												
Mixed upland	26	61	57	45	13	27	15	0	0	30	28	48
Aspen	31	64	9	8	0	86	3	0	0	44	28	9
Black spruce	17	45	94	92	2	4	2	0	0	36	14	87
Jack pine	21	56	99	2	96	1	0	0	0	52	15	80
Mean	23.8	56.5	64.8	36.8	27.8	29.5	4.0	0	0	43.0	21.3	56.0
Mackenzie												
Mixed	24	56	66	66	0	21	10	1	0	42	26	53
Aspen	24	70	10	7	2	80	8	0	0	70	20	2
Black spruce	12	43	95	88	0	0	3	0	3	47	10	88
Riparian	20	73	13	11	0	50	0	21	13	48	6	1
Mean	20.0	60.5	46.0	43.0	0.4	37.8	5.3	5.5	4.0	51.8	15.5	36.0

[a] Spruce includes both spruce and fir

(Eurasian robin, dark-eyed junco, chipping sparrow, and yellow-breasted bunting; see Appendix 1 for Latin names). Our observations indicate that these birds foraged predominantly above the ground during the period and in the habitats of our study. However, with ground-foraging birds it is often difficult to determine how much of their foraging time they spend on the ground, since there they are more difficult to observe. We will probably have to use more sophisticated technology to resolve this problem. We also include some cardueline finches (siskins and bullfinches), that are well known to feed on seeds extensively, even when rearing young (Newton 1972). In the forest habitats we studied, siskins and bullfinches forage commonly for foliage arthropods during the height of the breeding season. We considered flycatchers and other sit-and-wait predators that use long attack distances provided that a majority of the foraging attacks were directed towards prey that were resting or flushed from foliage or fine twigs (in this case, species for example in the genera *Contopus* and *Muscicapa* were excluded because our data indicated that most prey were flying arthropods).

Foraging observations

We made foraging observations 1 June–20 July, the peak breeding season in all study areas. We justify the restriction to a narrow season by noting that the nesting season is usually a period of relative stability in resource use and that a number of species show restricted forest habitat use. In addition, the nesting season is a period of relatively stable foraging behavior that is followed by a post-breeding period often characterized by a high degree of foraging plasticity.

To make regional comparisons, foraging observation were relatively broad brushed and the sampling consisted of gathering a small amount of data from a number of individuals spread out over different habitats. We walked different transects through the focal habitats (See Table 1) each day to ensure we observed different individuals. Because we attempted to maximize the sample size of all target species, we covered the different habitats more or less

equally. In addition, every effort was made to gather foraging data on every individual located – audibly or visually – to minimize the bias against birds that forage high in the trees or in dense foliage. During the breeding season there is often a bias towards gathering data on singing males. Males and females often forage at different heights and may even use different techniques or substrates (Morse 1980). Searching for birds by sight and by ear should minimize this. In fact, the overall mean percentage of singing males was 26% (2.9% SE) for North America and 36% (3.3% SE) for Europe with an overall range from 0 to 70% (these data were not consistently recorded for Siberia). We do not address this variation in our analysis but present the percentage of singing males for each species in Appendix 1.

We quantified foraging attack location and maneuvers, probably the most easily quantifiable aspects of foraging behavior, while ignoring interspecific variation in locomotory patterns associated with searching for prey. Clearly, the work of Robinson and Holmes (1982) and others shows that, although considering locomotion provides additional insight into interspecific differences in foraging behavior, locomotory patterns are well correlated with attack behavior and distance.

We recorded general location data for each individual for the first foraging maneuver. These data included an estimation of the height of the individual and the tree or shrub in which it was located. At the beginning of each season, all observers practised estimating foraging heights by calibrating estimates to those determined by range-finders, or to other known heights. We recorded the position of the bird in relation to the stem or trunk of the plant, classifying each sighting into inner, middle, and outer zone which are assigned the number 1–3 for the analysis. We estimated the foliage cover for a 1-m cube around each bird and assigned one of four classes: 1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%.

We used a modified version of the foraging classification system of Remsen and Robinson (1990). We preserved the most important aspect of this system which is the complete separation of foraging maneuver type and foraging substrate – the surface on which the prey item was located at the time a foraging attack is initiated (even

if a subsequently flushed prey is captured in the air). In the field, we recorded a number of different types of prey substrates (e.g., foliage type, foliage surface, twig, branch, air, curled leaf, dead curled leaf, infloresence, air), some of which were pooled for analysis.

Because foraging location and tree type generally do not change within short foraging bouts, the previously mentioned location variables were recorded once per individual. However, because foraging maneuver type changes frequently during short bouts, we recorded foraging attack behavior for up to five maneuvers per bird. We recorded the type of maneuver the bird used to capture prey in a manner consistent with Remsen and Robinson (1990). In addition, we made a further separation of foraging maneuvers into primary or secondary. A primary maneuver type is based on the body position and action of wings used to attempt to capture prey (e.g., down strike, upward strike, lunge, leap, stand, hang up, hang down). A secondary maneuver is added to the initial attack. For example, a strike maneuver is often followed by hovering in place or hanging on to the substrate or a flush pursuit, and standing is often accompanied by the bird stretching its legs and neck in a "reach". In all, we recorded 10,415 primary foraging maneuvers from 6227 individuals – 3401 maneuvers from 2774 individuals of 27 New World species and 7014 maneuvers from 3453 individuals of 31 Old World species.

Analysis

The analyses are based on mean values for foraging variables for each species. Based on the field observations, the following foraging variables were calculated for each species: percentage of foraging maneuvers directed towards foliage versus non-foliage substrates, the percentage of foliage-foraging maneuvers directed towards conifer needles versus leaves, the mean foraging zone (based on integer classes 1–3 corresponding to inner, middle, and outer), percentage of foraging maneuvers that were aerial, mean attack distance (cm) of all aerial maneuvers, mean foraging height (m), mean relative foraging height (bird height divided by tree height), percentage of foraging maneuvers with hovering as a secondary maneuver, percentage of foraging attacks with hanging as a primary or secondary maneuver, the percentage of foraging maneuvers with reaching as a secondary maneuver. We transformed variables for which the samples showed significant deviation from a normal distribution (Kolmogorov-Smirnof test; Statsoft 1995). We used arcsine, logarithmic, or square root transformation depending upon which gave the smallest d-value for the Kolmogorov-Smirnof test for departure from normality of the sample distribution. Arc-sine transformation was used for percentage conifer use, foliage use, relative height, and aerial attack frequency; log transformation was used for attack distance, hang and hover frequency; square root transformation was used for reach frequency.

