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Breeding forest birds in the Valdai Uplands, north-west Russia: assemblage composition, interspecific associations and habitat amplitudes

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Seven study plots (16.9–21.0 ha) were established in representative forest habitats in the northern part of the Valdai Uplands. The breeding birds were censused by the mapping method during four to five years, from 1985 to 1989. Forty-six pigeon, woodpecker and passerine species were found to have at least half a territory in the total plots during the study period. *Anthus trivialis* was the only species that nested in sphagnum bog pine forest. In other plots, *Fringilla coelebs* was the most numerous species. The average total densities ranged from 33 territories/km^2 (bog pine forest) to 1027 territories/km^2 (mesic grey alder forest). The average species richness and average total density were strongly positively correlated. Grey alder forest specialists were most closely associated. Spruce forest species formed a very distinct group, but the association among them was fairly low. There was a positive correlation between habitat amplitude and total sample size across 23 common species for the period 1986–1989. *Turdus pilaris*, *T. iliacus*, *Hippolais icterina*, *Sylvia borin*, *S. atricapilla* and *Anthus trivialis* had much narrower habitat amplitudes than could be expected on the basis of their sample sizes, whereas *Turdus philomelos*, *Parus cristatus* and *P. montanus* had much broader amplitudes. The expected number of habitats in a standard sample of 14 territorial pairs was highest in *Turdus philomelos*, *Erithacus rubecula* and *Fringilla coelebs*. Species which could be expected to be found in many habitats tended to occupy them more evenly.

1. Introduction

Quantitative information on species abundances in different habitats within the same geographical region is necessary for solving many fascinating ecological problems. The habitat distribution of individual bird species and the structure of bird assemblages in European boreal forests have been studied for a fairly long period (e.g. Palmgren 1930, Merikallio 1946a,b, Vtorov & Drozdov 1960, Toropanova & Dubinin 1962, Haapanen 1965, 1966, Butev 1969, Järvinen & Väisänen 1976, 1978, 1980). However, as Haila et al. (1980:87) emphasized, "... few studies have as yet covered all the major habitats of a certain region". In this paper I analyse the composition of forest bird assemblages and habitat relations among the most common species in the northern part of Valdai Uplands. According to the phytogeographical zonation proposed by Ahti et al. (1968), the study area lies at the northern border of a south-boreal "island", within a slightly continental section of the hemiboreal zone. Thus, the data presented here are of biogeographical interest. The main purposes of this paper are

1) to present a description of breeding bird assemblages in some representative forest habitats of the region,
2) to measure the degree of habitat association of the common species, and
3) to estimate the habitat amplitudes of common species and to search for the relationship between habitat distribution and local abundance.

A detailed discussion of short-term stability patterns and an analysis of relationships between bird assemblage parameters and vegetation characteristics will be published elsewhere.

2. Study area

The study area lies between Moscow and Leningrad in the surroundings of the town Valdai, Novgorod Region; its approximate position is 57°57′–58°10′ N, 33°5′–33°30′ E, and it lies 180 to 240 m above sea level. Climatically, Valdai belongs to the boreal zone, having a relatively long cold season; the mean temperatures of the warmest months are above +10°C (type VIII(VI2) in Walter & Lieth 1964). The mean annual temperature is +3.2°C, the average for July being +16.9°C and that for January –9.6°C. The period with mean day temperatures above +10°C lasts on average for 128 days, usually from mid-May to mid-September. This is one of the most cloudy and humid localities of the Novgorod Region. Mean annual precipitation is 830 mm. A steady snow cover lasts on average for 140 days, usually from the last week of November to mid-April (Fedorova 1972, Korotkov 1986, 1991). In forests, however, the duration of the snow cover is usually much longer.

The predominant recent forms of relief are considered to have been created during the last glaciation (Vatkovskii et al. 1974, Glazovskaya 1980). The study area is a mosaic of moraine hills, eskers, kames, depressions and sandar. There are many lakes of different size, Lake Valdaiskoje being the largest (19.7 km^2). As a result of the irregular topography, many different plant communities occur close to each other. Forest covers more than 70 % of the area. Spruce, pine and birch forests predominate (in the Valdai Forest, 38, 29 and 22 %, respectively). The forests have two main components: 1) boreal forests (class Vaccinio-Piceetea according to the Braun-Blanquet syntaxonomy) with a relatively poor herb-dwarf shrub layer (*Vaccinium myrtillus* and *V. vitis-idaea* are abundant) and a high abundance of boreal green mosses (*Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum rugosum*, *D. scoparium*), and 2) rich mesic forests (Querco-Fagetea) with a high abundance of nemorose species, especially in the field layer. Oligotrophic bog sphagnum (Vaccinietea uliginosi) and rich swampy (Alnetea glutinosae) forests are also present (Korotkov 1986, 1991, Korotkov & Morozova 1986).

3. Study plots

Field studies were conducted in Valdai Forest and its surroundings from 1985 to 1989. The seven study plots (denoted below as A to G) represent practically the whole spectrum of the predominant forest types and the plant species richness of the forest associations in this locality. The distances between the plots ranged from 1.5 to 7 km. The plots were largely distinguished by their configurations. The plant species nomenclature follows Cherepanov (1981) (vascular plants), Savich-Lyubitskaya & Smirnova(1968) and Melnichuk (1970) (Bryophyta).

A: 60-year-old sphagnum pine forest (Fig. 1A); 16.9 ha in size. The pines are low: up to about 8 m high in the centre and up to about 14 m high in the peripheral parts of the bog (cover 20–60 %). The herb-dwarf shrub layer (cover 25–35 %) is dominated by *Ledum palustre*, *Chamaedaphne calyculata*, *Eriophorum vaginatum*, *Rubus chamaemorus*, *Vaccinium uliginosum*, and

Melampyrum pratense. In the moss layer (cover 95 %), the dominants are *Sphagnum magellanicum*, *S. angustifolium*, *S. fuscum*, *Aulacomnium palustre* and *Pleurozium schreberi* (the last-named especially on hummocks around trunks).

B: 130-year-old moderately barren pine forest (Fig. 1B, C); 21.0 ha. In the tree layer, two sublayers can be distinguished. The upper (cover 40–55 %, height 25–32 m) is composed of pine with an admixture of spruce. On average 4 (range 2–10) dead standing pines per 50×50 m^2 were present here before sanitation cutting (see below). The lower tree sublayer (cover 40–65 %, up to 22–25 m high) is composed of spruce. Dead standing spruces are fairly frequent. The shrub layer (defined as woody vegetation 0.5–2 m in height) (cover 0–15 %) consists mainly of *Picea* saplings. The herb-dwarf shrub layer (cover 1–15 %) is dominated by *Vaccinium myrtillus*, *V. vitis-idaea*, *Melampyrum pratense*, *Goodyera repens*, *Calluna vulgaris*, and *Convallaria majalis*. The moss-lichen layer (cover 70–90 %) is composed mostly of boreal green mosses. A clear gradient exists between the "shadiest" part of the plot (maximum height of the lower tree sublayer; shrub layer practically absent; herb layer cover ca. 1 %) (Fig. 1C) and the "lightest" part (minimum height of lower tree sublayer; many *Picea* saplings; herb layer cover 5–15 %; small patches of *Cladonia* spp. and *Cetraria islandica* in moss-lichen cover) (Fig. 1B).

C: 50-year-old cowberry pine forest with small stands of 40–100-year-old spruces (Fig. 1D); 17.5 ha. A small part of the plot (250 m long) borders a power line (Fig. 1E). The pines are 17–20 m (up to 25 m) and the spruces up to 25–28 m in height (cover 40–75 %). The shrub layer (cover 5–30 %) is composed of *Picea* saplings and *Juniperus communis* with some admixture of *Sorbus aucuparia*, *Alnus incana* and *Betula pubescens* saplings. The herb-dwarf shrub layer (cover 10–30 %) is dominated by *Vaccinium vitis-idaea*, *Melampyrum pratense*, *Convallaria majalis*, *Calluna vulgaris*, and *Calamagrostis arundinacea*. The moss-lichen layer (cover 65–85 %) as in plot B.

D: 50–60-year-old birch-pine and birch forest (Fig. 1F); 19.9 ha. The tree layer consists of two sublayers. The upper (cover 45–60 %, height 20–27 m) is composed of *Betula pubescens* and *Pinus* with an admixture of *Picea* and *Populus tremula*. There is one pine-dominated patch (ca. 1.8 ha in size) in the central part of the plot. The lower canopy (cover 15–40 %, up to 15–17 m in height) consists mainly of spruce and birch. The shrub layer (cover 5–20 %) is composed of *Picea* saplings with an admixture of *Frangula alnus*, *Salix cinerea* and *Sorbus aucuparia*. Due to the irregular topography, dry, wet and swampy patches alternate with each other. *Vaccinium myrtillus*, *V. vitis-idaea*, *Calamagrostis arundinacea* and *Melampyrum pratense* are the most abundant species in the herb-dwarf shrub layer of the dry and wet patches (cover 15–20 %). The boreal green mosses predominate on the dry patches, whereas *Sphagnum* spp., *Polytrichum commune* and *P. strictum* are especially abundant on the wet patches (total cover 25–90 %). Rich swampy patches (herb cover up to 80 %) bear chiefly *Athyrium filix-femina*, *Filipendula ulmaria*, *Crepis paludosa*, *Equisetum sylvaticum*, *Naumburgia thyrsiflora*, *Sphagnum squarrosum*, and *Climacium dendroides*. Besides the three main types, several intermediate plant subcommunities are present.

