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Short-term fluctuations in a south-taiga bird assemblage: support for an "individualistic" view

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Short-term variability patterns among forest breeding bird assemblages were analysed on the basis of annually repeated mapping censuses conducted during 1985–1989 in several study plots in the Valdai Uplands, northwest Russia. For most species, there was no evidence that variability in breeding numbers has been strongly limited by any mechanisms operating in the breeding grounds. Only in the Wood Warbler, in a birch-dominated forest, did the number of territories vary less than could be explained by chance. When the data from a variety of forest habitats were pooled and analysed together, a prevalence of parallel density fluctuations among species was found. However, there were considerable interhabitat differences in fluctuation patterns. At the habitat level, the highest variability of total bird numbers, and the significant preponderance of parallel density fluctuations among species were found in the richest assemblage with the highest number of congeneric species (grey alder forest). Even secondary hole-nesters gave no indications of compensatory density fluctuations. There was little evidence of competitive density interactions at the assemblage level. Individualistic responses of species to environment, stochastic processes, predation pressure on the key species, and heterospecific attraction seem to be more important in determining bird assemblage variability and creating interhabitat differences in fluctuation patterns.

1. Introduction

"The most fundamental question in community ecology is: why are communities the way they are?" (Begon et al. 1988:762). There are two main "paradigms" in community ecology and, as a result, two different sets of hypotheses concerning this question. First, competitive interactions are supposed to create structured community patterns and determine their stability. Communities close to an equilibrium resulted from resource limitations, and were more or less "saturated" by individuals and species. Population changes driven by both intra- and interspecific interactions are produced, first of all, by environmental variations in time and space. According to another view, stochastic effects are important in determining community patterns (see Wiens 1989a for a review of both paradigms).

Investigating the nature of variability is a good way to separate the alternative explanations. Järvinen (1979, see also Järvinen & Väisänen

1976, Glowacinski 1981, Noon et al. 1985, Helle & Mönkkönen 1986, Solonen 1986, Virkkala 1989, 1991a, b) proposed an intuitively lucid approach to evaluate bird assemblage stability on the basis of annually repeated censuses: an assemblage is more stable the less its properties vary from year to year. He found a south-north gradient in variability among European breeding bird assemblages, which seemed to be correlated with latitudinal changes in environmental predictability.

The aims of this paper are to examine short-term population fluctuations of breeding birds in various south taiga habitats and to search for interhabitat differences in variability among bird assemblages at a local scale. I try to answer the following questions: Are fluctuations of breeding numbers of individual species and assemblages in the study plots produced by stochastic processes exclusively, or do the amplitudes of these fluctuations indicate that some powerful stabilizing mechanisms or destabilizing factors are at work? Are there any evidences that southern taiga bird assemblages are stabilized by some forces operating in the breeding grounds? Do species with similar migratory habits tend to fluctuate in a parallel way (see Enemar et al. 1984, Järvinen & Rajasärkkä 1992)?

2. Methods

2.1. Study plots

The data were collected in the Valdai District of the Novgorod Region, in northwest Russia (57°57′–58°10′N, 33°5′–33°30′E). According to the phytogeographical zonation proposed by Ahti et al. (1968), the study area lies at the northern border of a small south-boreal "island" within the hemiboreal zone. Forest covers more than 70% of the area in this locality. Bird censuses were conducted by the author in forest stands typical to the area during 1985–1989; the plots are described in Morozov (1992). I used the following criteria for inclusion (see Järvinen 1979, Noon et al. 1985): 1. The study plot (or a part of it selected) should not have undergone considerable changes in habitat during the course of the study. 2. The study period should cover at least 3 years. The distances between the study plots ranged from 1.5 to 7 km. There were no major changes in the areas of the main habitat types in the study area within a radius of at least 10 km during the study period.

I initially analysed variability in species breeding numbers at the separate plot level (see Table 1). In most coniferous plots, however, sample sizes were too small. To minimize the effect of small sample sizes, I combined data from several primordially separate study plots. To examine variability at the habitat level, separate plots were grouped into three major habitat types:

Long boled pine and birch-pine forests (hereafter called pine forests). I combined a 130-year-old pine forest, a 50-year-old cowberry pine forest, and a 14.7-ha part of a birch-pine forest (some birch-dominated and/or swampy patches in the latter plot were excluded). The distances between the plots ranged from 1.5 to 2 km. Total area was 42.3 ha. The study period was from 1986 to 1989.

Spruce forests. Two nemorose spruce plots almost bordered on each other. The distance between "mainland" (nemorose) and island spruce forests was 3.8 km. After the 1987 breeding season, spruce stands were subjected to so-called sanitation cutting (partial removal of dead spruces; see Morozov 1992). Although the structure of the main layers and habitat configuration, as a whole, changed only slightly, it is for this reason that more attention is given here to the period from 1985 to 1987 (total area 31.0 ha). However, the 1986–1989 period is also considered for comparative purposes (total area 39.1 ha, since in 1986, censuses started also in the nemorose spruce plot with no lower canopy; see Table 1).