Because species-typical foraging patterns arise from the combination of a variety of individual characteristics, such as foraging attack method and foraging site (Holmes et al. 1979), we relied largely upon multivariate analysis. Specifically, we employ forward stepwise discriminant function analysis (DFA, Statsoft 1995; F to include = 1.00) to distinguish foraging characteristics of Old World and New World species using a combination of a minimal number of variables for each of the paired habitat comparisons (i.e., middle taiga sites and south taiga sites). We examine the efficacy of the classification functions by examining the a posteriori classification table. In addition, we examine the phylogenetic pattern by plotting the group classifications on a phylogenetic tree derived from Sibley and Ahlquist (1990) using MacClade software (Maddison and Maddison 1992).

Results

Overall differences in breeding foraging variables

The DFA of foraging data from middle taiga sites (Appendix 1) produced a significant function (Wilks'

lamda = 0.18, $F_{8,23} = 13.3$, $P < 0.0001$) with the following variables included in the analysis: use of foliage (0.29 factor loading), use of coniferous foliage (0.24), cover (0.007), hover frequency (−0.06), attack frequency (0.05), reach frequency (0.18), hang frequency (0.006), and foraging height (0.06). Of these only percent conifer (0.24 factor loading), percent use of foliage (0.29), and percent of maneuvers using "reach" (0.18) had loadings greater than 0.1 and can be considered important in contributing to the discrimination. The DFA of south taiga sites also produced a significant function (Wilks' lamda = 0.51, $F_{4,39} = 9.42$, $P < 0.0001$) with the following variables: foliage frequency (−0.59) conifer frequency (−0.38), cover (0.15), and attack frequency (0.02) with only the first three variables having loadings with absolute values greater than 0.1. The a posteriori classification for the middle taiga sites was correct for 97% of the species, with only the coal tit incorrectly classified as a New World species. The classification for the south taiga sites was correct for 85% of the species: black-capped chickadee, philadelphia vireo, chestnut-sided warbler, and American redstart were misclassified as Old World species and the icterine warbler, wood warbler, and goldcrest were misclassified as New World species.

The Palaearctic and Nearctic assemblages differed consistently between both pairs of sites in percentage use of conifer versus broad-leafed vegetation and percentage use of foliage (Fig. 1). The average Canadian species foraged from conifer needles for about 50% of the maneuvers directed toward foliage (47.4% Ontario, 52.3% Mackenzie), whereas this value was 26% for the Russian species (28.4% Siberia, 24.7% Kostroma). The variation between sites was significant
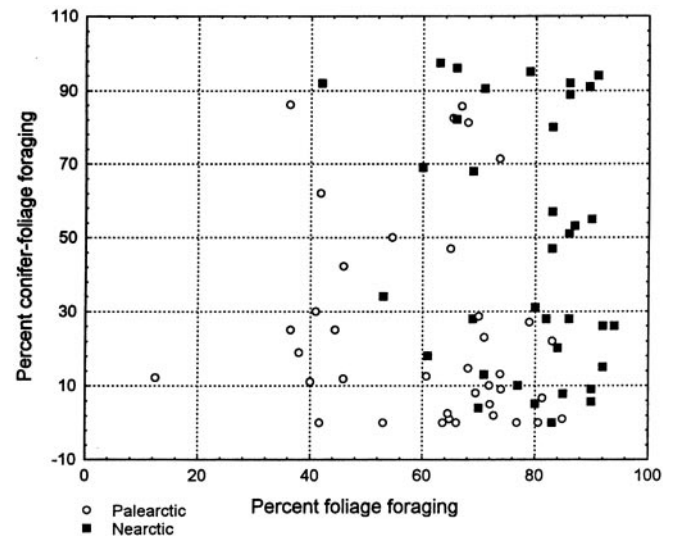
Fig. 1 Percentage of foraging maneuvers directed towards foliage (needles or leaves) versus percentage of foliage maneuvers directed towards conifer needles. Each point represents a species or population

($F_{3,72} = 4.12$, $P = 0.009$) and the pairwise comparisons between Siberia and Mackenzie and Kostroma and Ontario were significant using planned comparisons ($F_{1,72} = 9.2$, $P = 0.006$ and $F_{1,72} = 5.9$, $P = 0.017$, respectively). Ten of the 17 Mackenzie species (59%) foraged from conifer foliage for more than 50% of the observations, whereas only 3 of the 17 Siberian species (17%) did so. Similarly, 9 of the 21 Ontario species (43%) foraged from conifer foliage a majority of the time versus 4 of 23 (17%) for the European site. Canadian species foraged from foliage (as opposed to twigs, branches, and other substrates) on average 79% (75.5% Ontario, 81.4% Mackenzie) of the time versus 61% for Russian species (59.8% Kostroma, 62.1% Siberia). The overall variation between sites was significant ($F_{3,72} = 8.3$, $P = 0.0005$) as was the difference between paired sites ($F_{1,72} = 13.03$. $P = 0.005$, and $F_{1,72} = 13.1$, $P = 0.005$ for southern and middle taiga sites, respectively).

Selective use of conifer foliage

Because use of conifer foliage is one of the consistent variables distinguishing the species assemblages in sites on the two continents, we conducted one additional analysis. We examined the degree to which foliage gleaners selected either broad-leaved or coniferous vegetation, as they could be selecting this foliage rather than responding passively to differences in relative availability. We calculated the difference between percentage conifer-foliage foraging versus the mean estimated percentage conifer foliage within 25 m of the focal bird (these data were not gathered for the Siberian samples). Plotting this percentage deviation against the percentage conifer-foliage foraging (Fig. 2) revealed a strong relationship between the two variables ($r^2 = 0.69$). This indicates that species that have a high proportional use of conifer foliage also use this foliage out of proportion to its estimated relative abundance (and the same applies to broad-leafed foliage).