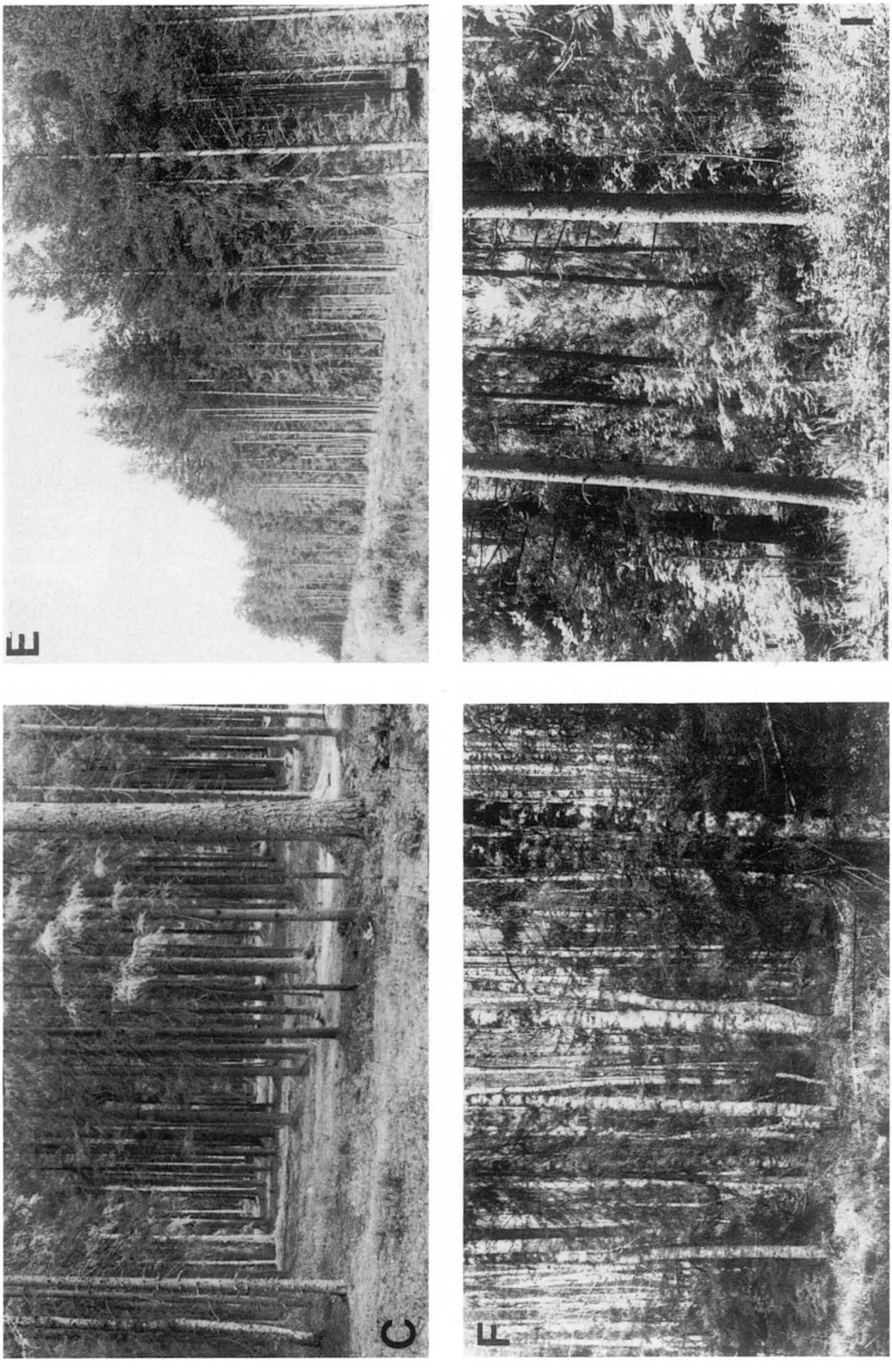
E: Spruce forest with a complete series of *Picea* generations up to about 140 years old (Fig. 1G); 19.5 ha. The plot is situated on the largest forested island (ca. 1.4 km^2 in size) of Lake Valdaiskoje. In the upper canopy (cover 25–40 %, height 26–35 m), pines are also frequent. On average, one (range 0–4) dead standing spruce per 50×50 m^2 was present before sanitation cutting. The lower canopy is formed by *Sorbus aucuparia* and young spruces. The shrub layer (cover up to 45 %) is also composed mainly of *Picea* and *Sorbus* saplings. The luxuriant herb-dwarf shrub layer (cover 35–75 %) is dominated by *Dryopteris assimilis*, *Oxalis acetosella*, *Maianthemum bifolium*, *Galeobdolon luteum*, *Vaccinium myrtillus*, *Stellaria nemorum*, *Rubus idaeus*, *Trientalis europaea*, and *Carex digitata*. In the moss layer (cover 5–65 %, on average 20–40 %), boreal green mosses, *Rhodobryum roseum* and *Brachythecium starkei*, are especially abundant.

F: 100-year-old luxuriant spruce forest (Fig. 1H, I); 19.6 ha. This plot consists of two parts (11.5 ha and 8.1 ha in size), hereafter named F1 and F2, respectively. In the upper canopy (cover 30–70%, height 27–37 m), *Pinus* and *Betula pubescens* occur sparsely. On average, 2–3 (range 0–7) dead standing spruces per 50×50 m^2 were found here before sanitation cutting. In F1 (Fig. 1I), the lower canopy (cover 5–35 %) is composed of *Picea*, *Sorbus aucuparia*, *Alnus incana*, *Padus avium*, *Salix caprea* and *Betula pubescens*. In F2 the lower canopy is practically absent. The shrub layer (cover 15–35 % in F1 and 5–20 % in F2) consists of *Sorbus aucuparia*, *Lonicera xylosteum*, *Picea* saplings and *Padus avium* with an admixture of *Salix caprea*, *Ribes spicatum*, *Sambucus racemosa*, *Alnus incana* saplings, and *Daphne mezereum*. In the luxuriant herb layer (cover 65–80 %), nemorose species are abundant, dominants being *Oxalis acetosella*, *Stellaria nemorum*, *Galeobdolon luteum*, *Equisetum pratense*, *Dryopteris assimilis*, *Anemone nemorosa*, *Calamagrostis arundinacea*, and *Maianthemum bifolium*. There are many sites where dead spruces have been blown down or removed during sanitation cutting. Such gaps (up to 0.4 ha in size) (Fig. 1H) are overgrown by *Rubus idaeus*, *Urtica dioica*, *Mercurialis perennis*, *Aconitum septentrionale*, and *Calamagrostis arundinacea*. The moss layer (cover 5–30 % in F1 and 15–40% in F2) is dominated by *Brachythecium starkei*, *Rhodobryum roseum*, *Cirriphyllum piliferum*, *Mnium affine*, *M. seligeri*, and *Plagiochila asplenioides*. Boreal green mosses are also present, but are not dominant. The number of uprooted trees is highest in this plot.

G: 20–50-year-old predominantly mesophytic grey alder forest with luxuriant herb layer (Fig. 1J, K); 18.4 ha. The plot stretches for ca. 1.5 km (maximum width 215 m) along the lake shore (south-north direction). In some parts of the plot the slope is as big as 30–35°. There are a few ravines with brooks which flow into the lake. On the opposite boundary of the plot the forest adjoins open or semi-open areas (meadows, arable land, young deciduous forests). In the tree layer (cover 40–75 %, height 15–19 m), *Sorbus aucuparia*, *Salix myrsinifolia*, *S. caprea* and *Padus avium* are frequent. The average age of *Alnus incana* is about 20 yrs, but it varies, reaching a maximum (40–50 yrs) near the shoreline. A few mature aspens, birches, spruces and pines protrude above the main canopy. The shrub layer (cover 20–35 %) consists of *Padus avium*, *Alnus incana* and *Sorbus aucuparia* saplings and *Ribes spicatum*. The herb layer (cover 45–80 %, up to 1.5 m in height) is dominated by *Stellaria nemorum*, *Angelica sylvestris*, *Rubus idaeus*, *Equisetum sylvaticum*, *E. pratense*, *Athyrium filix-femina*, *Urtica dioica*, *Anemone nemorosa*, *A. ranunculoides*, *Crepis paludosa*, *Filipendula ulmaria*, *Campanula latifolia*, and *Aegopodium podagraria*. The moss layer is diverse but poorly developed (cover up to 10–15 %, but less than 1 % in many sites); dominants are *Atrichum undulatum*, *Cirriphyllum piliferum*, *Brachythecium rutabulum*, *Mnium cuspidatum*, *Eurhynchium swartzii*, and *Climacium dendroides*.

Unfortunately, plots B, E and F were subjected to so-called sanitation cutting during the study period. As a result, in B dead pines were cut on more than half the area between the 1988 and 1989 breeding seasons. These trees were sawn into logs (0.5–1 m long), stacked and left at the spot for the whole of the 1989 breeding season. In E, many dead standing spruces and windfallen spruces were sawn up and taken away from the plot during winter 1987/88. In August 1987, some trees in plot F were felled by the gale; during autumn 1987 and winter 1987/88 windfallen trees and some dead standing spruces were sawn up, stacked and left lying on the spot. Some parts of plot F were also subjected to sanitation cutting during winter 1988/89 and spring 1989; most of these new stacks of logs were removed from the plot before 28 April 1989. Fortunately, in all the plots the structure of the lower canopy, shrub, field and moss layers remained practically unchanged, and the habitat "physiognomy" as a whole changed only slightly from a human point of view. It is obvious, however, that removal of dead trees from these plots may have been of great importance for the subsequent determination of the bird assemblage composition. A few cases of transient cattle driving through a small part (2.3 ha) of plot G also took place yearly from late May onwards. There were no major changes in the proportions or in the areas of the main habitat types in the study area within a radius of at least 10 km during the study period.

Fig. 1. Photographs of the plots censused in Valdai. — A. *Sphagnum* pine forest. Plot A (July 1982). — B. Moderately barren pine forest. Plot B. The "lightest" part of the plot (2 August 1990). — C. Moderately barren pine forest. Plot B. The "shadiest" part of the plot (2 August 1990). — D. Cowberry pine forest. Plot C (July 1982). — E. Cowberry pine forest. Plot C (2 August 1990). — F. Birch forest. Plot D. Dry patch (26 May 1982). — G. Island spruce forest. Plot E (5 August 1990). — H. An extensive gap in luxuriant spruce forest. Plot F1 (4 August 1990). — I. Luxuriant spruce forest. Plot F1 (4 August 1990). — J. Grey alder forest. Plot G (17 April 1990, but such an aspect is usually observed in late April to early May). — K. Grey alder forest. Plot G (1 August 1990).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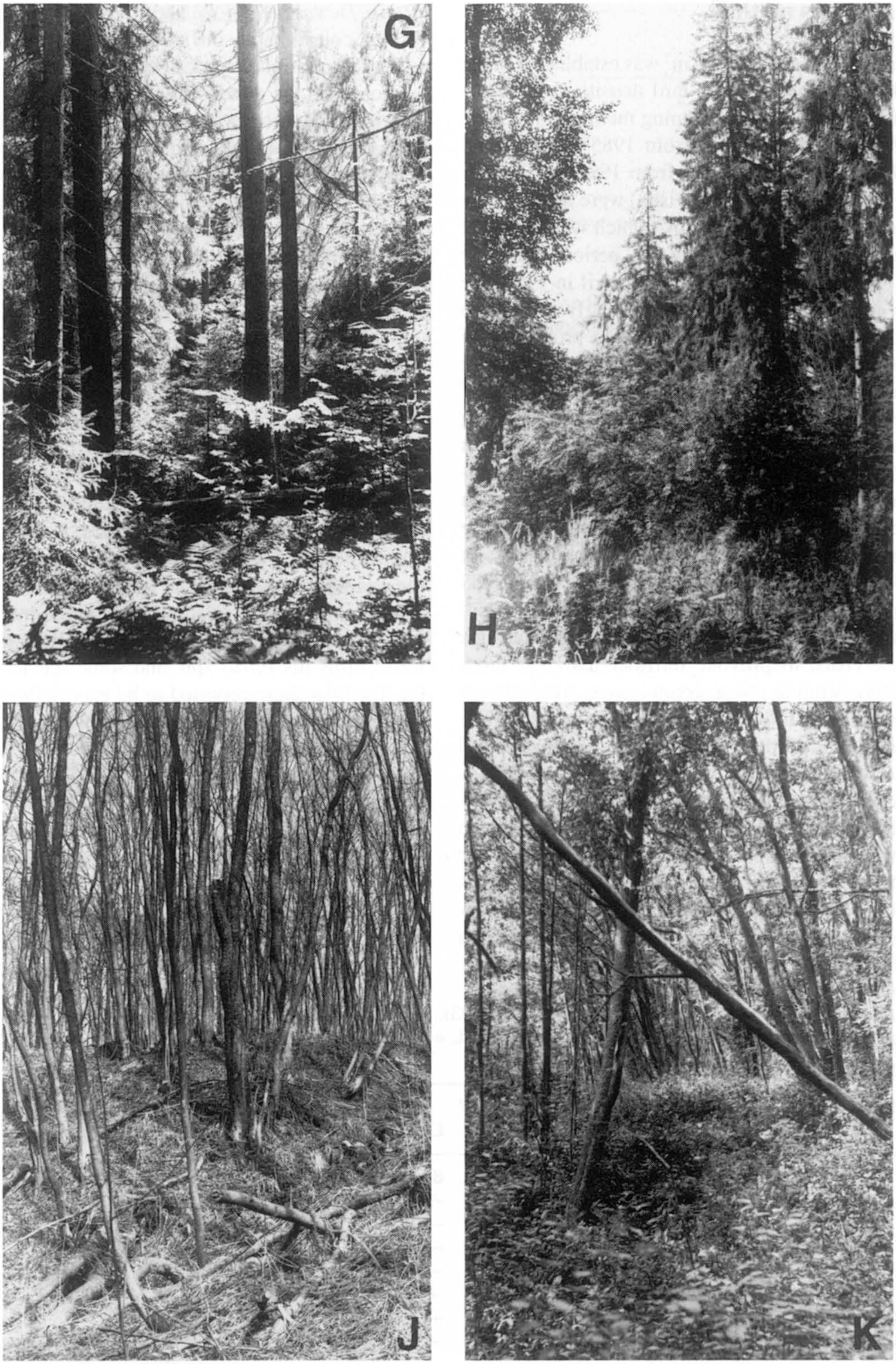
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4. Census method