Grey alder forest. Finally, 4-year data (1986–1989) from a low-growing *Sphagnum* pine forest, both long-boled pine stands, birch-pine and birch forest, birch-aspen patch within spruce forest, grey alder forest, and a 8.0-ha part of a nemorose spruce forest (with lower canopy) not subjected to sanitation cutting, were pooled (hereafter called "pooled data"; the sample area is 92.1 ha) to analyse variability in a large sample. Note that pooled data are not merely the sum of data from long-boled pine, spruce, and alder forests. They do not include the data from most spruce stands because the latter ones were subjected to sanitation cutting during the 1986–1989 period (see Table 1). At the same time, pooled data contain additional small sets of data from bog pine, birch, and birch-aspen stands.

2.2. Bird census method

Bird species' abundances were estimated by territory mapping. Each plot was visited from nine to thirteen times yearly between late April–early May (from mid-April in 1989) and early July (late June in 1985). The detailed information about the year-to-year distribution of numbers of morning, afternoon, and evening visits is given in Morozov (1992). For each plot, the minimum yearly number of morning visits was six. The proportion of evening visits was highest in 1986 (up to four out of ten visits for the 130-year-old pine forest). Most morning visits started before, or near a local sunrise, and continued from one and a half to five hours. Densely inhabited plots took much more time than those with low bird densities. Mid- and late-morning censuses (started 3.5–5 hours after a sunrise and finished before or near noon) were the only ones made in the *Sphagnum* pine forest during 1987–1989. Evening visits started about two hours before a sunset and usually finished with the fading of singing activity in the dusky species. The observer paid special attention to obtaining simultaneous records of singing males (see Tomiałojć 1980). Woodpeckers and the Fieldfare *Turdus pilaris* were censused almost exclusively by nest counts. In the alder forest, many Fieldfare nests were robbed during May in some years (see below). In 1986, due to the relatively late start of census work, the number of pairs of this species attempting to breed in this plot was presumably underestimated.

In the previous analysis (Morozov 1992), the minimum gradation used for interpreting edge clusters of registrations was half a breeding territory. On the contrary, whole numbers of territories are the only ones used in this study. In questionable situations, halves of territories were reinterpreted as whole ones. In spite of this, the re-evaluation of species maps produced estimates similar to the previous ones. The revised estimates and the classification of migratory habits are given in the Appendix. The analysis is restricted to pigeon, woodpecker and passerine species. The Hooded Crow *Corvus cornix* (few

Table 1. Study plots and census periods. Periods including years of sanitation cuttings are given in brackets.

Stand characteristics	Plot size (ha)	Census period
Low-growing 60-year-old sphagnum pine forest	16.9	1986–89
130-year-old moderately barren pine forest with a poor herb cover, and a complete cover of green mosses. The lower canopy is formed by spruce	10.2	1986–89
50-year-old cowberry pine forest with small stands of 40–100-year-old spruces	17.5	1986–89
50–60-year-old birch-pine and birch forest represented by a mosaic of wet and dry patches. The lower canopy is formed by spruce	19.9	1986–89
Rich spruce forest with a complete series of *Picea* generations up to about 140 years old. The plot is situated within the forested island (ca. 1.4 km^2 in size)	19.5	1985–87 (1986–89)
100-year-old nemorose spruce forest with lower canopy	11.5	1985–87 (1986–89)
100-year-old nemorose spruce forest without lower canopy	8.1	(1986–89)
Birch-aspen patch within a spruce forest	3.5	1986–89
20–50-year-old predominantly mesophytic grey alder forest with luxuriant herb layer. The plot stretches for ca. 1.5 km (maximum width 215 m) along the lake shore.	16.1	1986–89

breeding pairs in the island spruce forest each year), the Siskin *Carduelis spinus* and the Crossbill *Loxia curvirostra* are excluded from the present analysis.

2.3. Stability measurements

It is preferable to make the logarithmic transformation of the primary data when population variability is studied (Williamson 1972, Fowler & Cohen 1985). However, following Helle & Mönkkönen (1986), I did not transform the data here. The transformation should have been done from N+1 breeding territories because many species had no territories in some years in a given habitat type. The proportion of zero-observations was too high to be sure that transformation would have improved the data quality.

A certain amount of stochastic variation in numbers of breeding territories is expected in the study plots, even if the source population is stable from year to year. It is reasonable to expect an increase in stochastic variation with a decreasing local breeding density: the "checkerboard effect" using Wiens's (1981, 1989b) terminology. If numbers of territories of a species, in the plot, in different years behave as a random (Poisson) variate, the variance should approximately equal the mean. Comparing observed variabilities with expected ones (see Svensson et al. 1984, Helle & Mönkkönen 1986, Järvinen & Rajasärkkä 1992), I tried to find significantly more or significantly less variable species than could be explained by chance alone. The F-test was used for comparing observed and expected variances. The numbers of degrees of freedom used were the number of study years minus 1 and infinity for observed and expected variances, respectively (O. V. Burskii, N. G. Chelintsev, personal communication).

The ratio of the total sample density variance over the sum of the individual species density variances (the so-called Järvinen's Ratio, V) was used to test the independence of species' density fluctuations at the assemblage level. If the ratio is significantly less than 1.0, compensatory fluctuations are stronger than parallel ones, and if the ratio is significantly greater than 1.0, parallel fluctuations prevail (Schluter 1984, see also James & Boecklen 1984, Brawn et al. 1987). Compensatory fluctuations would suggest competitive density interactions.