Phylogenetic pattern

We have plotted the classification New World type and Old World foraging type onto phylogenetic trees (Fig. 3) based on the MacClade analytical program (Maddison and Maddison 1992) using the phylogenetic inference of Sibley and Ahlquist (1990). We use the classification of the DFA even where this resulted in a misclassification of the actual continent of origin. Inspection of the tree reveals that foraging type is not restricted to a single clade in each continent: the New World type occurs predominantly in the distally located Emberizinae and the Old World type occurs in the Muscicapidae, Sylviodae and basal groups of the Fringillidae. However, the New World type dominates in the basal Corvidae, Vireonidae, and Tyrannidae clades as well.
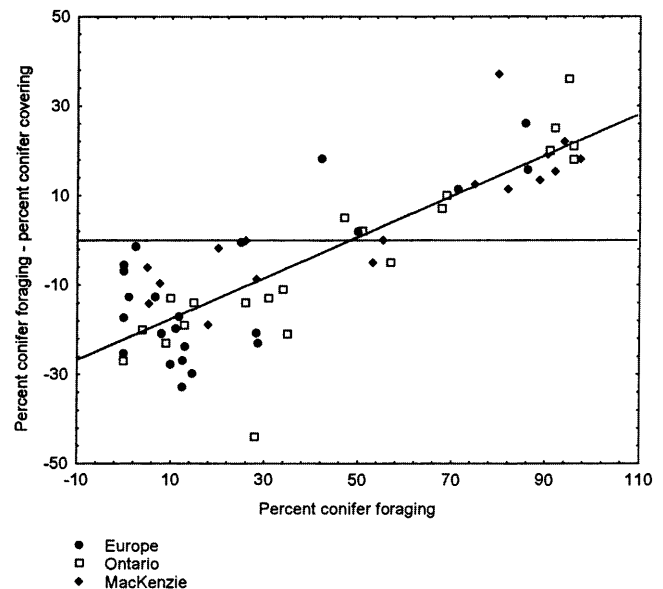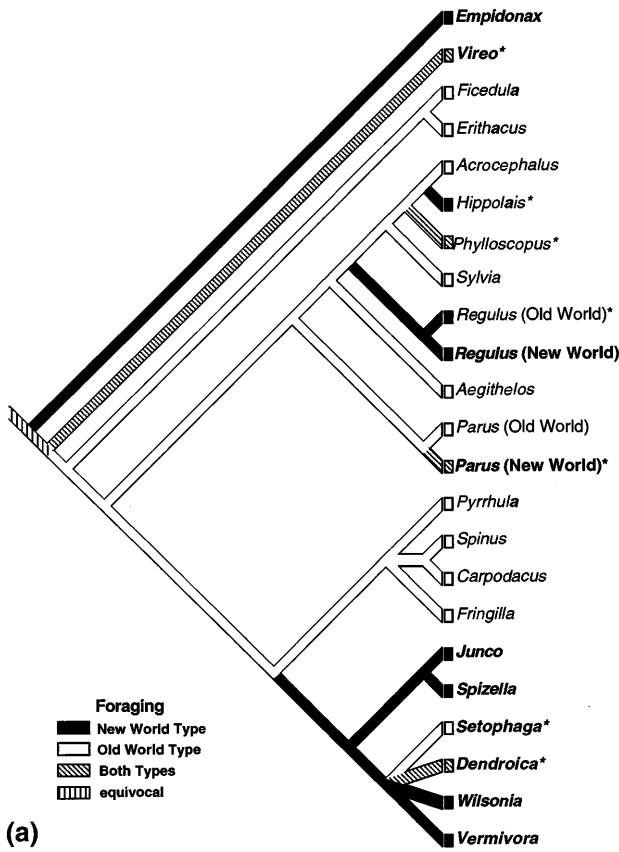

Fig. 2 The mean difference between the percentage of foliage foraging maneuvers directed towards conifer needles and the percentage conifer foliage within 25 m of focal bird versus the estimated percentage conifer canopy cover (conifer cover/conifer + broad-leafed cover). Each point represents a species from Europe, Ontario, or MacKenzie, sites where cover data were recorded. The horizontal line indicates no selection
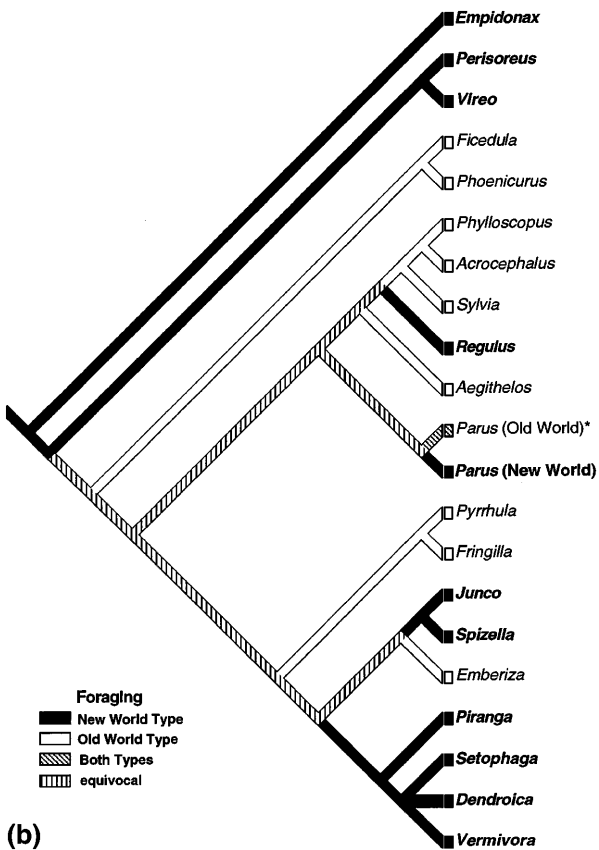
Discussion

Differences between Russian and Canadian boreal forest foliage gleaners

The data show overall divergence in foraging behavior of foliage-gleaning birds of the Palaearctic and Nearctic boreal forests. The strongest and most consistent discriminating variables were degree of specialization on foliage and the relative use of conifer foliage. The Palaearctic assemblage comprised more generalists species that commonly use substrates other than foliage, and within foliage insectivory, more species of Nearctic foliage gleaners concentrated on coniferous versus broad-leafed foliage.