A grid system of 50×50 m^2 was established in the plots and the breeding bird densities were estimated by a territory mapping method. Plots B, E and F1 were censused from 1985 to 1989, and plots A, C, D, F2 and G from 1986 to 1989. At least ten visits (up to 13 visits) were made yearly to each plot, except plot A (which was visited at least nine times), during the period from late April – early May (from mid-April in 1989 due to unusually mild winter and early spring) to early July (late June in 1985). The proportion of evening censuses was highest in 1986 (up to five out of twelve visits for F1 and up to four out of ten visits for F2 and B). Mid- and late-morning censuses were the only ones made in plot A in 1987–1989 (Table 1). The total time expenditures are given in Table 2. I paid special attention to obtaining simultaneous records of singing males, following the recommendations of Tomiałojć (1980). For *Erithacus rubecula* in 1987 and 1988, and *Luscinia luscinia* in 1987, a playback of conspecific songs was also used during a few visits, to provoke territory males to more active singing. Nest counts were used almost exclusively to census woodpeckers and *Turdus pilaris* and partially for *Turdus iliacus*. I also tried to find nests of any other species in passing. A very large proportion of *T. pilaris* nests was usually robbed during May in plot G. In 1986, due to the relatively late start of census work, the number of *T. pilaris* pairs attempting to breed within this plot was probably underestimated. Some species, especially *Prunella modularis*, *Muscicapa striata*, *Turdus philomelos* and *Pyrrhula pyrrhula*, caused considerable difficulties during census and interpretational work. The identification of territories on the species maps was based on the international recommendations (Pinowski & Williamson 1974), but account was also taken of the conclusions and recommendations of Nilsson (1977), Svensson (1979), Tomiałojć (1980) and Tomiałojć & Lontkowski (1989). Practically all the censuses (except two visits in 1986) and species map evaluation were performed by the author.

The mapping method is considered to be one of the most accurate. E.g., this method provides nearly 100 % accuracy in censusing some species of *Phylloscopus* warblers (Enemar et al. 1979, Tomiałojć 1980, Tiainen & Bastian 1983, Hogstad 1984). However, there are some serious problems as well (see Tomiałojć 1980, Ralph & Scott 1981, Verner 1985 for reviews). First of all, the census efficiency is strongly affected by the relationship between the species-specific acceptance level and visit efficiency (Svensson 1979, Kwak & Meijer 1985). Among European forest birds tits *Parus* spp. and some species of the Turdidae were reported to be especially difficult to census by the mapping method, partly due to their low visit efficiency (Nilsson 1977, Tomiałojć 1980, Kwak & Meijer 1985, Tomiałojć & Lontkowski 1989).

Subsequent analysis was restricted to pigeon, woodpecker and passerine species that had at least half a territory in one of the plots in one of the years. Most of the computing work was done by the program BIODIV (Baev & Penev 1990).

Table 1. The number of visits to the study plots (A–G). .5 indicates that approximately half the plot area was censused during one of the visits. — M = morning, L = mid- and late morning, A = noon and afternoon, E = evening visits.

Plot	1985			1986			1987				1988			1989		
	M	A	E	M	L	E	M	L	A	E	M	L	E	M	L	E
A	–	–	–	3	3	3	–	8	1	–	–	11	–	–	9	–
B	9.5	1	2	6	–	4	7	–	–	3	10	–	1	9	1	2
C	–	–	–	7	–	3	8	–	–	2	10	–	1	10	–	1
D	–	–	–	7	–	3	7	–	–	3	10	–	1	10	–	1
E	12	–	1	7	–	3	6	–	1	3	10	–	1	11	–	–
F1	9.5	–	2.5	7.5	–	5	7	–	–	3	10	–	2	11	–	–
F2	–	–	–	6	–	4	7	–	–	3	10	–	2	11	–	–
G	–	–	–	8	–	2	7	–	1	2	11	–	–	12	–	–

5. Results and discussion

5.1. Species composition

The results of the censuses are given in the Appendix (see also Table 2). Forty-six pigeon, woodpecker and passerine species were found having at least half a territory on the seven study plots during the study period. Twenty two (48 %) of them were detected in one plot only, 13 of these (28 %) being recorded as breeding only in plot G. *Anthus trivialis* was the only species nesting in plot A. In other plots (except plot G in 1989), the most numerous species was *Fringilla coelebs*.

Table 2. Total time expenditures (hours/ 10 ha) during visits, and the observed numbers of territorial pairs and species in 1985–1989.

Plot		1985	1986	1987	1988	1989
A:	Visits	–	12.6	11.8	12.8	10.2
	Pairs	–	6	6	4	6.5
	Species	–	1	1	1	1
B:	Visits	18.7	11.4	11.1	13.4	16.5
	Pairs	26	21	25.5	26	28.5
	Species	7	5	7	10	9
C:	Visits	–	15.1	15.4	19.8	22.9
	Pairs	–	25	22.5	24.5	33
	Species	–	8	7	11	9
D:	Visits	–	16.6	16.7	19.2	22.4
	Pairs	–	57.5	55	56	53
	Species	–	12	9	16	12
E:	Visits	26.9	18.5	18.6	20.1	23.4
	Pairs	94	102	114.5	100.5	116
	Species	16	15	18	21	19
F:	Visits	32.7[a]	24.8	23.9	27.1	28.6
	Pairs	36[a]	69.5	83.5	85	73.5
	Species	15[a]	14	17	19	17
G:	Visits	–	35.9	35.1	34.4	55.5
	Pairs	–	164.5	177	157.5	254.5
	Species	–	23	21	24	23

[a] For F1 only.

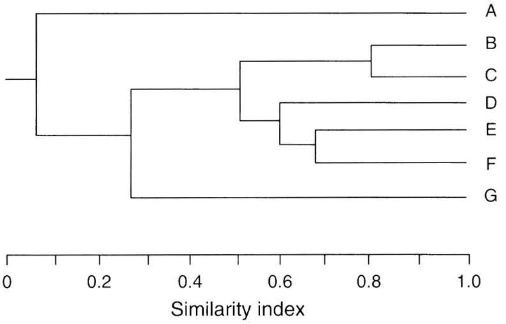

Fig. 2. A dendrogram illustrating the similarity of the bird assemblages studied.

The annual bird densities were averaged over the 1986–1989 period (Table 3), to minimize the possible "checkerboard" effect (see Wiens 1981) and to give a single comparable abundance estimate for each species in each plot. The assemblages studied were compared with the quantitative version of the Czekanowski-Sørensen similarity index (Huhta 1979: formula 8, Pesenko 1982: form "a"):

$$I_{cs} = \frac{2\sum_{i} \min(n_{ij}, n_{ik})}{\sum_{i} n_{ij} + \sum_{i} n_{ik}}.$$

Here n_{ij} and n_{ik} are the average densities of the *i*th species in the assemblages *j* and *k*, respectively. A dendrogram showing the relations between the assemblages is presented in Fig. 2. The average linkage method was used to construct this dendrogram, as explained by Cody (1974). The bird assemblages of dry pine (B, C) and rich spruce (E, F) forests constitute the two most compact groups. Note that bird assemblage of birch-pine forest (D) has more affinities to the latter.

Besides the species listed in Table 3, *Loxia curvirostra* and *Carduelis spinus* were regularly observed in coniferous plots (see Appendix), especially in E and F. Both are known to be nomadic species. The first could not be adequately censused because the greater part of the population normally breeds in late winter and early spring (von Haartman 1969, Malchevskii & Pukinskii 1983). The status of *C. spinus* individuals inhabiting the Baltic region and northwest Russia during April–June is poorly known (Paevskii 1970, Malchevskii & Pukinskii 1983). This species was unusually numerous in 1985, though its abundance gradually decreased from April to mid-June. Interestingly, in 1985 *C. spinus* was also very abundant during the period of spring migration through the Kurische Nehrung (Paevskii 1990) and during the breeding season in Finland (Haila et al. 1987, Väisänen et al. 1989). Some birds undoubtedly bred in Valdai this year

Table 3. Average densities (territories/km^2) and average frequencies (%, in parentheses) of pigeon, woodpecker and passerine species in the study plots for the period 1986–1989. A dash indicates that a species had less than half a territory within a plot during this period. See text for details and the Appendix for complete data.