Bird assemblage stability was expressed by a coefficient of variation (CV, %) for variations in: 1) total bird density, DN; 2) the expected number of species in a random sample of 80 territorial pairs, Es, calculated by rarefaction (James & Rathbun 1981); 2) species diversity, D′; 4) and evenness, G′. Järvinen (1979) and many other researchers used Shannon's (H′) and Pielou's (J′) indices to measure diversity and evenness, respectively. Both measures were avoided here because of their unsatisfactory mathematical properties and dubious biological interpretation (see Hurlbert 1971, DeBenedictis 1973, Goodman 1975, Molinari 1989 for criticism). Instead, I used the inverse of the Simpson's measure of concentration (D′) figuratively interpreted as the number of very abundant species and the calibrated version of Alatalo's index (G′) (Molinari 1989).

The average annual species turnover (ST) was calculated as the arithmetic average of $ST = (I+E)/(S_1+S_2)$, where I and E are the numbers of species "immigrated" and "disappeared" between the years 1 and 2, respectively, and S_1 and S_2 are the total numbers of species in the years 1 and 2, respectively. ST-values were calculated for successive years only (Järvinen 1979).

3. Results

3.1. Fluctuations in the pooled data

The relationship between mean population size and its variance is shown in Fig. 1. In most species, no significant difference was found between observed variance and variance calculated assuming that the number of territories vary as a Poisson variate. Only the Fieldfare showed significantly more variability in the number of breeding pairs than could be explained by chance ($N = 18.3$, observed coefficient of variation $CV = 106.0\%$, expected $CV = 23.4\%$, $F = 20.51$, $P < 0.001$).

The observed variability of total bird numbers was significantly higher than expected ($N = 346.8$, observed $CV = 14.5\%$, expected $CV = 5.4\%$, $F = 7.33$, $P < 0.001$) being the result of the preponderance of parallel density fluctuations

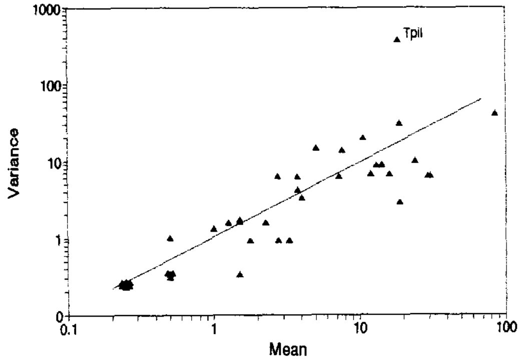

Fig. 1. Relationship between mean number of territories censused ($\bar{N}$) and its variance among species in the pooled data. The straight line represents the equality between the variance and the mean expected for randomly fluctuating populations. Tpil = the Fieldfare. Note logarithmic scales. The point corresponding to the Nuthatch ($\bar{N}$ = 1.0, Variance = 0) is omitted.

among species (V = 4.29, P < 0.001). At the migratory group level, residents and partial migrants (N = 32.5, observed CV = 42.8%, expected CV = 17.5%, F = 5.96, P < 0.005) and short-distance migrants (N = 171.7, observed CV = 15.5%, expected CV = 7.6%, F = 4.15, P < 0.01) seemed to be more unstable than tropical migrants (N = 118.2, observed CV = 11.2%, expected CV = 9.2%, F = 1.47, n. s.). However, high variability in short-distance migrants as a group is mainly explained by fluctuations in the Fieldfare (excluding the Fieldfare, N = 153.5, observed CV = 5.4%, expected CV = 8.1%, F = 2.20, n. s.). Parallel fluctuations significantly prevailed among residents and partial migrants (V = 3.58, P < 0.005) and tropical migrants (V = 2.12, P < 0.05). A nearly significant preponderance of parallel fluctuations was found also among short-distance migrants (V = 1.60, P < 0.1).

3.2. Inter-habitat differences in variability

Total bird densities fluctuated in an independent way among pine, spruce and alder samples during 1986–1989 (V = 1.22, n.s.). The same was true for the Chaffinch *Fringilla coelebs* densities (V = 0.82, n.s.). In the Robin *Erithacus rubecula*, another numerous species with a broad habitat amplitude, densities in the three forest types fluctuated reciprocally (V = 0.35, P < 0.025).

In most species, no significant differences were found between observed and expected variances at the habitat (Fig. 2) and separate plot levels. There are four exceptions. The Fieldfare in the grey alder forest (F = 20.51, P < 0.001), the Wood Warbler *Phylloscopus sibilatrix* in spruce forests during 1985–1987 (N = 16.0, observed CV = 70.4%, expected CV = 25.0%, F = 7.94, P < 0.001), and the Willow Warbler *Phylloscopus trochilus* (N = 1.8, observed CV = 135.0%, expected CV = 75.6%, F = 3.19, P < 0.025) in pine forests demonstrated significantly more variability than expected according to the Poisson distribution. On the contrary, the number of the Blackcap *Sylvia atricapilla* territories in spruce forests during 1986–1989 varied less than could be explained by chance (N = 6.5, observed CV = 8.9%, expected CV = 39.2%, F = 19.50, P < 0.025). However, for the Willow Warbler and the Blackcap total sample sizes are too small (7 and 26 territories, respectively) to draw any serious conclusions.

In the Wood Warbler, the high variability observed in spruce stands is the result of a situation in 1985 when the species was unusually scarce in the Valdai. A high variability in the Wood Warbler is also observed if the island spruce forest is analysed alone (numbers of territories are 2, 16, 17 for the period from 1985 to 1987; N = 11.7, observed CV = 71.9%, expected CV = 29.3%, F = 6.03, P < 0.025). The Fieldfare is a colonial species and the position of its colonies, as well as the breeding success in the grey alder forest, were changing unpredictably from year to year (Fig. 3).