Systematic differences in the foraging behavior of foliage-gleaning birds between the continents could result from historical and contemporary differences in boreal forest habitats between the continents. Alternatively, because the Palaearctic and Nearctic assemblages are dominated by species of different major phylogenetic groups, there may be explanations associated with unknown phylogenetic constraints. We reject an overriding phylogenetic-constraints argument for two reasons. The first is based on natural history considerations. We have examined foraging behavior in this study because the general lability of behaviors minimizes the fixed effect of design and phylogeny on morphological features (Terborgh and Robinson 1985). The characteristics most consistently distinguishing the two avifaunas – use of foliage and use of conifer foliage – are particularly

(a)

Foraging
- New World Type
- Old World Type
- Both Types
- equivocal

(b)

Foraging
- New World Type
- Old World Type
- Both Types
- equivocal

◄

Fig. 3 Distribution of the two foraging classes distinguished by a discriminant function analysis (DFA) contrasting species from comparable sites in Canada and Russia: Mackenzie versus Siberia (**A**) and Ontario versus Kostroma (**B**). Foraging type classification is indicated by shading. Palaearctic taxa (actual distribution) are indicated in *bold*. The MacClade program displays the inferred ancestral character based on consistency of the character state in the taxa of a particular clade. Where the character state is not consistent it is displayed as *equivocal*. Taxa containing species that were misclassified to continent in the DFA are indicated with an *asterisk*

flexible. The second is based on heuristic analysis of the phylogenetic distribution of New World and Old World foraging types. Although the New World foraging types, as determined by the DFA, are concentrated in the distally located Emberizinae clade, they involve species of groups (Corvidae, Tyrannidae) that are basal to the Passeriform phylogenetic tree. It is also noteworthy that two members of the Old world Sylviid warblers were classified in the New World foraging type, and three members of the New World vireos and wood warblers were classified in the Old World foraging type (Fig. 3). Because simple phylogenetic divergence cannot explain the differences we have documented, we will focus the rest of discussion on possible historical ecological factors that could explain the overall pattern of intercontinental differences.

Differences in present-day habitat

When specific plots are not matched between regions, as in this study, comparisons are confounded by differences in availability of particular habitat components. In particular, differences in availability of conifer foliage might help explain the difference in the number of species that forage predominantly in conifer foliage. It should be noted that the arguments for difference in availability do not easily explain the other feature that distinguishes Palaearctic and Nearctic foliage-gleaning birds documented here. For example, it would be difficult to argue that a systematic difference in the structure of the vegetation between the continents explains the greater number of species that are specialized on foliage versus twig and branch gleaning at the Nearctic sites.

However, the potential effect of the differential abundance of conifers in our Palaearctic and Nearctic sites is clearer. The vegetation data show that conifers, particularly the "dark conifer" spruce-fir element, were more prevalent in most habitats in the New World than Old World sites (Table 1). The standardized average proportion of conifer crown cover was 58% across our Nearctic versus 37% in the Palaearctic habitats. This difference is even greater (40 vs 22%) for spruce and firs. Therefore, the greater number of conifer-arthropod foraging species could simply reflect differences in relative tree abundance at the study sites rather than either an active selection of one foliage type over another or a general continental difference in preference.

Although the overall greater relative abundance of conifers at the specific New World sites used in this study may provide a partial explanation, the relationship between percent conifer foliage use and proportion of canopy cover (Fig. 2) suggests that a substantial degree of specialization results from true preference and active selection. Furthermore, consideration of what has been published of the natural history of boreal forest birds further suggests that the specialization on coniferous foliage by more Nearctic species is not restricted to the sites of this study and their particular habitat configuration. The close association between a number of New World warblers and dark coniferous vegetation is both well known and well studied (MacArthur 1958; Rabenold 1978; Morse 1980; Sabo and Holmes 1983) and to a large degree independent of the particular site of study. Parrish (1995) showed that the preference of populations of black-throated green warblers for coniferous or broad-leafed vegetation was largely intrinsic and unrelated to relative abundance of foliage types. To our knowledge, few Palaearctic foliage-gleaning birds have been reported to have a strong tendency to selectively forage in coniferous trees. For a broad overview of how ornithologists perceive the use of conifer versus broad-leafed foliage in the species considered in this study, we examined the breeding habitat classifications provided by Ehrlich et al. (1988, 1994). These accounts are based largely upon information summarized by the life history series of A.C. Bent and Cramp et al. (see Ehrlich et al. 1988, 1994 for full citations). For three species of Siberian birds (dusky, pallas', and yellow-browed warblers), we referred directly to Cramp and Brooks (1992). Based on these accounts, we find that species for which conifer-dominated habitats are listed as the first or primary habitat correspond closely to those species showing preference for conifer foliage in this study (Appendix 1) and that 58% of the Nearctic versus 16% of the Palaearctic species show primary association with coniferous vegetation. Note that these figures refer to habitat and not foraging preference; however, there appears to be a high correlation between these two (for example, Fig. 2).

The greater relative abundance of conifers, particularly spruce and fir, at our New World sites is probably not idiosyncratic, but represents a real continent-level difference. One factor that contributes to the greater abundance of the dark conifer element in the Nearctic communities is differences in the natural re-establishment of dark conifer species after disturbance. Both natural fire or logging (without reseeding and vegetation management – important in some regions of the boreal forest) favor the re-establishment of broad leafed stands (birch or aspen) in the boreal forest (Kozlenko 1987; Welsh 1987). Since conifer stands can take 100–500 years to become re-established after the initial disturbance, an increase in logging will shift the natural balance between coniferous and broad-leaved stand to primarily broad-leafed stands. Re-establishment of dark coniferous forests appears to take longer in the Palae-

arctic than the Nearctic boreal zone (Walter 1979; Kozlenko 1987; Scott 1995).