Species	A	B	C	D	E	F	G
Columba palumbus	–	1.2 (1.0)	–	–	–	–	–
Dendrocopos major	–	–	–	2.5 (0.9)	5.1 (1.0)	–	2.7 (0.3)
D. minor	–	–	–	–	–	–	2.7 (0.2)
Picoides tridactylus	–	–	–	–	1.3 (0.2)	–	–
Anthus trivialis	33.3 (100.0)	–	–	12.5 (4.5)	3.2 (0.6)	19.8 (4.8)	19.1 (1.9)
Oriolus oriolus	–	–	–	–	–	–	5.5 (0.5)
Corvus cornix	–	–	–	–	12.8 (2.3)	–	–
Troglodytes troglodytes	–	–	–	1.3 (0.5)	1.9 (0.4)	17.9 (4.5)	–
Prunella modularis	–	–	6.5 (4.4)	5.0 (1.7)	35.3 (6.4)	37.1 (9.2)	5.4 (0.6)
Locustella fluviatilis	–	–	–	–	–	1.3 (0.4)	–
Acrocephalus dumetorum	–	–	–	–	–	–	6.8 (0.6)
A. palustris	–	–	–	–	–	–	0.7 (0.1)
Hippolais icterina	–	–	–	–	–	–	44.3 (4.2)
Sylvia atricapilla	–	–	–	–	9.6 (1.7)	21.1 (5.3)	123.3 (12.4)
S. borin	–	–	–	–	–	5.1 (1.3)	85.8 (8.6)
S. curruca	–	–	–	–	1.3 (0.2)	–	–
Phylloscopus trochilus	–	1.8 (1.4)	2.2 (1.3)	7.5 (2.8)	28.9 (5.2)	3.9 (0.9)	83.8 (8.3)
Ph. collybita	–	–	0.7 (0.5)	1.9 (0.7)	10.3 (1.9)	11.5 (3.0)	–
Ph. sibilatrix	–	10.1 (8.1)	15.8 (10.5)	70.2 (25.3)	66.0 (11.9)	28.1 (7.2)	19.1 (1.9)
Ph. trochiloides	–	–	–	–	1.3 (0.2)	1.3 (0.3)	–
Regulus regulus	–	13.1 (10.5)	19.4 (12.6)	6.3 (2.3)	57.1 (10.3)	55.0 (13.8)	–
Ficedula hypoleuca	–	–	–	3.1 (1.1)	12.8 (2.2)	3.8 (0.9)	96.0 (9.6)
F. parva	–	–	–	3.8 (1.3)	–	1.3 (0.3)	–
Muscicapa striata	–	1.2 (1.2)	–	–	3.2 (0.6)	19.2 (4.7)	15.7 (1.5)
Phoenicurus phoenicurus	–	1.2 (1.0)	1.4 (1.0)	–	2.6 (0.5)	1.3 (0.3)	–
Erithacus rubecula	–	20.8 (17.6)	22.9 (14.9)	43.9 (15.8)	54.5 (9.9)	21.7 (5.5)	45.6 (4.6)
Luscinia luscinia	–	–	–	–	–	–	19.8 (1.9)
Turdus pilaris	–	–	–	–	2.6 (0.4)	–	103.5 (8.9)
T. merula	–	–	–	–	–	–	2.7 (0.3)
T. iliacus	–	–	–	–	–	–	72.9 (7.2)
T. philomelos	–	6.0 (4.8)	9.3 (6.3)	12.5 (4.5)	25.0 (4.4)	11.5 (2.8)	20.5 (1.9)
T. viscivorus	–	2.4 (1.9)	–	–	–	–	–
Aegithalos caudatus	–	–	–	0.6 (0.2)	–	–	–
Parus palustris	–	–	–	–	–	–	19.1 (1.8)
P. montanus	–	1.2 (1.0)	8.6 (5.3)	6.3 (2.3)	17.3 (3.0)	0.7 (0.2)	6.8 (0.7)
P. cristatus	–	5.4 (4.2)	4.3 (2.6)	6.3 (2.3)	7.0 (1.2)	4.5 (1.1)	–
P. ater	–	–	–	–	1.3 (0.2)	–	–
P. caeruleus	–	–	–	–	–	–	2.7 (0.3)
P. major	–	–	–	–	1.3 (0.2)	–	18.4 (1.8)
Sitta europaea	–	–	–	–	–	–	5.4 (0.5)
Certhia familiaris	–	5.4 (4.3)	–	1.3 (0.5)	20.5 (3.7)	16.0 (4.0)	–
Fringilla coelebs	–	50.6 (43.1)	58.0 (39.6)	90.3 (32.4)	169.2 (30.6)	107.4 (27.2)	194.8 (19.2)
F. montifringilla	–	–	–	–	–	–	2.7 (0.2)
Carpodacus erythrinus	–	–	–	–	–	–	0.7 (0.1)
Pyrrhula pyrrhula	–	–	1.4 (1.0)	1.3 (0.4)	3.9 (0.7)	8.9 (2.4)	–
Emberiza rustica	–	–	–	1.3 (0.4)	–	–	–
Total	33.3	120.4	150.5	277.9	555.3	398.4	1026.5

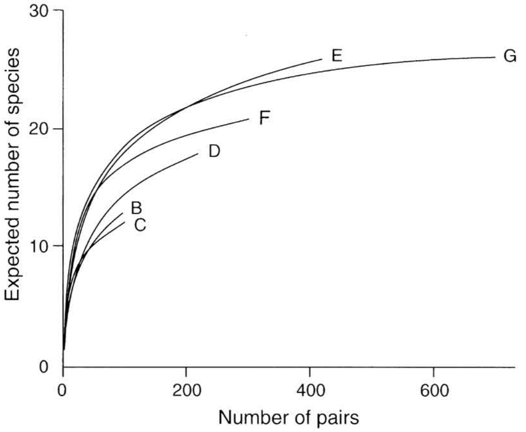

Fig. 3. The expected numbers of species in samples of different sizes for assemblages B–G. Data of four census years (1986–1989) pooled.

as fledgelings were observed. However, we obtained no conclusive breeding records of *C. spinus* or *L. curvirostra* from the plots in 1985, or in the other years studied.

5.2. Species richness and total density

The actual number of species in each plot is not the best measure of species richness in this study, since the plot areas are somewhat different. Therefore, the expected number of species was calculated by rarefaction (James & Rathbun 1981). The rarefaction curves are shown in Figs. 3 and 4. To give an averaged picture, the pooled data for 1986–1989 were used for their construction; after summation for individual species, half territory numbers were rounded up to the nearest integer. Habitat A, followed by habitats B and C, had the lowest number of species, while E and G had the highest numbers, both for the absolute number of territorial pairs (Fig. 3) and per unit area (Fig. 4). Grey alder forest (G) contained three times more species per 10 ha than dry pine forests (B, C).

The range of total densities was extremely wide, being 31 times as high in plot G as in plot A. The average species richness and average total density were positively correlated (Fig. 5). The low total densities in dry pine (plots B, C) and birch (D) forest communities represent the combined result of both a lower number of species and lower densities of some abundant species with broad habitat amplitudes (especially *Fringilla coelebs*). A strong positive correlation between bird species richness and total density was also found in south Swedish (Nilsson 1979) and Polish (Tomiałojć et al. 1984) forests but it is not a general rule. For example, no significant correlation was found in northeastern Finland between the expected number of species in a 15-pair sample and total density in the course of secondary succession ($r = 0.24$, $P > 0.5$, $n = 10$; based on data from Helle 1985a).

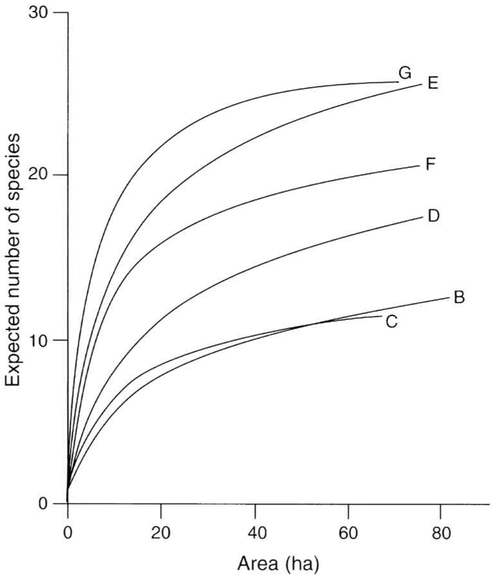

Fig. 4. The expected species/area relationships for assemblages B–G. Data of four census years (1986–1989) pooled. For each plot, the sample area is calculated as plot area multiplied by four.

The bird assemblages of dry pine forests in Valdai seem to be impoverished in comparison with those of some central European pine-dominated stands censused by the mapping method (cf. Glowacinski 1979, Cieślak 1982, 1984, Piotrowska & Wolk 1983, Mosimann et al. 1987). Such differences may be the result of different habitat physiognomy and floristics and of the character of the surroundings. The Valdai densities are close to those (128–140 pairs/km^2) found by Enemar (1964) in pine forest in Swedish Lapland. At the same time, the average total density in Valdai "mainland" spruce forest (plot

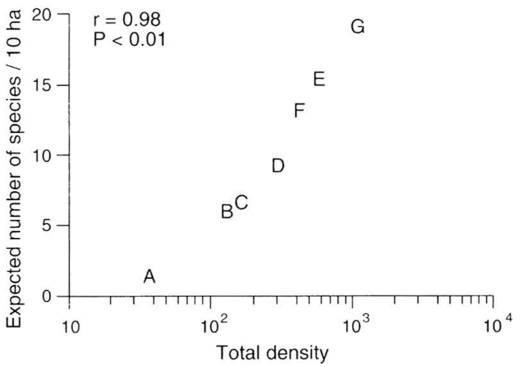

Fig. 5. The relationship between the average number of species expected per 10 ha and the average total density (territories/km^2) for the period 1986–1989 in the bird assemblages studied (A–G).

F) is within the range of typical values (250–450 territories/km^2) found in spruce forests in central Europe. The higher density in the island spruce plot (E) is also in accordance with the central European trend (see Oelke 1980). Finally, the total densities in my alder forest are on average one quarter of those reported for grey alder forest in central Norway (Saether 1980). The difference is mainly due to the extraordinarily high densities of *Turdus pilaris*, *Fringilla coelebs* and *Turdus iliacus* in the Norwegian plot. However, on the whole, Valdai grey alder forest is among the densely inhabited rich deciduous forests of northern Europe (e.g., see Enemar 1966).

5.3. Interspecific associations

The similarity of habitat selection of each pair of species was examined using the association index (Hurlbert 1978: eq. 11, see also Haila et al. 1980, Tiainen et al. 1983):

$$L = \frac{A}{XY} \sum_j \frac{x_j \cdot y_j}{a_j} .$$

Here x_j and y_j are the total numbers of territories of the two species in plot j over the period 1985–1989, X and Y are the respective total numbers of territories in all the plots, a_j is the area of plot j multiplied by four or five (by four plus area of F1 for plot F), depending on the number of study years, and A the total sample area (the sum of a_j values). The index value is 0 if the species have no plot in common, 1 if both species use each plot in proportion to its area and greater than 1 if the high and the low densities of the species tend to coincide.

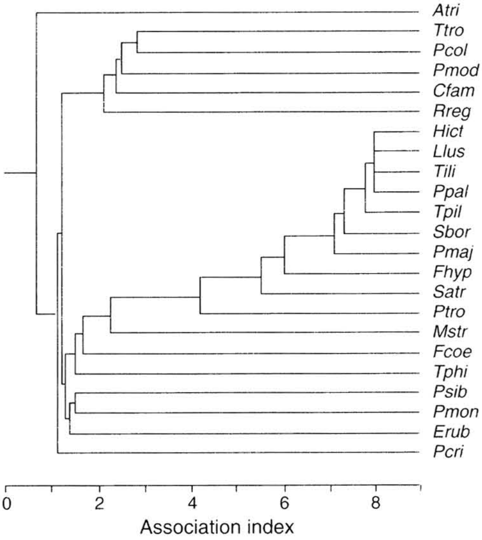

Fig. 6. Interspecific associations among the 23 common bird species. See Appendix for abbreviations of species names and text for details.

To demonstrate habitat relations among the most abundant species (at least 14 territories censused in all plots during 1985–1989), a dendrogram was constructed by the average linkage method (Fig. 6). Grey alder forest specialists form the cluster of the most closely associated species (central part of figure). There is a smooth transition between the "core" of this cluster (*Hippolais icterina*, *Luscinia luscinia*, *Turdus iliacus*, *Parus palustris*) and the most generalized species, which concentrate in the lower part of the dendrogram. Note that there are three pairs of congeners (*Turdus iliacus* – *T. pilaris*, *Parus palustris* – *P. major*, *Sylvia borin* – *S. atricapilla*) among the most closely associated common species. Spruce forest species form a very distinct group (the upper part of the dendrogram), but the association among them is fairly low. *Anthus trivialis* is negatively associated with all groups.