Another interesting exception is the Wood Warbler in a birch-pine and birch forest. If this plot (19.9 ha in size) is analysed separately, the numbers of territories of the species are 14, 16, 15, and 15 for the period from 1986 to 1989. Thus, in a birch-dominated stand Wood Warblers showed significantly less variability than expected on the basis of random distribution (N = 15.0, observed CV = 5.4%, expected CV = 25.8%, F = 22.86, P < 0.025).

In both pine and spruce forests, the observed variability of total bird numbers did not deviate significantly from the expected amount. In the

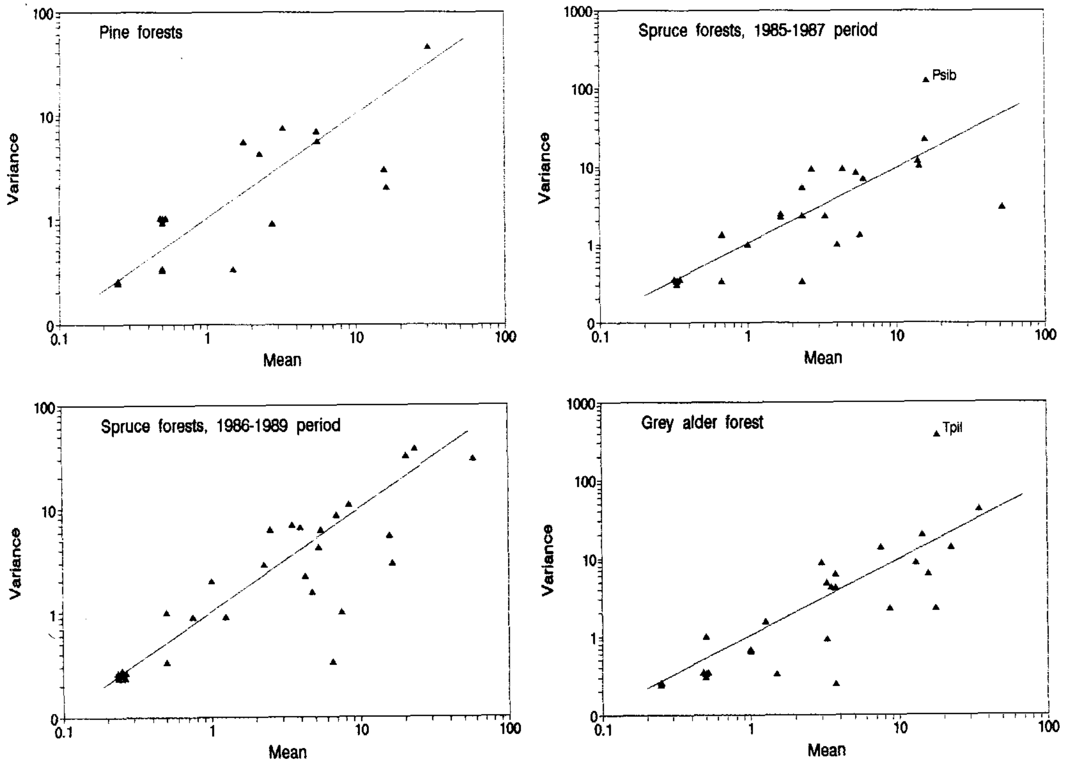

Fig. 2. Relationship between mean number of territories censused (N̄) and its variance among species for three forest habitats studied. See Fig. 1 for legend. Psib = the Wood Warbler, Tpil = the Fieldfare. For grey alder forest, the point corresponding to the Nuthatch (N̄ = 1.0, Variance = 0) is omitted.

grey alder forest, in contrast, the total number of pairs varied annually more than could be explained by chance (N = 186.0, observed CV = 23.4%, expected CV = 7.3%, F = 10.18, $P < 0.001$). Even after excluding the Fieldfare from the analysis, variability of the total bird number remained relatively high (N = 167.8, observed CV = 14.8%, expected CV = 7.7%, F = 3.67, $P < 0.025$). Parallel density fluctuations among bird species significantly prevailed in the alder forest, whereas no clear patterns emerged in the pine and spruce stands. Considerable interhabitat differences in fluctuation patterns were found also for the migratory groups (Table 2). The differ-

Table 2. Järvinen's Ratio (V) for the bird assemblages and migratory groups studied. WA = whole assemblage, r = residents and partial migrants, s = short-distance migrants, t = tropical migrants. * P < 0.05, ** P < 0.005, *** P < 0.001.

		V			
Forest type	Census period	WA	r	s	t
Pine	1986–1989	0.71	3.25**	0.60	1.35
Spruce	1985–1987	1.65	0.45*	0.15***	1.60
	1986–1989	0.63	1.80	0.05***	0.59
Alder	1986–1989	3.64**	0.74	1.99*	2.03*
(excluding the Fieldfare)		(4.28***)		(2.04*)	

Fig. 3. Locations of the Fieldfare nests (dots, circles, stars) in the grey alder forest during 1986–89. Circles indicate nests destroyed earlier than 31 May. Stars indicate nests built significantly or presumably later than 31 May. Arrows indicate sites of assumed nesting of pairs whose nests were not found. The area delineated by the dotted line was also censused but excluded from the analysis to avoid the probable effect of cattle grazing.

ences in variability of total bird density (Table 3) were significant between alder and both coniferous forest types during 1986–1989 ($F = 212.0$, $P < 0.001$ for alder and pine forests; and $F = 101.3$, $P < 0.005$ for alder and spruce forests), and between spruce forests during 1985–1987 and pine forests during 1986–1989 ($F = 11.52$, $P < 0.05$).