Large-scale conversion of the landscape from dark conifer to deciduous-pine has already occurred, for example, in the boreal zone of European Russia where areas of the once dominant spruce forest are restricted to small remnants (K. Preobzazhenskaya, personal communication) due to human activities primarily within the past 50–80 years. The lack of many species of foliage-gleaning species strongly associated with conifers in Palaearctic forests compared to the Nearctic forests suggests that the effects of the conversion of boreal forest on bird diversity may be more pronounced in the New World.

Divergent histories of boreal forests

Nevertheless, the degree of divergence found between the Palaearctic and Nearctic avifaunas appears to be too great to be easily explained by existing ecological conditions. First, the degree of specialization on foliage cannot be explained by differences in habitat availability. In addition, the strikingly low species richness of conifer-specialized foliage gleaners is difficult to understand given the abundance of coniferous vegetation in Palaearctic boreal communities. Therefore, we now look to historical differences to explain the divergence in foraging behavior.

The Pleistocene history of vegetation was quite different between Eurasia and North America (Frenzel 1968; Frenzel et al. 1992; Webb et al. 1993; Adams and Faure 1995) and this is believed to explain the greater degree of habitat specialization and regional diversity in the eastern Nearctic compared to the western Palaearctic avifaunas (Mönkkönen 1994; Blondel and Mourer-Chauvire 1998). In addition, major differences in the distribution of forest during the glacial maxima, particularly boreal coniferous forest, conform to the major distinctions we report here between the foliage-gleaning birds of the two continents. The greater diversity of canopy species, particularly those associated with dark coniferous tree species, in the Nearctic can be related to the large aerial extension of spruce-pine forest-steppe in eastern North America versus the small pockets of birch-pine forest which may have persisted near the Italian Alps, the Carpathian, and the Caucasus Mountains during the glacial maxima (Adams and Faure 1995). The distribution of boreal forest in Siberia is more poorly known, but at best, a small belt of boreal vegetation may have persisted in the extreme south, as well as the Far East.

Because of their great impact on forest vegetation, glaciations in Eurasia may have eliminated bird species most specialized on the forest canopy, particularly the canopy of dark coniferous (spruce and fir) vegetation, leaving more ecologically plastic species, an argument made by Mönkkönen (1994) more generally for habitat selection. Even in the absence of such differential

extinction, Pleistocene vegetation changes have created a selective environment that favors ecological plasticity in species. The hypothesis that loss and fragmentation of boreal forest during the Pleistocene has contributed to the lack of specialization of foliage-gleaning birds needs to be investigated for the remaining boreal forest regions, including the south Asian mountains and the Russian far east. With respect to southern Asia, it appears that there were no significant boreal forest refugia (Adams and Faure 1995), and it is therefore consistent with the hypothesis that Price (1991) found only two of nine species of sylviids in the mountains of Kashmir to show a preference for coniferous vegetation.

As an alternative to long-term climate-based changes in vegetation, the greater degree of more recent human impact on the forests of the western Palaearctic than the Nearctic has been posited as a possible reason for the greater apparent degree of ecological generalization in European forest birds (Scmiegelow et al. 1997). However, it should be noted that we found qualitatively similar differences between the birds of the relatively pristine central Siberian and northwestern Canadian study sites as we did with the more disturbed European and eastern Canadian sites. Furthermore, the northern Russian boreal forest, although highly altered, is not nearly so fragmented as the forests of western Europe. Finally, although more distant in time, the degree of habitat loss imposed upon the boreal forest by the advance of the glaciers must have far exceeded that caused by more recent human activities. Mönkkönen and Welsh (1994) argued that the present-day European avifauna is little affected by fragmentation because it consists of species that survived the vegetation changes of the Pleistocene.

Biogeography of the arthropod prey base

The pulse of food (arthropod) abundance has been related to the species richness of migratory foliage-gleaning birds in Nearctic boreal forests (Rabenold 1978). However, the high abundance of migratory canopy-foliage-gleaning birds in the European boreal site (Greenberg et al. 1999) does not support the idea that lower food abundance explains the lower richness of canopy foliage gleaners in the Palaearctic sites. However, it is possible that a relatively low abundance of arthropods in Old World conifers, if documented, might account for the relatively low number of conifer-foraging species. We know of no data to examine this possibility. The work of Bryant et al. (1989), mostly on deciduous boreal trees, at least suggests that general differences in anti-herbivore chemical defenses can occur within species or genera at the broad geographic level in the boreal forest, and this regional variation could underlie foraging differences in birds foraging in habitats with taxonomically similar floras. Helle and Mönkkönen (1990) hypothesized that the diversity of the prey base (arthropods) could have been more greatly reduced during Pleistocene glaciations in Eurasia because of their

great impact on forest vegetation and floras (Grubb 1987; Latham and Ricklefs 1993; but see Currie and Paquin 1987). However, as far as we know there is no direct support for this. Niemelä et al. (1994) found "remarkable similarity" in species richness of carabid beetles in mature forests of Finland and eastern Canada, and Coope (1987) suggested that Pleistocene events caused few global extinctions in arthropod assemblages. Even if an impact on arthropod diversity were established, its relationship to abundance is unclear.