It is interesting to compare my results with those of Haila et al. (1980), since I followed their operational approach in this study. Their data came from the mainland of Åland archipelago, censused by the line transect method. Three species of Valdai spruce forests (*Phylloscopus collybita, Prunella modularis, Regulus regulus*) were members of the spruce forest group on Åland as well. *Troglodytes troglodytes* has been recorded exclusively in spruce forests, but it was not included in the analysis due to the small sample size. However, *Certhia familiaris* was interpreted to be a species of luxuriant deciduous and mixed forests on Åland. Three out of eight species from the Åland spruce forest group, namely *Phylloscopus sibilatrix, Erithacus rubecula* and *Turdus philomelos*, seem to be somewhat more ubiquitous in Valdai forests. Most of the grey alder forest specialists of Valdai (*Turdus iliacus, T. pilaris, Hippolais icterina, Sylvia borin, S. atricapilla, Parus major, Ficedula hypoleuca*) belong to the group of species of luxuriant deciduous and mixed forests on Åland. *Fringilla coelebs* and *Phylloscopus trochilus* were also the members of the latter group. Interestingly, the cluster of pine forest species (on Åland: *Anthus trivialis, Parus cristatus, P. montanus* and *P. ater*) is absent from the Valdai dendrogram. Helle (1985b) made a similar analysis in relation to forest succession in northeastern Finland. Five successional stages, from clear-felled areas to climax forests (in both dry and moist sites), were sampled by one-visit censuses. The picture was quite different from those revealed in southern Finland and Valdai. The species formed five distinct groups, mainly corresponding to different stages of forest succession. *Turdus iliacus, Sylvia borin, Parus major* and *Ficedula hypoleuca*, which were all found to be grey alder forest specialists in Valdai, belonged to four different groups. At the same time such species as *Sylvia borin, Erithacus rubecula, Phylloscopus collybita, Regulus regulus, Parus montanus* and *Fringilla coelebs* were all members of one distinct group.

5.4. Habitat amplitudes

The habitat amplitude of a species is the combined result of the number of habitats occupied and the evenness of numerical distribution across the habitats. Following Haila et al. (1980), I used index

$$A_h = \exp H', \text{ where } H' = \sum_j -p_j \ln p_j ,$$

to measure the habitat amplitudes of the species. Here p_j is the average frequency (see Table 3) of a species for the *j*th plot over the period 1986–1989. In this study, A_h may range from 1 to 7. A_h values were calculated for the 23 most common species (at least 14 territories censused in all the plots during 1986–1989) (Table 4).

Some studies on birds have revealed positive correlations between the number of habitats occupied or/and habitat amplitude and local abundance. Such a relationship has been found both across many species (McNaughton & Wolf 1970, Brown 1984, Helle 1985b, Maurer 1990) and for individual species across many years (O'Connor 1981, 1986). Two main causes may be involved (Helle 1985b). Firstly, this relationship may be a consequence of sample size (chance) only. Secondly, it can be produced by intraspecific competition in abundant species. Broader habitat amplitudes in abundant bird species may be a result of territorial behaviour forcing "surplus" individuals into suboptimal habitats (Brown 1969, Fretwell 1972, O'Connor 1981, 1986, 1987). It seems improbable, however, that the latter mechanism operates alone, since a positive relationship between habitat amplitude and abundance has been found in many other groups of organisms (McNaughton & Wolf 1970, Hanski 1982, Brown 1984).

The relationship between habitat amplitude and sample size over the period 1986–1989 is shown in Fig. 7. Nine species are of special interest. *Turdus pilaris, T. iliacus, Hippolais icterina, Sylvia borin, S. atricapilla* and *Anthus trivialis* had much narrower habitat amplitudes than could be expected on the basis of their sample sizes, whereas *Turdus philomelos, Parus cristatus* and *P. montanus* had much broader amplitudes. The rather narrow habitat amplitude in *Ficedula hypoleuca* may be attributed to the shortage of natural tree holes in most of the Valdai plots. Note, that all grey alder forest specialists are concentrated in the lower left half of Fig. 7, below the regression line. Again, I compared these results with those from Finland. There are many differences. For example, on Åland *Parus cristatus*, *P. montanus*, *Turdus philomelos*, *T. pilaris* and *T. iliacus* did not deviate substantially from the general trend. *Regulus regulus* and *Phylloscopus trochilus* had narrow amplitudes in relation to their total abundances, whereas *Certhia familiaris* and *Parus major* showed the opposite patterns (Haila et al. 1980). The same was observed in northeastern Finland for *Parus major* and *Phylloscopus trochilus* (Helle 1985b). In the Valdai scatter plot, the latter four are situated not far from the regression line in comparison with other common species. Unlike the patterns found in Valdai, *Fringilla coelebs* and *Turdus philomelos* in northeastern Finland had narrow habitat amplitudes in relation to their abundances. Such discrepancies are undoubtedly partially the result of different biotope recognition and choice by the observers and/or the preponderance of different habitat types in the data sets. The census method may be of some importance, since not only stationary birds are included in one-visit censuses. I believe, however, that, on the whole, the differences mentioned above reflect actually existing regional differences in species habitat distribution and amplitudes. For example, as noted by Helle (1985b), the habitat amplitude in *Fringilla coelebs* differs clearly between the inner and the northern parts of the range.

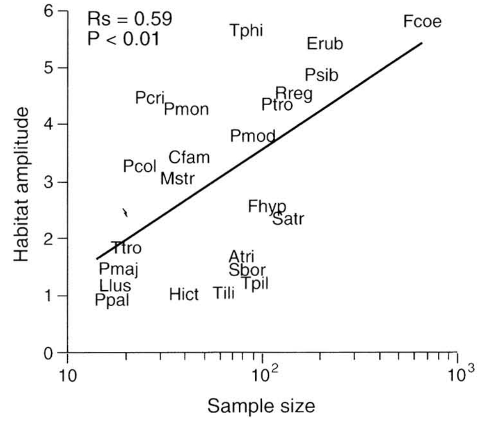

Fig. 7. The relationship between habitat amplitude and sample size (the number of territorial pairs) in the period 1986–1989 among 23 common species. See Appendix for species abbreviations.

Table 4. Habitat amplitude (A_h), the expected number ± *SD* of plots occupied in a random sample of 14 pairs (NPO), and the evenness of habitat distribution (*EHD*) of the common bird species during 1986–1989. The sample size (total number of territories) is given in parentheses after the species name.

Species	A_h	*NPO*	*EHD*
Anthus trivialis (64.5)	1.6	4.29 ± 0.57	0.07
Trogl. troglodytes (16.5)	1.8	2.75 ± 0.45	0.16
Prunella modularis (69)	3.8	3.90 ± 0.82	0.53
Hippolais icterina (32.5)	1.0	1.00 ± 0.00	
Sylvia atricapilla (114.5)	2.3	2.51 ± 0.55	0.43
S. borin (67)	1.5	1.62 ± 0.49	0.24
Phylloscopus trochilus (96)	4.5	3.53 ± 1.02	0.43
Ph. collybita (19)	3.2	3.68 ± 0.58	0.49
Ph.sibilatrix (163)	4.9	4.81 ± 0.87	0.50
Regulus regulus (117)	4.5	4.10 ± 0.73	0.74
Ficedula hypoleuca (86)	2.5	2.68 ± 0.77	0.22
Muscicapa striata (30)	3.0	3.33 ± 0.61	0.37
Erithacus rubecula (161.5)	5.4	5.32 ± 0.73	0.67
Luscinia luscinia (14.5)	1.0	1.00 ± 0.00	
Turdus pilaris (78)	1.2	1.33 ± 0.47	0.10
T. iliacus (53.5)	1.0	1.00 ± 0.00	
T. philomelos (65)	5.6	5.37 ± 0.70	0.74
Parus palustris (14)	1.0	1.00 ± 0.00	
P. montanus (31)	4.3	4.81 ± 0.76	0.45
P. cristatus (21.5)	4.4	4.94 ± 0.24	0.60
P. major (14.5)	1.4	1.93 ± 0.26	0.19
Certhia familiaris (34)	3.4	3.36 ± 0.54	0.71
Fringilla coelebs (514)	5.8	5.18 ± 0.77	0.81

Admittedly, pooling the data of several years may conceal possible year-to-year changes in habitat amplitude, e.g. caused by overall population fluctuations (see Svärdson 1949, Hildén 1965, Fretwell 1972, O'Connor 1981, 1986, 1987) or by changes in the habitat structure of study plots due to sanitation cuttings (see section 3). Unfortunately, for most Valdai species annual sample sizes were too small to calculate habitat amplitudes. Annual habitat amplitudes for the seven most numerous species (at least 14 territories censused in all the plots in each of the four years) are given in Table 5. The year-to-year variation of *Ah* reaches its maximal values in *Ficedula hypoleuca* (*CV* = 45 %) and *Phylloscopus trochilus* (32 %) being very low in *Fringilla coelebs* (2 %), *Erithacus rubecula* (4 %) and *Sylvia atricapilla* (5 %). However, a sampling size effect is of great importance in determining year-to-year variation even among these species.

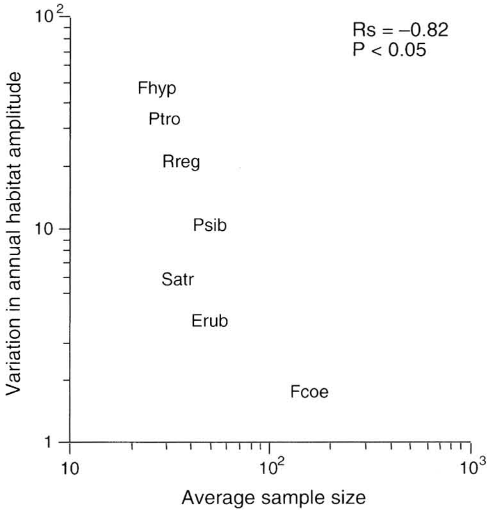

Fig. 8. The relationship between variation in annual habitat amplitude (%) and average sample size (the number of territorial pairs) in the period 1986–1989 among the seven most common species. See Appendix for species abbreviations.

There is a negative relationship between the average sample size and the variation in annual habitat amplitude (Spearman's rank correlation $R_s = -0.82$, $P < 0.05$, $n = 7$) (Fig. 8).

The first component of habitat amplitude — the number of habitats occupied — is also strongly affected by sample size ($R_s = 0.56$, $P < 0.01$, $n = 23$). In order to remove this influence, I used rarefaction to calculate the expected number of plots occupied in a random sample of 14 territorial pairs (see Helle 1985b). The highest values were found in *Turdus philomelos*, *Erithacus rubecula* and *Fringilla coelebs* (Table 4). It must be noted that the total sample size and the expected number of habitats in a random sample of 14 pairs are positively correlated too ($R_s = 0.44$, $P < 0.05$, $n = 23$). The result agrees with that of Helle (1985b) and suggests that the sample size effect alone is insufficient to explain the relationship between habitat amplitude and local abundance.