It is widely accepted that local breeding densities of hole-nesting species, which do not excavate their own holes, are limited by the availability of suitable cavities (von Haartman 1957, 1971, Hildén 1965, Van Balen et al. 1982; but see Brawn & Balda 1988, Waters et al. 1990 for criticism). For this reason, my special interest was in this guild which reached relatively high densities in the alder forest only (15.8±2.5 territories/10 ha). The guild was sharply dominated by the Pied Flycatcher *Ficedula hypoleuca*, but three tit species (*Parus major*, *P. palustris*, *P. caeruleus*) and the Nuthatch *Sitta europaea* were also present. The hypothesis tested was that compensatory density fluctuations should prevail among guild members if interspecific competition for cavities is important. However, contrary to this expectation, a nearly significant preponderance of parallel fluctuations was found for the study period ($V = 1.69$, $P < 0.1$).

Unlike the patterns of variability in total bird densities, the least variability of species richness, evenness and species diversity, and the least species turnover rate tended to occur in the alder forest, whereas the highest ones were in the pine forests (Table 3). However, the differences in the variability of Es, G′ and D′ between forest types were not significant (F-test).

4. Discussion

Using the terminology of Svensson et al. (1984:347–348), most populations in the Valdai study plots "behaved as if there were stable source populations from which the plots took a random sample every year". For most species, there is no evidence that variability in breeding bird numbers, at both the pooled data and the habitat levels, has

Table 3. Means and coefficients of variation (CV, %) for total bird density (territories/10 ha) (DN), species richness (Es), diversity (D′) and evenness (G′), and average species turnover ($\overline{ST}$) in three forest types.

Forest type	Census period	DN		Es		D′		G′		$\overline{ST}$
		Mean	CV	Mean	CV	Mean	CV	Mean	CV	
Pine	1986–1989	20.8	8.9	11.3	18.3	5.1	29.6	0.33	23.4	0.245
Spruce	1985–1987	50.8	12.4	16.1	5.5	6.3	20.0	0.21	18.0	0.172
	1986–1989	51.8	5.2	16.9	7.2	7.6	16.6	0.25	13.0	0.196
Alder	1986–1989	115.5	23.4	17.9	3.9	10.0	7.4	0.38	10.5	0.161

been strongly limited by any mechanisms operating in the breeding grounds. The only significant exception is the Wood Warbler in a birch-dominated forest.

Since the birch forest is presumably the optimal habitat for the Wood Warbler in the Valdai (Morozov 1992), the low variability in breeding numbers can be due to intraspecific competition. However, territory mapping showed that even the birch-dominated plot was never tightly saturated by Wood Warblers. Probably, low variability reflects the compromise between aspirations to establish a territory in a highly attractive habitat and to scatter territories and/or nests to minimize the risk of nest predation (see Krebs 1971, Tomiałojć et al. 1984, Wesolowski et al. 1987, Martin 1988).

In the pooled data, parallel density fluctuations prevailed among species. However, this pattern is mainly due to the alder forest, since parallel fluctuations were not found in the pine or the spruce forests (Table 2). The latter is also true, if 4-year data from pine and spruce forests are pooled ($V = 0.64$, $P < 0.5$). Thus, different fluctuation patterns emerge in different habitat types within the very same area.

In the pooled data, species with similar migratory habits tended to fluctuate in parallel ways. Total numbers of birds belonging to different migratory groups also fluctuated in synchrony ($V = 2.35$, $P < 0.025$). However, this parallelism in the pooled data conceals considerable interhabitat differences in fluctuation patterns at the migratory group level (Table 2). To summarize, in the pooled data parallel density fluctuations among residents prevailed mainly due to the pine forests, whereas among tropical migrants parallel fluctuations prevailed mainly due to the alder forest. A nearly significant preponderance of parallel density fluctuations among short-distance migrants, in the pooled data, resulted from the same pattern in the alder forest, and excluding a considerable part of the spruce stands (see section 2.1) where compensatory fluctuations significantly prevailed.

The surprising result is a significant preponderance of compensatory density fluctuations among short-distance migrants for both periods, and among residents and partial migrants during the period 1985–1987 in spruce forests (Table 2). I see no ecologically reasonable explanations for these patterns. In short-distance migrants during 1986–1989, the compensatory pattern resulted from opposite trends in the numbers of the Chaffinch (decreased, see Appendix) and totals of other species (increased) (excluding the Chaffinch, $V = 0.88$, n. s.). During 1985–1987, an increase in numbers of the Wren *Troglodytes troglodytes* and the Dunnock *Prunella modularis* compensated for the opposite trend in the Robin, the Song Thrush *Turdus philomelos,* and the Chiffchaff *Phylloscopus collybita*. Most species mentioned (except the Chiffchaff) during the breeding season forage frequently, or almost exclusively, on the ground and theoretically can be partially limited by the same food resources. However, they differ substantially in many other aspects of their ecologies, and it seems doubtful that the short-term compensatory fluctuations that emerged reflect competitive interactions among them. A competition-based explanation of compensatory fluctuations in residents and partial migrants for the period 1985–1987 (two woodpecker and two tit species with low desities, the Goldcrest *Regulus regulus*, the Treecreeper *Certhia familiaris*, and the Bullfinch *Pyrrhula pyrrhula*) seems even more doubtful from this point of view.