Perhaps more important than a greater loss of arthropod species in Palaearctic forests would be the loss of keystone outbreak species that resulted from the Pleistocene forest loss. By keystone outbreak species, we refer to defoliating species that occur predictably, over large enough regions, and achieve high enough local densities to impact bird diversity at a regional or continental scale. In particular, the eastern spruce budworm (*Chirostoneura fumiferana*) appears to play a fundamental role in the diversity of bird species in the Nearctic boreal forest (MacArthur 1958; Morse 1980). For example, at least five of the Nearctic species (Tennessee, bay-breasted, Cape May, and blackburnian warblers and chipping sparrow; Erskine 1977) have been thought to have a strong association with budworm gradations, and populations of many other species (Erskine 1977) are found most abundantly in the presence of high populations of this outbreak lepidopteran. Spruce budworm gradations have a high local impact, often spread over huge areas of Nearctic boreal forest, and appear to have long, but relatively predictable cycles (Royama 1984). The intensity and scope of these cycles may explain the apparent support for increased bird diversity. Much of the eastern boreal forest experienced spruce budworm outbreaks in the late 1970s and early 1980s and budworm populations were peaking in the western boreal forest in the early 1990s. In fact, compilation of cumulative defoliation in this period depicts a wave moving through the boreal forest (Natural Resources Canada 1996; also references in Royama 1984). The global population of a number of species, as measured at netting stations or Breeding Bird Survey routes in a large area, is correlated with the occurrence of large-scale budworm outbreaks in eastern Canada (Hussell et al. 1992). In contrast, our review of the Russian and Fenno-Scandinavian literature and the field work conducted for over 20 years at the Yenissey site (O. Boursky, personal communication) showed that local outbreaks of Lepidoptera larvae have been documented, but they are local and do not change the species composition of the foliage-gleaning guild. The one exception is the Siberian silkworm (*Dendrolimus sibericus*) which can affect up to 10% of the dark coniferous forest of southern Siberia each year (Kondakov 1974); however, these caterpillars are well defended and consumed by few birds (Frolov 1938; Rozhkov and Reymers 1958). We are not familiar with any reports of bird populations on a continental scale correlated with the epidemic of a specific defoliating insect.

The lack of a similar Eurasian system seems to be another fundamental difference between Eurasian and Canadian coniferous forests that can be related to forest history. Consider that the spread of spruce budworms is facilitated by its occurrence in large topographically uniform and climatologically and ecologically similar areas (Royama 1984). With high-intensity herbivory at the very high population levels experienced during some outbreaks, local forest patches may be severely damaged and many trees killed outright. This should cause periodic extinction of local budworm populations (Royama 1984) except where adults can readily disperse to other favorable sites which would be more likely in larger areas of appropriate habitat. From a geographic perspective, dependence on large uniform tracts of habitat may explain the common observation that outbreak insects are thought to be more important and assert a greater impact on bird density and species richness in the northern boreal, as opposed to the western Cordilleran (Wiens 1975) and Appalachian (Rabenold 1978) forests in the New World. From an historical perspective, large-scale defoliating systems may also have been differentially impacted by the disparate degrees of forest loss and fragmentation in Nearctic and Palaearctic forests during Pleistocene glaciations. While dark coniferous vegetation is widespread in North American, European and southern Siberian boreal forest, tracts of such forest were only common in North America during the Pleistocene and were greatly restricted (to southern Siberia) in Eurasia, where extreme fragmentation would not have favored forest outbreak species. In summary, loss of keystone irruption species, exemplified presently in the Nearctic boreal forest by the spruce budworm, could be another result of the extreme isolation of remnant boreal forest in the Palaearctic during the ice age peaks.

Conclusions

We found the Nearctic foliage-gleaning bird assemblages to consist of more species that are specialized on the foliage substrate, and strongly associated with coniferous vegetation. These differences are consistent with a boreal forest biota that has been less severely eliminated, fragmented, and floristically modified during ongoing ice ages than its Palaearctic equivalent.

Appendix 1 Mean values for foraging variables for boreal forest birds[a]

Species	Site	n	CON (%)	FOL (%)	ATT (%)	ATDI (cm)	HA (%)	HO (%)	RE (%)	HT (%)	RHT (%)	ZON	COV	Male (%)
North America														
Yellow-bellied flycatcher (*Empidonax flaviventris*)	O	17, 26	28.0	69.0	96.2	120.0	0.0	20.0	0.0	9.1	65.0	2.19	1.38	59
Alder flycatcher (*Empidonax alnorum*)	M	17, 20	18.0	61.0	100.0	108.8	0.0	16.7	0.0	8.5	66.0	2.41	1.38	6
Least flycatcher (*Empidomax minimus*)	O	92, 104	10.0	77.0	99.0	92.1	1.9	24.0	0.0	10.2	64.0	1.99	1.47	30
	M	61, 74	7.8	85.0	99.0	98.1	0.0	16.2	0.0	12.3	60.4	2.14	1.45	15
Gray jay* (*Perisoreus canadensis*)	M	60, 75	97.4	63.0	1.3	20.0	6.4	0.0	25.3	6.9	51.0	2.26	2.01	0
Black-capped chickadee (*Parus atricapillus*)	O	106, 118	34.0	53.0	20.5	41.6	48.3	5.0	10.2	9.2	60.0	2.07	1.63	12
Boreal chickadee* (*Parus hudsonicus*)	O	23, 39	96.0	66.0	5.7	22.7	20.5	3.0	10.3	11.7	68.0	2.30	1.89	0
	M	80, 106	90.5	71.0	20.3	35.0	41.5	1.0	17.9	12.7	64.7	2.10	1.94	0
Golden-crowned kinglet* (*Regulus satrapa*)	O	49, 65	96.0	66.0	54.4	21.9	13.2	25.0	0.0	10.3	59.0	2.26	1.98	31
Ruby-crowned kinglet* (*Regulus calendula*)	O	41, 53	91.0	89.5	50.0	17.5	10.8	17.9	17.1	10.6	60.0	2.28	2.02	7
	M	81, 89	92.0	86.0	58.0	13.0	8.0	28.5	18.0	8.2	67.0	2.61	1.77	
Warbling vireo (*Vireo gilvus*)	M	59, 73	5.7	90.0	72.5	38.9	8.2	24.7	13.7	10.1	72.0	2.30	1.91	20
Philadelphia vireo (*Vireo philadelphicus*)	O	32, 35	0.0	83.0	68.6	49.0	8.5	19.0	11.4	13.7	81.0	2.60	2.06	44
Red-eyed vireo (*Vireo olivaceus*)	O	112, 121	9.0	90.0	70.7	64.7	14.0	14.1	14.0	10.6	65.0	2.23	1.90	39
	M	59, 83	26.0	92.0	73.3	67.5	2.4	21.7	7.3	10.5	71.5	2.22	1.98	22
Tennessee warbler* (*Vermivora peregrina*)	O	78, 80	31.0	80.0	12.4	33.0	7.5	24.0	41.3	9.6	72.0	2.49	2.01	18
	M	162, 210	55.4	90.0	11.3	39.8	14.7	8.1	35.2	8.3	70.0	2.56	1.90	13
Nashville warbler* (*Vermivora ruficapilla*)	O	108, 125	28.0	82.0	16.0	18.8	8.0	5.9	25.6	8.9	72.0	2.50	1.90	39

Appendix 1 (Contd.)