For the 19 common species inhabiting more than one plot, the evenness of frequency distribution across the plots (*EHD*) was also calculated (Table 4) using the calibrated version of Alatalo's index (Molinari 1989):

$$EHD = (\arcsin F_h / 90)\, F_h, \text{ when } F_h > \sqrt{\tfrac{1}{2}}$$

$$EHD = F_h^{\,3}, \text{ when } F_h \leq \sqrt{\tfrac{1}{2}},$$

where

$$F_h = \frac{B_h - 1}{A_h - 1}, \qquad B_h = \frac{1}{\sum\limits_j p_j^2}.$$

Interestingly, the expected number of plots occupied and the evenness of numerical distribution across the plots are positively correlated ($R_s = 0.69$, $P < 0.01$, $n = 19$; except for *Fringilla coelebs*, $R_s = 0.65$, $P < 0.01$, $n = 18$) (Fig. 9), i.e. the species found in many habitats tended to occupy them more evenly. This is also true if the absolute territory numbers are used instead of frequencies in the *EHD* calculations ($R_s = 0.85$, $P < 0.01$, $n = 19$, and $R_s = 0.84$, $P < 0.01$, $n = 18$, respectively).

Table 5. Annual habitat amplitudes A_h (sample sizes, in parentheses) for seven most numerous bird species in the years 1986–89.

Species	1986	1987	1988	1989
Sylvia atricapilla	2.3 (33.5)	2.4 (27.5)	2.2 (24)	2.5 (29.5)
Phylloscopus trochilus	2.8 (19)	2.9 (26.5)	4.9 (19)	5.1 (31.5)
P. sibilatrix	4.9 (45)	3.9 (44)	4.7 (36)	4.4 (38)
Regulus regulus	4.6 (22)	2.9 (21)	4.5 (33.5)	4.5 (40.5)
Ficedula hypoleuca	1.0 (17)	3.3 (24)	2.6 (21)	1.9 (24)
Erithacus rubecula	5.3 (40.5)	5.5 (41)	5.5 (40)	5.1 (40)
Fringilla coelebs	5.7 (136)	5.7 (137)	5.8 (117.5)	5.9 (123.5)

6. Concluding remarks

The essential features of the habitat are well known for some of the species studied, as a result of previous investigations in adjacent regions in Europe. *Regulus regulus* is a good example, since its dependence on spruce during the breeding season has long been well known (Palmgren 1932, Ptushenko & Inozemtsev 1968, von Haartman 1969, Malchevskii & Pukinskii 1983). In Valdai, this species was also especially numerous in two spruce plots (E, F) (Table 3). In B, the breeding territories were concentrated in the "shady" part of the plot, where mature and medium-sized spruces were especially abundant. In C and D, the *R. regulus* males established their territories exclusively in patches with a high abundance of mature spruces, and some of these patches were occupied from year to year. As regards some other species, however, it is very difficult to explain the existing patterns of habitat distribution with one or a few main factors. For example, *Phylloscopus sibilatrix* is known to prefer mature deciduous forests in many regions of Europe (Aschenbrenner 1966, Haapanen 1966, Fouarge 1968, Tiainen et al. 1983), although geographical differences in habitat preferences exist (see Svärdson 1949, von Haartman 1969). Also, this species demonstrates a tendency to aggregation during the breeding period (Svärdson 1949). In this study, the highest densities were found in birch-dominated plots, but almost the same densities were recorded in island spruce forest (except in 1985, when the overall species' density was unusually low) (Table 3, Appendix). Interestingly, in grey alder forest the *P. sibilatrix* males seemed to locate their singing territories in sites with single trees and small groups of birches and aspens. Some aspen- and birch-dominated patches (including those with young stands) in the neighbourhood of plot G have been occupied from year to year. What is common to all the habitats mentioned? And why were the densities in "mainland" spruce forest constantly lower than in the island one?

The habitat distribution of *Troglodytes troglodytes* is another mystery. In the "mainland" spruce plot, the males occupied territories up to about 6 ha in size. The territory numbers and positions remained very similar from year to year and the first broods were observed within most territories. At the same time, the few territories distinguished in different years in the island spruce plot were located in different places and no broods were found, although special attention was paid to this species. Females were never seen within the territories distinguished. Why is the density in island spruce forest low in comparison with the "mainland" value? It can hardly be the result of nest site shortage (see Armstrong 1956, Wesolowski 1983), since uprooted spruces are available in both plots. The abundance of spruce bushes, which were also found to be very important nest sites in the neighbouring Leningrad Region (Malchevskii & Pukinskii 1983), is much higher in island forest.

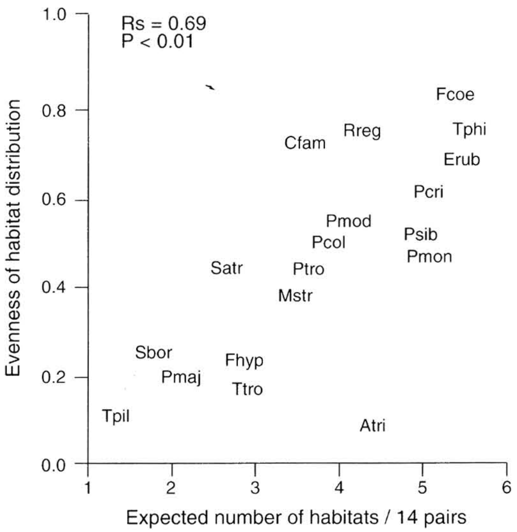

Fig. 9. The relationship between the expected number of habitats in a standard sample of 14 pairs and the evenness of habitat distribution in the period 1986–1989 among 23 common species. See Appendix for species abbreviations.

It is necessary to remember that birds of many species spend a considerable amount of time outside their singing territories (Lack 1954, Hinde 1956, Ferry et al. 1981, Møller 1987, Hanski & Haila 1988). Food collecting and extra-pair copulations are the possible main functions of such behaviour. Thus, besides the breeding habitat suitability *per se*, the probability of finding food, nest-material or a partner for extra-pair copulation in adjacent areas may be an important component of the habitat quality *sensu lato* (see also Haila 1988). Finally, a serious conceptual difficulty is encountered in attempts to explain the observed patterns of habitat distribution. As van Horne (1983) stressed, density alone is an insufficient indicator of habitat quality. Data on nest productivity and offspring survival are needed to support the assumption about the positive correlation between the density of a species and habitat quality.

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References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5:169–211.

Armstrong, E. A. 1956: Territory in the wren Troglodytes troglodytes. — Ibis 98:430–437.

Aschenbrenner, L. 1966: Der Waldlaubsänger (Phylloscopus sibilatrix). — A. Ziemsen Verlag, Wittenberg Lutherstadt. 76 pp.

Baev, P. V. & Penev, L. D. 1990: BIODIV — a program for calculating of biological diversity parameters and cluster analysis. — Inst. Animal Evol. Morphol. Ecol. Moscow.

Brown, J. L. 1969: The buffer effect and productivity in tit populations. — Amer. Nat. 103:347–354.

Brown, J. H. 1984: On the relationship between abundance and distribution of species. — Amer. Nat. 124:255–279.

Butev, V. T. (Бутьев, В. Т.) 1969: [Structure of bird communities of the northern taiga in the European part of the USSR.] (In Russian) — In: [Ornithology in the USSR] 1:153–165. Ilim, Aschabad.

Cherepanov, S. K. (Черепанов, С. К.) 1981: [Vascular plants of the USSR.] (In Russian) — Nauka, Leningrad. 509 pp.

Cieślak, M. 1982: Zgrupowanie ptaków legowych rezerwatu Czapliniec, nadleśnictwo Radzyń Podlaski. (In Polish with English summary) — Notatki Ornithol. 23:65–69.

— 1984: Wyniki ilościowych badań ptaków legowych w nadleśnictwie Sobibór. (In Polish with English summary) — Notatki Ornithol. 25:25–30.

Cody, M. L. 1974: Competition and the structure of bird communities. — Princeton, N. J. 318 pp.

Enemar, A. 1964: Småfågelfaunans täthet och sammansättning i några skogsbiotoper längs övre Vindelälven år 1963. — Fauna och Flora 59:1–23.

— 1966: A ten-year study on the size and composition of a breeding passerine bird community. — Vår Fågelvärld, Suppl. 4:47–94.

Enemar, A., Klaesson, P. & Sjöstrand, B. 1979: Accuracy and efficiency of mapping territorial willow warblers Phylloscopus trochilus. — Oikos 33:176–181.

Ferry, C., Frochot, B. & Leruth, Y. 1981: Territory and home range of the blackcap (Sylvia atricapilla) and some other passerines, assessed and compared by mapping and capture-recapture. — Stud. Avian Biol. 6:119–120.

Fedorova, T. G. (Федорова, Т. Г.) 1972: [The climate of Valdai town.] (In Russian) — Gidrometeoizdat, Leningrad. 35 pp.

Fouarge, J. G. 1968: Le Pouillot siffleur Phylloscopus sibilatrix Bechstein. — Gerfaut 58:179–368.

Fretwell, S. D. 1972: Populations in a seasonal environment. — Princeton Univ. Press, Princeton, N. J. 217 pp.

Glazovskaya, M. A. (Глазовская, М. А.) (ed.) 1980: [Ecology and productivity of the forests of Nechernozemje.] (In Russian) — Izd. Moskovskogo Univ., Moscow. 142 pp.

Glowacinski, Z. 1979: Some ecological parameters of avian communities in the successional series of a cultivated pine forest. — Bull. Acad. Polonaise Sci., Ser. Sci. Biol., Cl. II 27:169–177.

Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — Ann. Zool. Fennici 2:153–196.

— 1966: Bird fauna of the Finnish forests in relation to forest succession. II. — Ann. Zool. Fennici 3:176–200.

von Haartman, L. 1969: The nesting habits of Finnish birds. I. Passeriformes. — Comment. Biol. Soc. Sci. Fennicae 32:1–187.

Haila, Y. 1988: Calculating and miscalculating density: the role of habitat geometry. — Ornis Scand. 19:88–92.

Haila, Y., Järvinen, O. & Väisänen, R. A. 1980: Habitat distribution and species associations of land bird populations on the Åland Islands, SW Finland. — Ann. Zool. Fennici 17:87–106.

Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga, southern Finland. — Ornis Fennica 64:90–106.

Hanski, I. 1982: Dynamics of regional distribution: the core and satellite species hypothesis. — Oikos 38:210–221.

Hanski, I. K. & Haila, Y. 1988: Singing territories and home ranges of breeding chaffinches: visual observation vs. radio-tracking. — Ornis Fennica 65:97–103.

Helle, P. 1985a: Effects of forest regeneration on the structure of bird communities in northern Finland. — Holarctic Ecol. 8:120–132.

— 1985b: Habitat selection of breeding birds in relation to forest succession in Northeastern Finland. — Ornis Fennica 62:113–123.

Hildén, O. 1965: Habitat selection in birds. A review. — Ann. Zool. Fennici 2:53–75.

Hinde, R. A. 1956: The biological significance of the territories of birds. — Ibis 98:340–369.

Hogstad, O. 1984: The reliability of the mapping and standard check methods in making censuses of willow warbler Phylloscopus trochilus populations during the breeding season. — Fauna Norvegica, Ser. C, Cinclus 7:1–6.

van Horne, B. 1983: Density as a misleading indicator of habitat quality. — J. Wildl. Managem. 47:893–901.

Hurlbert, S. H. 1978: The measurement of niche overlap and some relatives. — Ecology 59:67–77.