At the habitat level, contrary to expectations, the highest variability of total bird numbers, and the significant preponderance of parallel density fluctuations among species were found in the richest assemblage with the highest number of congeneric species (grey alder forest). In the alder forest, even secondary hole-nesters gave no indications of interspecific competition. Unlike the result obtained by Järvinen (1979) at the geographical scale, an interhabitat gradient of total density variability in this study seems to be opposite to the gradients of variability of species richness, evenness, and species diversity (Table 3). Variability of total bird numbers in the Valdai alder forest ($CV = 23.4\%$) was substantially higher than in the central European and southern Scandinavian communities analysed by Järvinen (1979, see also Wasilewski 1979, Solonen 1986) (CV from 1.2 to 16.2%). Actually, it falls into the range of values typical for northern European communities.

I suppose that the instability of total bird numbers and the prevalence of parallel density fluctuations among species in the alder forest are mainly explained by the presence of the Fieldfare. In the area surrounding their nests, birds of this species usually attack predators and try to drive them away. Although the data of different authors regarding the breeding success of this species are contradictory, when comparing colonies versus solitary nesting pairs (see Hogstad 1983; Haas 1985; Fetisov 1988 for a review), the presence of its colonies seems to be attractive for some small- and medium-sized bird species (Slagsvold 1979, 1980, Gubin et al. 1990, Vengerov 1990). Most likely, the behaviour of Fieldfares also protects the nests of other species against predators. In the Valdai alder forest, Fieldfares had settled and started to build nests before many other species had fully occupied their breeding territories. However, in the Fieldfare, the number of breeding pairs, the location of colonies, the nesting success, and the dates of ravaging of colonies by predators unpredictably varied from year to year (Fig. 3). I suspect that territory establishment and subsequent breeding densities of some species in the alder forest have been partially predetermined by the patterns of settlement and subsequent fates of Fieldfare colonies and solitary pairs. The prevalence of parallel density fluctuations was observed among both early (mass arrival usually starts before 10 May) and late arriving migrant species (mass arrival starts after 10 May) (excluding the Fieldfare, $V = 3.02$, $P < 0.01$ and $V = 2.04$, $P < 0.05$, respectively), but not among residents ($V = 0.74$, $P > 0.05$). Moreover, the presence of early arriving species attracted by Fieldfare colonies may be an additional indicator of favourable conditions for species arriving later (see Mönkkönen et al. 1990). Thus, my hypothesis is that the Fieldfare, being locally the highly "unpredictable" species itself, also destabilizes local densities of some other bird species. This can also partially explain the lack of synchrony in fluctuations of the Chaffinch densities in the three habitat types analysed together. In the pine and the spruce forests for the period 1986–1989, Chaffinch densities tended to fluctuate in a more parallel way ($V = 1.87$, $P < 0.1$). Unfortunately, the results of the mapping method are insufficient to test these suppositions. Individual marking of birds of presumably "accompanying" species, detailed mapping of their territories, and experimental manipulations in Fieldfare colonies are necessary to provide enough reliable evidences to test these suppositions.

In the forest communities studied in the Valdai, bird species richness and plant species richness were closely positively correlated (Morozov & Morozova 1990). Thus, the grey alder forest provides a good example of a community which, at the local scale, combines the highest variability of total bird numbers with the highest bird and plant species richness, contrary to the old belief that complex communities are more stable than simple ones.

To conclude, there is little evidence of competitive density interactions at the assemblage level. Individualistic responses of species to environment, stochastic processes, predation pressure on the key species, and heterospecific attraction seem to be more important in determining the year-to-year variability of bird assemblages studied and creating interhabitat differences in fluctuation patterns.

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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.

Begon, M., Harper, J.L. & Townsend, C. R. 1988: Ecology: individuals, populations and communities. — Blackwell Scientific Publ., Oxford.

Brawn, J. D. & Balda, R. P. 1988: Population biology of cavity-nesters in northern Arizona: do nest sites limit breeding densities? — Condor 90:61–71.

Brawn, J. D., Boecklen, W. J. & Balda, R. P. 1987: Investigations of density interactions among breeding birds in ponderosa pine forests: correlative and experimental evidence. — Oecologia (Berlin) 72:348–357.

DeBenedictis, P. A. 1973: On the correlations between certain diversity indices. — Amer. Nat. 107:295–302.

Enemar, A., Nilsson, L. & Sjöstrand, B. 1984: The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. — Ann. Zool. Fennici 21:321–338.

Fetisov, S. A. (Фетисов, С. А.) 1988: The character of settlement and productiveness of Fieldfare in the lakes of Sebezh. (In Russian) — In: Abstracts of the 12th Eastern Baltic Ornithological Conference: 229–230. Vilnius.

Fowler, J. & Cohen, L. 1985: Statistics for ornithologists. — BTO Guide No.22, BTO, Tring.

Glowacinski, Z. 1981: Stability in bird communities during the secondary succession of a forest ecosystem. — Ekol. Polska 29:73–95.