Species	Site	n	CON (%)	FOL (%)	ATT (%)	ATDI (cm)	HA (%)	HO (%)	RE (%)	HT (%)	RHT (%)	ZON	COV	Male (%)
Yellow warbler	M	49, 71	5.1	80.0	46.4	14.7	8.5	1.5	28.2	5.1	73.0	2.40	2.03	20
(*Dendroica petechia*)														
Chestnut-sided warbler	O	61, 70	4.0	70.0	47.1	16.6	2.8	15.8	17.1	8.4	69.0	2.14	1.88	52
(*Dendroica pensylvanica*)														
Magnolia warbler*	O	115, 139	47.0	83.0	49.5	24.9	1.4	13.0	15.1	7.4	60.0	2.32	1.94	55
(*Dendroica magnolia*)	M	95, 111	28.0	86.0	54.0	16.6	1.8	16.2	28.0	5.4	53.5	2.26	1.84	42
Cape May warbler*	O	41, 41	95.0	79.0	17.6	30.0	3.4	0.0	13.9	15.3	78.0	2.89	2.17	31
(*Dendroica tigrina*)														
Yellow-rumped warbler*	O	143, 167	69.0	60.0	30.8	38.3	4.2	14.4	15.0	9.4	63.0	2.19	1.71	
(*Dendroica coronata*)	M	212, 272	88.8	86.0	44.3	30.0	5.2	14.7	18.3	10.4	71.0	2.56	2.03	19
Black-throated green warbler*	O	34, 40	26.0	94.0	46.3	21.7	2.0	31.0	22.1	11.3	73.0	2.50	1.95	38
(*Dendroica virens*)														
Blackburnian warbler*	O	114, 147	57.0	83.0	40.1	32.4	4.8	22.0	18.4	13.6	72.0	2.54	2.22	43
(*Dendroica fusca*)														
Bay-breasted warbler*	O	98, 118	51.0	86.0	35.3	53.3	1.7	12.0	11.0	10.1	64.0	2.54	1.95	45
(*Dendroica castanea*)	M	15, 20	80.0	83.0	30.0	23.5	11.0	5.6	11.0	9.3	62.7	2.45	2.44	42
American redstart	O	103, 119	13.0	71.0	78.7	43.3	0.8	20.0	3.3	8.7	62.0	2.10	1.72	47
(*Setophaga ruticilla*)	M	106, 132	20.2	84.0	79.8	64.8	2.3	16.7	9.0	5.9	59.5	2.30	1.68	13
Canada warbler	O	20, 28	15.0	92.0	82.1	33.4	0.0	30.7	0.0	4.3	58.0	2.11	1.57	50
(*Wilsonia canadensis*)														
Western tanager*	M	58, 86	53.2	87.0	55.8	73.9	3.5	11.6	9.3	12.7	65.0	2.45	2.07	10
(*Piranga ludoviciana*)														
Chipping sparrow*	O	109, 116	68.0	69.0	26.1	20.2	1.4	3.5	12.1	7.2	54.0	2.46	1.89	29
(*Spizella pusilla*)	M	184, 211	94.0	91.0	11.6	19.2	1.0	3.3	32.0	10.2	69.3	2.61	2.01	4
Dark-eyed junco*	O	28, 28	92.0	42.0	29.8	22.7	0.0	10.0	10.7	6.2	45.0	2.14	1.50	36
(*Junco hyemalis*)	M	43, 47	82.1	66.0	26.1	35.0	6.4	0.0	8.5	3.8	47.0	2.50	1.95	2
Eurasia														
Eurasian robin	E	45, 68	11.1	40.0	81.8	94.1	0.0	13.2	9.9	5.1	50.1	2.00	1.48	24
(*Erithacus rubecula*)														
Eurasian redstart	S	34, 50	18.7	38.0	95.0	100.7	0.0	16.0	0.0	7.3	54.0	2.12	1.57	
(*Phoenicurus phoenicurus*)														
Blythe's reed warbler	E	108, 201	0.0	76.8	38.5	35.7	5.0	5.5	27.0	3.0	54.5	2.27	1.96	33
(*Acrocephalus dumetorum*)	S	57, 98	9.0	74.0	29.7	34.3	1.1	5.1	20.4	3.5	52.0	2.48	2.21	
Icterine warbler	E	56, 104	6.7	81.3	53.8	40.6	0.7	10.6	23.0	8.2	64.0	2.29	1.82	62
(*Hippolais icterina*)														
Garden warbler	E	145, 223	1.1	64.8	40.7	30.0	5.4	8.5	22.4	5.3	60.0	2.19	1.96	44
(*Sylvia borin*)														
Lesser whitethroat	S	131, 260	23.0	71.0	37.5	83.3	5.0	3.1	10.8	7.5	59.0	2.12	1.93	
(*Sylvia curruca*)														
Whitethroat	E	62, 108	2.5	64.5	36.5	28.7	2.8	8.3	34.3	3.7	59.2	2.20	2.08	47
(*Sylvia communis*)														
Blackcap	E	62, 112	0.0	80.7	48.2	63.5	5.4	4.5	16.1	7.1	62.2	2.31	1.96	55
(*Sylvia atricapilla*)														
Wood warbler	E	160, 304	14.7	68.2	83.3	48.6	1.6	22.4	6.6	7.8	59.3	2.26	1.41	62
(*Phylloscopus sibilitrax*)														
Willow warbler	E	269, 432	8.0	69.5	56.9	29.2	5.1	15.5	18.3	7.8	64.7	2.50	2.00	30
(*Phylloscopus trochilus*)														
Chiffchaff	E	70, 136	28.6	70.0	50.5	58.7	2.8	19.1	14.0	9.7	68.3	2.28	1.97	47
(*Phylloscopus collybita*)	S	81, 309	9.0	74.0	42.7	64.7	3.7	37.8	16.4	7.3	70.0	2.39	1.78	
Dusky warbler	S	44, 190	0.0	63.4	34.8	65.6	3.7	8.4	12.1	2.8	66.0	2.20	2.00	
(*Phylloscopus fuscatus*)														
Arctic warbler	S	108, 399	2.0	72.7	66.7	66.2	1.1	25.3	4.0	5.5	69.0	2.20	2.00	
(*Phylloscopus borealis*)														
Greenish warbler	E	176, 330	13.1	73.9	72.4	26.0	3.6	14.9	9.0	9.7	64.7	2.37	1.89	62
(*Phylloscopus trochiloides*)														
Yellow-browed warbler	S	281, 411	5.0	72.0	51.8	45.6	4.1	17.3	4.7	6.1	54.0	2.12	1.74	
(*Phylloscopus inornatus*)														
Goldcrest*	E	136, 242	85.7	66.9	53.7	15.5	17.4	27.3	14.5	11.3	66.2	2.44	1.93	38
(*Regulus regulus*)														
Pied flycatcher	E	79, 118	12.5	60.8	84.4	176.0	1.7	6.8	2.5	9.0	53.4	1.79	1.41	39
(*Ficedula hypoleuca*)														
Red-breasted flycatcher	E	44, 94	12.5	36.4	85.2	166.6	2.1	9.6	3.0	8.3	55.9	1.81	1.27	70
(*Ficedula parva*)	S	33, 82	25.0	12.5	95.6	111.4	2.4	2.4	1.2	4.9	43.0	2.26	1.18	
Willow tit	E	261, 481	30.0	41.8	30.1	23.4	46.6	3.1	10.0	9.9	61.2	2.10	1.66	
(*Parus montanus*)	S	59, 159	62.1	41.0	5.5	45.0	49.1	7.1	12.0	8.7	59.0	1.19	1.83	