Huhta, V. 1979: Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after clear-cutting. — Oecologia (Berlin) 41:11–23.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98:785–800.

Järvinen, O. & Väisänen, R. A. 1976: Between-year component of diversity in communities of breeding land birds. — Oikos 27:34–39.

— 1978: Habitat distribution and conservation of land bird populations in northern Norway. — Holarctic Ecol. 1:351–361.

— 1980: Quantitative biogeography of Finnish land birds as compared with regionality in other taxa. — Ann. Zool. Fennici 17:67–85.

Korotkov, K. O. (Коротков, К. О.) 1986: [Syntaxonomical analysis of Valdai forests.] (In Russian) — Bashkirskij Univ., Ufa. Ph.D. thesis. 291 pp. + appendix 273 pp.

— 1991: [Phytosociology of Valdai forests.] (In Russian) — Nauka, Moscow.

Korotkov, K. O. & Morozova, O. V. (Коротков, К. О. & Морозова, О. В.) 1986: [Class Querco-Fagetea. Forests of the Valdai Forestry.] (In Russian) — In: Mirkin, B. M. (Миркин, Б. М.) (ed.), [Classification of vegetation of the USSR]: 121–133. Izd. Moskovskogo Univ., Moscow.

Kwak, R. & Meijer, R. 1985: Species-specific acceptance levels in the mapping method. — In: Taylor, K., Fuller, R. J. & Lack, P. C. (eds.), Bird census and atlas studies:73–81. BTO, Tring.

Lack, D. 1954: The natural regulation of animal numbers. — Clarendon Press, Oxford. 343 pp.

Malchevskii, A. S. & Pukinskii, Yu. B. (Мальчевский, А. С. & Пукинский, Ю. Б.) 1983: [The birds of the Leningrad Region and adjacent areas] 2. (In Russian) — Izd. Leningradskogo Univ., Leningrad. 504 pp.

Maurer, B. A. 1990: The relationship between distribution and abundance in a patchy environment. — Oikos 58:181–189.

McNaughton, S. J. & Wolf, L. L. 1970: Dominance and the niche in ecological systems. — Science 167:131–139.

Melnichuk, V. M. (Мельничук, В. М.) 1970: [A guide to the true mosses of the Middle and South of the European part of the USSR.] (In Russian) — Naukova Dumka, Kiev. 442 pp.

Merikallio, E. 1946a: Über regionale Verbeitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I. Allgemeiner Teil. — Ann. Zool. Soc. Vanamo 12(1):1–140.

— 1946b: Über regionale Verbeitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. II. Spezieller Teil. — Ann. Zool. Soc. Vanamo 12(2):1–120.

Molinari, J. 1989: A calibrated index for the measurement of evenness. — Oikos 56:319–326.

Møller, A. P. 1987: Intruders and defenders on avian breeding territories: the effect of sperm competition. — Oikos 48:47–54.

Mosimann, P., Naef-Daenzer, B. & Blattner, M. 1987: Die Zusammensetzung der Avifauna in typischen Waldgesellschaften der Schweiz. — Ornithol. Beob. 84:275–299.

Nilsson, S. G. 1977: Estimates of population density and changes for titmice, Nuthatch, and Treecreeper in southern Sweden — an evaluation of the territory mapping method. — Ornis Scand. 8:9–16.

— 1979: Density and species richness of some forest bird communities in South Sweden. — Oikos 33:392–401.

O'Connor, R. J. 1981: Habitat correlates of bird distribution in British census plots. — Stud. Avian Biol. 6:533–537.

— 1986: Dynamical aspects of avian habitat use. — In: Verner, J., Morrison, M. L. & Ralph, C. J. (eds.), Wildlife 2000. Modeling habitat relationships of terrestrial vertebrates: 235–240. Univ. Wisconsin Press, Madison.

— 1987: Organization of avian assemblages — the influence of intraspecific habitat dynamics. — In: Gee, J. H. R. & Giller, P. S. (eds.), Organization of communities. Past and present: 163–183. Blackwell, Oxford.

Oelke, H. 1980: The bird structure of the European spruce forest biome — as regarded from breeding bird censuses. — In: Oelke, H. (ed.), Bird census work and nature conservation: 201–209. Göttingen.

Palmgren, P. 1930: Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands. — Acta Zool. Fennica 7:1–218.

— 1932: Zur Biologie von Regulus r. regulus (L.) und Parus atricapillus borealis Selys. Eine vergleichend-ökologische Untersuchung. — Acta Zool. Fennica 14:1–113.

Paevskii, V. A. (Паевский, В. А.) 1970: Migrational peculiarities of the Siskin in Europe. (In Russian) — In:

Viksne, J., Vilks, E. K. & Mihelson, H. A. (eds.), Proc. Seventh Baltic Ornithol. Conf.: 69–75. Zinatne, Riga.

— 1990: Population dynamics of birds according to trapping data on the Courish Spit of the Baltic Sea during twenty seven years. (In Russian with English summary) — Zool. Zh. 69(2):80–93.

Pesenko, Yu. A. (Песенко, Ю. А.) 1982: [Principles and methods of quantitative analysis in faunistical investigations.] (In Russian) — Nauka, Moscow. 287 pp.

Pinowski, J. & Williamson, K. 1974: Introductory informations of the Fourth Meeting of the International Bird Census Committee. — Acta Ornithol. 14:152–164.

Piotrowska, M. & Wolk, K. 1983: Breeding avifauna in coniferous forests of the Bialowieza primaeval forest. — Acta Ornithol. 19:81–95.

Ptushenko, E. S. & Inozemtsev, A. A. (Птушенко, Е. С. & Иноземцев, А. А.) 1968: [Biology and economic significance of birds of the Moscow Region and adjacent areas.] (In Russian) — Izd. Moskovskogo Univ., Moscow. 461 pp.

Ralph, C. J. & Scott, J. M. (eds.) 1981: Estimating numbers of terrestrial birds. — Stud. Avian Biol. 6, Cooper Ornithol. Soc., Los Angeles. 630 pp.

Saether, B.-E. 1980: The composition of the bird community in a Grey Alder forest in Central Norway during a four-year period. — Fauna Norvegica, Ser. C, Cinclus 3:80–83.

Savich-Lyubitskaya, L. I. & Smirnova, Z. N. (Савич-Любицкая, Л. И. & Смирнова, З. Н.) 1968: [A guide to the sphagnous mosses of the USSR.] (In Russian) — Nauka, Leningrad. 112 pp.

Svärdson, G. 1949: Competition and habitat selection in birds. — Oikos 1:157–174.

Svensson, S. 1979: Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. — J. Appl. Ecol. 16:61–68.

Tiainen, J. & Bastian, H.-V. 1983: The accuracy and efficiency of territory mapping tested on willow warblers Phylloscopus trochilus and chiffchaffs Ph. collybita. — Ornis Fennica 60:112–116.

Tiainen, J., Vickholm, M., Pakkala, T., Piiroinen, J. & Virolainen, E. 1983: The habitat and spatial relations of breeding Phylloscopus warblers and the goldcrest Regulus regulus in southern Finland. — Ann. Zool. Fennici 20:1–12.

Tomiałojć, L. 1980: The combined version of the mapping method. — In: Oelke, H. (ed.), Bird census work and nature conservation: 92–106. Göttingen.

Tomiałojć, L. & Lontkowski, J. 1989: A technique for censusing territorial song thrushes Turdus philomelos. — Ann. Zool. Fennici 26:235–243.

Tomiałojć, L., Wesolowski, T. & Walankiewicz, W. 1984: Breeding bird communities of primaeval temperate forest (Bialowieza National Park, Poland). — Acta Ornithol. 20:241–310.

Toropanova, T. A. & Dubinin, N. P. (Торопанова, Т. А. & Дубинин, Н. П.) 1962: Birds of the forest zone. I. Birds of the pine, spruce and broad-leaved woods in the subzone of merged woods and in the southern taiga area. (In Russian with English summary) — Bull. Moskovskogo Obshch. Isp. Prir. 67(5):50–60.

Väisänen, R. A., Hildén, O. & Pulliainen, E. 1989: Suomen pesivä maalinnusto 1979–88 piste- ja linjalaskentojen valossa. — Lintumies 24:60–67.

Vatkovskii, O. S., Golovenko, S. V., Grishina, L. A., Kuznetsov, G. V., Lazukova, G. G., Titelman, I. Z. & Fedorov, S. F. (Ватковский, О. С., Головенко, С. В., Гришина, Л. А., Кузнецов, Г. В., Лазукова, Г. Г., Тительман, И. З. & Федоров, С. Ф.) 1974: [Ecology and productivity of geochemically autonomous spruce forests of Valdai.] (In Russian) — In: Kovda, V. A. (Ковда, В. А.) (ed.), [Soils and the productivity of plant communities] 2:89–141. Izd. Moskovskogo Univ., Moscow.

Verner, J. 1985: Assessment of counting techniques. — Current Ornithology 2:247–302.

Vtorov, P. P. & Drozdov, N. N. (Второв, П. П. & Дроздов, Н. Н.) 1960: [Summer-autumn bird communities of taiga landscapes of the Vologda District.] (In Russian) — Ornitologiya 3:131–138.

Walter, H. & Lieth, H. 1964: Klimadiagramm-Weltatlas. — VEB Gustav Fischer Verlag. Jena.

Wesolowski, T. 1983: The breeding ecology and behaviour of wrens living under primaeval and secondary conditions. — Ibis 125:499–515.

Wiens, J. A. 1981: Scale problems in avian censusing. — Stud. Avian Biol. 6:513–521.

Appendix. Primary data (number of territories or nests) from bird censuses made by the mapping method in seven study plots (A—G) in Valdai, north-west Russia, in 1985–1989.
+ = species was observed within a plot during the study period, but had less than half a territory located there (including migrants). † = displaying male observed on three consequtive visits in the same place, ‡ = brood.