Goodman, D. 1975: The theory of diversity-stability relationship in ecology. — Quart. Rev. Biol. 50:237–266.

Gubin, A. G., Preobrazenskaya, E. S. & Bogoljubov, A. S. (Губин, А. Г., Преображенская, Е. С. & Боголюбов, А. С.) 1990: Ecological characters of the Fieldfare (Turdus pilaris) and the Redwing (T. iliacus) in the places of their joint inhabitance. (In Russian with English summary) — In: Kurochkin, E. N. (Курочкин, Е. Н.) (ed.), Modern ornithology 1990:117–121. Nauka, Moscow.

von Haartman, L. 1957: Adptation in hole-nesting birds. — Evolution 11:339–347.

— 1971: Population dynamics. — In: Farner, D. S. & King, J. R. (eds.), Avian biology, Vol. 1:392–459. Academic Press, New York.

Haas, V. 1985: Colonial and single breeding in fieldfares, Turdus pilaris L.: a comparison of nesting success in early and late broods. — Behav. Ecol. and Sociobiol. 16:119–124.

Helle, P. & Mönkkönen, M. 1986: Annual fluctuations of land bird communities in different successional stages of boreal forest. — Ann. Zool. Fennici 23:269–280.

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

Hogstad, O. 1983: Is nest predation really selecting for colonial breeding in Fieldfares Turdus pilaris? — Ibis 125:366–369.

Hurlbert, S. H. 1971: The nonconcept of species diversity: a critique and alternative parameters. — Ecology 52:577–586.

James, F. C. & Boecklen, W. J. 1984: Interspecific morphological relationships and the densities of birds. — In: Strong, D. R. Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. (eds.), Ecological communities: conceptual issues and the evidence: 458–477. Princeton Univ. Press, Princeton, New Jersey.

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

Järvinen, A. & Rajasärkkä, A. 1992: Population fluctuations in two northern land bird communities: effects of habitat, migration strategy and nest-site. — Ornis Fennica 69:173–183.

Järvinen, O. 1979: Geographical gradients of stability in European land bird communities. — Oecologia (Berlin) 38:51–69.

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

Krebs, J. R. 1971: Territory and breeding density in the Great Tit, Parus major L. — Ecology 52:1–22.

Martin, T. E. 1988: Processes organizing open-nesting bird assemblages: competition or nest predation? — Evolutionary Ecology 2:37–50.

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

Mönkkönen, M., Helle, P. & Soppela, K. 1990: Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (Parus spp.): heterospecific attraction in northern breeding bird communities? — Oecologia (Berlin) 85:218–225.

Morozov, N. S. 1992: Breeding forest birds in the Valdai Uplands, north-west Russia: assemblage composition, interspecific associations and habitat amplitudes. — Ann. Zool. Fennici 29:7–27.

Morozov, N. S. & Morozova, O. V. 1990: Relationship between avian population parameters and floristic richness in forest communities. — In: Doklady Biological Sciences, May 1990, Proceedings of the Academy of Sciences of the USSR: 711–714. Plenum Publishing Corporation, New York.

Noon, B. R., Dawson, D. K. & Kelly, J. O. 1985: A search for stability gradients in North American breeding bird communities. — Auk 102:64–81.

Schluter, D. 1984: A variance test for detecting species associations, with some examples applications. — Ecology 65:998–1005.

Slagsvold, T. 1979: The Fieldfare Turdus pilaris as a key species in the forest bird community. — Fauna norvegica, Ser.C, Cinclus 2:65–69.

— 1980: Habitat selection in birds: on the presence of other bird species with special regard to Turdus pilaris. — J. Anim. Ecol. 49:523–536.

Solonen, T. 1986: Stability of a bird community in southern Finland. — Ornis Scand. 17:106–116.

Svensson, S., Carlsson, U. T. & Liljedahl, G. 1984: Structure and dynamics of an alpine bird community, a 20-year study. — Ann. Zool. Fennici 21:339–350.

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

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

Van Balen, J. H., Booy, C. J. H., Van Franeker, J. A. & Osieck, E. R. 1982: Studies on hole-nesting birds in natural nest sites. 1. Availability and occupation of natural nest sites. — Ardea 70:1–24.

Vengerov, P. D. (Венгеров, П. Д.) 1990: Ecological peculiarities of the Chaffinch (Fringilla coelebs L.) in colonies of the Fieldfare (Turdus pilaris L.). (In Russian) — Ekologija (Sverdlovsk) 3:89–90.

Virkkala, R. 1989: Short-term fluctuations of bird communities and populations in virgin and managed forests in Northern Finland. — Ann. Zool. Fennici 26:277–285.

— 1991a: Annual variation of northern Finnish forest and fen bird assemblages in relation to spatial scale. — Ornis Fennica 68:193–203.

— 1991b: Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. — Oikos 62:59–66.

Wasilewski, A. 1979: Interspecific competition in relation to homeostasis in bird communities. — Memorabilia Zoologica 32:37–47.

Waters, J. R., Noon, B. R. & Verner, J. 1990: Lack of nest site limitation in a cavity-nesting bird community. — J. Wildl. Managem. 54:239–245.

Wesolowski, T., Tomiałojć, L. & Stawarczyk, T. 1987: Why low numbers of Parus major in Bialowieza Forest — removal experiments. — Acta Ornithol. 23:303–316.