Appendix 1 (Contd.)

Species	Site	n	CON (%)	FOL (%)	ATT (%)	ATDI (cm)	HA (%)	HO (%)	RE (%)	HT (%)	RHT (%)	ZON	COV	Male (%)
Pallas Warbler* (*Phylloscopus proregulus*)	S	35, 115	82.4	65.4	50.0	59.7	7.0	12.2	6.1	18.8	77.0	2.25	23.18	
Crested tit* (*Parus cristatus*)	E	80, 119	86.2	36.3	33.0	16.5	32.8	10.1	13.0	9.2	61.8	2.21	1.53	27
Blue tit (*Parus caerulus*)	E	27, 56	25.0	44.4	16.4	48.6	48.2	5.4	3.0	9.1	67.9	2.19	1.50	
Great tit (*Parus major*)	E	74, 111	11.8	46.0	34.3	37.2	34.2	9.9	5.4	7.2	60.1	2.15	1.79	
Coal tit*(*Parus ater*)	E	19, 27	71.4	73.7	48.0	30.0	29.6	18.5	0.0	13.6	72.6	2.38	2.19	
	S	26, 41	81.2	68.0	37.0	32.0	41.5	12.2	6.0	14.0	64.0	2.36	1.92	
Long-tailed tit (*Aegilithos caudatus*)	E	24, 32	0.0	41.7	25.0	9.3	65.6	3.2	3.0	7.8	60.4	2.30	1.60	22
	S	21, 57	0.0	53.0	15.0	28.0	71.9	3.2	1.7	5.9	69.0	2.50	1.60	
Chaffinch (*Fringilla coelebs*)	E	363, 572	10.0	71.9	36.9	58.0	2.6	15.6	10.0	9.5	64.3	2.29	1.90	30
	S	37, 71	27.0	79.0	47.3	78.9	2.8	19.7	7.0	9.0	67.0	2.37	2.06	
Brambling (*Fringilla montifringilla*)	S	139, 335	22.0	83.0	31.7	67.4	2.6	11.0	6.5	9.6	67.0	2.19	1.99	
Eurasian siskin* (*Carduelis spinus*)	E	98, 148	42.2	45.9	8.3	14.9	38.5	0.7	17.6	10.3	70.5	2.59	1.70	13
Bullfinch* (*Pyrrhula pyrrhula*)	E	44, 82	50.0	54.6	50.2	62.8	4.9	36.6	1.2	8.1	58.7	2.23	1.70	9
	S	44, 87	47.0	60.5	38.0	41.4	2.3	21.8	16.0	10.4	64.0	2.66	2.21	
Scarlet rosefinch (*Carpodacus erythrinus*)	E	75, 99	0.0	66.1	16.6	16.2	3.0	1.5	23.5	4.4	72.6	2.40	2.06	27
Yellow-breasted bunting (*Emberiza aureola*)	S	73, 151	1.0	84.9	18.1	57.4	0.0	4.6	9.9	4.6	75.0	2.44	2.06	

[a] Abbreviations for variables are as follows: site (*O* Ontario, *M* Mackenzie, *E* Europe, *S* Siberia), *n* sample size (individuals, foraging maneuvers), *CON* percent conifer, *FOL* percent foliage, *ATT* percent aerial attacks, *ATDI* mean distance of aerial attack, *HA* percent hanging, *HO* percent hovering, *RE* percent Reach, *HT* bird height, *RHT* bird height/tree height × 100, *ZON* mean horizontal zone, *COV* mean cover class, *Male* percent singing males. * Species that is reported to be primarily associated with coniferous vegetation by Ehrlich et al. (1988, 1994), *n* is individuals, maneuvers

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