	Plot A				Plot B					Plot C				Plot D				Plot E					Plot F/F1					Plot G			
	86	87	88	89	85	86	87	88	89	86	87	88	89	86	87	88	89	85	86	87	88	89	85	86	87	88	89	86	87	88	89
Apla	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	+	1	+	/–	–/–	–/–	–/–	1/1	–	–	–	–
Aque	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	+/+	–/–	–	–	–	–
Aful	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	/–	–/–	–/–	–/–	–/–	–	–	–	–
Bcla	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	/–	–/–	–/–	–/–	+/+	–	–	–	–
Mmer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	+	/–	–/–	–/–	+/–	–/–	–	–	–	–
Bbut	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	/–	–/–	–/–	–/–	–/–	–	–	–	–
Fsub	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	/–	–/–	–/–	–/–	–/–	+	–	–	–
Ttet	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	/–	–/–	–/–	–/–	+/–	–	–	+	+
Turo	–	–	–	–	–	+	–	1	–	–	–	–	–	+	1	‡	†	–	–	–	–	–	/1	–/–	+/+	+/+	+/–	–	–	–	–
Bbon	–	–	–	–	–	–	–	–	+	+	–	+	+	+	+	‡	‡	–	–	+	+	–	/+	1/+	+/+	+/+	+/+	+	+	+	+
Toch	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/+	–/–	–/–	–/–	+/–	–	–	–	–
Ahyp	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	2–3	3	3	1
Srus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	/–	+/–	–/–	–/–	+/+	–	–	–	+
Ccan	+	–	+	+	–	+	–	+	+	–	–	–	–	+	+	+	+	–	–	–	–	–	/–	+/+	–/–	–/–	+/+	–	+	+	+
Aotu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	/–	–/–	–/–	–/–	–/–	–	–	–	–
Salu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	+/–	–	–	–	–
Ceur	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	–	–
Cpal	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/+	+/+	–/–	–/–	–/–	+	–	+	–
Stur	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	/–	–/–	+/+	–/–	–/–	–	+	–	–
Jtor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	+	–	–	–
Dmar	–	–	–	–	+	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	/–	+/+	+/+	–/–	+/+	–	–	–	–
Dmaj	+	–	–	+	–	+	–	–	–	+	+	+	+	1	–	1	+	1.5	3	+	1	+	/+	+/+	+/+	+/+	+/+	1	–	1	–
Dleu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	+	–	–	+
Dmin	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	/–	–/–	–/–	–/–	–/–	1	–	+	1
Ptri	+	–	+	+	+	+	+	–	+	–	–	–	–	–	+	–	+	+	–	1	–	+	/–	–/–	+/+	–/–	+/+	–	–	–	–
Atri	6	6	4	6.5	–	+	–	–	–	+	+	+	+	2.5	3	1.5	3	–	1	1	0.5	–	/0.5	1.5/1	5/2.5	5.5/2	3.5/1.5	4	6.5	0.5	3
Lcol	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	–	–
Oori	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	/–	–/–	+/+	–/–	–/–	0.5	0.5	1.5	1.5
Ggla	+	–	+	–	+	+	–	+	+	+	+	+	–	–	–	+	+	–	–	–	–	+	/+	+/+	+/+	+/+	+/+	+	+	+	–
Ppic	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	/–	–/–	–/–	–/–	–/–	+	+	+	–
Ccor	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	3	2.5	2.5	2	3	/+	–/–	+/+	–/–	–/–	+	+	+	+
Ttro	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	0.5	0.5	1	+	+	1	0.5	/2	2.5/2	3/2	4/2	4.5/2	–	–	–	+
Pmod	–	–	–	–	0.5	–	+	+	+	1	0.5	2	1	3	+	1	+	10.5	7	8.5	6	6	/5	5.5/3.5	6.5/3.5	10.5/6	6.5/5.5	1	2	1	+
Lflu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	1/1	–/–	–/–	–/–	–	–	+	–
Adum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	+/+	+/+	1	1	+	3
Apal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	0.5	–

	Plot A				Plot B					Plot C				Plot D				Plot E					Plot F/F1					Plot G			
	86	87	88	89	85	86	87	88	89	86	87	88	89	86	87	88	89	85	86	87	88	89	85	86	87	88	89	86	87	88	89
Hict	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	7.5	5	6	14
Satr	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	+	+	2	2	1	2.5	/1	4.5/2.5	5/5	4/3.5	3/2	27	20.5	19	24
Sbor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	–	+	/–	+/–	1.5/1.5	1/1	1.5/1.5	15	12	18.5	17.5
Scur	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	1	–	/–	–/–	–/–	–/–	–/–	–	–	–	–
Ptru	–	+	+	+	+	–	+	0.5	1	+	+	0.5	1	0.5	1	1	3.5	2	5.5	5	4.5	7.5	/+	0.5/0.5	1/1	1/1	0.5/0.5	12.5	19.5	11.5	18
Pcol	–	–	–	–	–	–	+	+	–	+	+	0.5	+	+	–	1.5	–	2	3	3	1	1	/1	1.5/1.5	1.5/1.5	1.5/1.5	4.5/4	–	–	+	–
Psib	+	+	–	+	+	1.5	–	2	5	3.5	1.5	3	3	14	15	14	13	2	15	15.5	9.5	11.5	/1	9/5	6.5/5.5	5/5	1.5/1	2	5.5	2.5	4
Ptrd	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	+	+	–	1	+	+	/+	–/–	–/–	1/1	+/+	–	–	–	–
Rreg	–	–	–	–	5.5	2	+	3	6	2	3	3	5.5	1.5	+	1.5	2	12.5	9	8.5	12.5	14.5	/8	7.5/4	9.5/3.5	13.5/6	12.5/8	–	–	+	+
Fhyp	–	+	–	+	–	–	–	+	–	–	–	+	+	+	1.5	1	+	2	+	3.5	2	4.5	/+	+/+	2/2	1/1	+/+	17	17	17	19.5
Fpar	–	–	–	–	+	–	+	+	–	–	–	–	+	2	0.5	0.5	+	–	–	–	+	–	/–	–/–	1/1	–/–	–/–	–	–	–	–
Mstr	+	–	–	–	+	1	+	+	+	+	+	+	+	+	–	+	+	4	+	1	1	0.5	/1	2.5/1.5	3/1.5	6.5/3	3/+	6	1	+	4.5
Ppho	–	–	–	–	0.5	+	1	+	+	1	+	+	–	–	–	–	–	2	2	+	–	+	/1	–/–	–/–	1/–	–/–	–	–	–	–
Erub	–	–	–	–	6	5	4	3.5	5	4	3	3	6	9	8.5	9.5	8	7.5	11	11	11	9.5	/1.5	5/4	4.5/3	4/3.5	3.5/3.5	6.5	10	9	8
Llus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	1	4	3.5	6
Tpil	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	+	+	2	/–	+/+	–/–	–/–	–/–	4.5	13	10	48.5
Tmer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	/+	–/–	–/–	+/+	–/–	+	–	1	1
Tili	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	+	+	+	+	+	/–	–/–	+/+	–/–	+/+	13	13	11	16.5
Tphil	–	–	+	+	1	+	3	1	1	0.5	2.5	1.5	2	2.5	3.5	1	3	3.5	4	5	3.5	7	/1	+/+	2.5/1	3/3	3.5/2.5	3.5	3.5	2	6
Tvis	+	–	–	–	+	+	+	1	1	–	–	+	+	–	–	–	–	–	–	–	–	–	/+	+/–	+/+	+/+	+/–	–	–	–	–
Acau	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–	0.5	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	–	+
Ppal	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	1	3	4	6
Pmon	+	+	+	+	+	–	+	1	+	1	+	2	3	0.5	–	1.5	3	+	0.5	5	3	5	/1	–/–	+/+	+/+	0.5/0.5	2	+	2	1
Pcri	+	+	+	+	3	+	2	1	1.5	+	0.5	0.5	2	+	2	1	2	1	+	1	1	3.5	/+	+/+	2/1	1/+	0.5/–	–	–	+	–
Pate	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	1	/–	–/–	+/+	–/–	–/–	–	–	–	–
Pcae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	2	–
Pmaj	–	–	–	–	–	–	–	–	–	+	+	–	–	–	–	–	–	+	–	–	1	+	/–	–/–	–/–	–/–	–/–	2.5	3.5	2.5	5
Seur	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	+	–	/+	–/–	–/–	–/–	–/–	1	1	1	1
Cfam	–	–	–	–	+	+	1	2.5	1	–	–	–	–	+	–	+	1	2	2	6	5	3	/2.5	2.5/1.5	5.5/3.5	1.5/1	3/3	–	–	–	–
Fcoe	+	+	+	+	9.5	11.5	13.5	10.5	7	12	11.5	7.5	9.5	20	20	18.5	13.5	37.5	34.5	34	32	31.5	/9	24/14.5	23.5/14.5	19/11.5	17.5/10.5	34	34.5	30	44.5
Fmon	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	+	+	+	–	–	+	–	/+	–/–	–/–	+/+	–/–	–	1	–	1
Cchl	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	+	–	–	–
Cspi	+	+	–	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	/+	+/+	+/+	+/+	+/+	+	+	+	+
Ccar	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	/–	–/–	–/–	–/–	–/–	–	–	–	–
Cery	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	+	+	0.5	+
Lcur	–	+	–	+	+	–	+	+	+	–	+	+	+	–	–	+	+	+	+	+	+	+	/+	+/+	+/+	+/+	+/+	–	–	–	–
Ppyr	–	–	–	–	–	+	–	+	+	+	+	1	+	+	–	1	+	+	+	+	1	2	/0.5	2/1	+/+	1/0.5	4/3	–	–	+	+
Ccoc	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	–	+
Ecit	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	/–	–/–	–/–	–/–	–/–	–	–	–	+
Erus	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	/–	–/–	+/+	–/–	–/–	–	–	–	–

Abbreviations of species names:

Apla	*Anas platyrhynchos*
Aque	*A. querquedula*
Aful	*Aythya fuligula*
Bcla	*Bucephala clangula*
Mmer	*Mergus merganser*
Bbut	*Buteo buteo*
Fsub	*Falco subbuteo*
Ttet	*Tetrao tetrix*
Turo	*T. urogallus*
Bbon	*Bonasa bonasia*
Toch	*Tringa ochropus*
Ahyp	*Actitis hypoleucos*
Srus	*Scolopax rusticola*
Ccan	*Cuculus canorus*
Aotu	*Asio otus*
Salu	*Strix aluco*
Ceur	*Caprimulgus europaeus*
Cpal	*Columba palumbus*
Stur	*Streptopelia turtur*
Jtor	*Jynx torquilla*
Dmar	*Dryocopus martius*
Dmaj	*Dendrocopos major*
Dleu	*D. leucotos*
Dmin	*D. minor*
Ptri	*Picoides tridactylus*
Atri	*Anthus trivialis*
Lcol	*Lanius collurio*
Oori	*Oriolus oriolus*
Ggla	*Garrulus glandarius*
Ppic	*Pica pica*
Ccor	*Corvus cornix*
Ttro	*Troglodytes troglodytes*
Pmod	*Prunella modularis*
Lflu	*Locustella fluviatilis*
Adum	*Acrocephalus dumetorum*
Apal	*A. palustris*
Hict	*Hippolais icterina*
Satr	*Sylvia atricapilla*
Sbor	*Sylvia borin*
Scur	*S. curruca*
Ptru	*Phylloscopus trochilus*
Pcol	*Ph. collybita*
Psib	*Ph. sibilatrix*
Ptrd	*Ph. trochiloides*
Rreg	*Regulus regulus*
Fhyp	*Fidecula hypoleuca*
Fpar	*F. parva*
Mstr	*Muscicapa striata*
Ppho	*Phoenicurus phoenicurus*
Erub	*Erithacus rubecula*
Llus	*Luscinia luscinia*
Tpil	*Turdus pilaris*
Tmer	*T. merula*
Tili	*T. iliacus*
Tphil	*T. philomelos*
Tvis	*T. viscivorus*
Acau	*Aegithalos caudatus*
Ppal	*Parus palustris*
Pmon	*P. montanus*
Pcri	*P. cristatus*
Pate	*P. ater*
Pcae	*P. caeruleus*
Pmaj	*P. major*
Seur	*Sitta europaea*
Cfam	*Certhia familiaris*
Fcoe	*Fringilla coelebs*
Fmon	*F. montifringilla*
Cchl	*Carduelis chloris*
Cspi	*C. spinus*
Ccar	*C. carduelis*
Cery	*Carpodacus erythinus*
Lcur	*Loxia curvirostra*
Ppyr	*Pyrrhula pyrrhula*
Ccoc	*Coccothraustes coccothraustes*
Ecit	*Emberiza citrinella*
Erus	*E. rustica*