Wiens, J. A. 1981: Scale problems in avian censusing. — In: Ralph, C. J. & Scott, J. M. (eds.), Estimating numbers of terrestrial birds: 513–521. Cooper Ornithological Society, Los Angeles.

— 1989a: The ecology of bird communities. Volume 1. Foundations and patterns. — Cambridge Univ. Press, Cambridge.

— 1989b: The ecology of bird communities. Volume 2. Processes and variations. — Cambridge Univ. Press, Cambridge.

Williamson, M. H. 1972: The analysis of biological populations. — Edward Arnold, London.

Appendix. Number of territories censuses by the mapping method in forest habitats of Valdai, north-west Russia, during 1985–89. Migratory habit (MG): r = resident or partial migrant, s = short-distance migrant, t = tropical migrant, e = overwinters east of Tibet, Gobi and the Altai-Sajan Mountain Region.

		Pooled data				Pine forest				Spruce forest							Grey alder forest			
		Area 92.1 ha				Area 42.3 ha				Area 31.0 ha			Area 39.1 ha				Area 16.1 ha			
Species	MG	-86	-87	-88	-89	-86	-87	-88	-89	-85	-86	-87	-86	-87	-88	-89	-86	-87	-88	-89
Dendrocopos major	r	2	–	2	–	1	–	1	–	2	3	–	3	–	1	–	1	–	1	–
D. minor	r	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
Picoides tridactylus	r	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–
Anthus trivialis	t	15	17	10	15	2	3	2	4	1	2	4	3	7	7	4	4	6	1	3
Oriolus oriolus	t	1	1	2	2	–	–	–	–	–	–	–	–	–	–	–	1	1	2	2
Troglodytes troglodytes	s	1	1	2	3	–	–	–	–	3	2	2	3	3	5	6	–	–	–	–
Prunella modularis	s	8	7	10	4	2	1	2	1	18	12	13	14	16	19	14	1	2	1	–
Locustella fluviatilis	t	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–
Acrocephalus dumetorum	t	1	1	–	3	–	–	–	–	–	–	–	–	–	–	–	1	1	–	3
A. palustris	t	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Hippolais icterina	t	6	5	6	13	–	–	–	–	–	–	–	–	–	–	–	6	5	6	13
Sylvia atricapilla	s–t	28	22	21	25	–	–	–	–	1	5	7	7	7	6	6	27	20	19	24
S. borin	t	15	13	19	17	–	–	–	–	–	–	2	–	2	1	2	15	13	19	16
S. curruca	t	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Phylloscopus trochilus	t	13	23	15	24	–	–	2	5	2	7	7	7	7	7	9	12	20	10	16
Ph. collybita	s	2	2	4	3	–	–	2	–	3	4	5	5	5	3	6	–	–	–	–
Ph. sibilatrix	t	26	32	30	30	15	15	14	18	3	22	23	27	24	17	15	1	6	2	4
Ph. trochiloides	t	–	–	1	–	–	–	–	–	–	–	1	–	1	1	–	–	–	–	–
Regulus regulus	r	8	6	12	16	4	3	6	9	21	14	12	18	19	28	30	–	–	–	–
Ficedula hypoleuca	t	17	18	19	21	–	–	1	–	2	–	6	–	6	3	5	17	17	17	20
F. parva	t	3	2	1	–	2	–	–	–	–	–	1	–	1	–	–	–	–	–	–
Muscicapa striata	t	6	3	2	5	–	–	–	–	5	2	3	3	5	9	5	6	1	–	5
Phoenicurus phoenicurus	t	1	1	–	–	1	1	–	–	3	2	–	2	–	1	–	–	–	–	–
Erithacus rubecula	s	30	28	30	34	17	14	16	17	10	16	16	17	18	17	14	7	10	8	10
Luscinia luscinia	t	1	4	4	6	–	–	–	–	–	–	–	–	–	–	–	1	4	4	6
Turdus pilaris	s	5	11	10	47	–	–	–	–	–	–	–	–	–	–	2	5	11	10	47
T. merula	s	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
T. iliacus	s	12	13	10	17	–	–	–	–	–	–	–	–	–	–	–	12	13	10	17
T. philomelos	s	9	13	11	15	3	8	4	7	5	5	7	5	8	8	13	4	4	3	4
Aegithalos caudatus	r	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Parus palustris	r	1	3	4	7	–	–	–	–	–	–	–	–	–	–	–	1	3	4	7
P. montanus	r	4	–	8	8	2	–	5	6	1	1	5	1	5	3	7	2	–	1	1
P. cristatus	r	–	3	2	6	–	2	2	5	1	–	2	–	3	2	4	–	–	–	–
P. ater	r	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
P. caeruleus	r	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
P. major	r	3	4	2	4	–	–	–	–	–	–	–	–	–	1	–	3	4	2	4
Sitta europaea	r	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1
Certhia familiaris	r	2	2	1	4	–	–	–	2	5	4	9	4	11	7	6	–	–	–	–
Fringilla coelebs	s	89	90	76	86	35	38	25	25	51	54	51	65	61	55	53	35	32	29	44
F. montifringilla	s	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1
Carpodacus erythrinus	t	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Pyrrhula pyrrhula	r	1	–	3	2	–	–	2	–	1	1	–	2	–	2	6	–	–	–	–
Emberiza rustica	e	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–