

## **The Breeding Bird Community of a Primaeval Temperate Forest (Białowieża National Park, Poland) at the End of the 20th Century**

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# The breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland) at the end of the 20<sup>th</sup> century

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**Abstract.** The 1995–1999 results of the mapping technique censuses carried out in permanent plots situated in three types of old-growth primeval BNP stands (ash-alder riverine, oak-hornbeam, mixed coniferous) are presented and contrasted with the data gathered in the same plots in the late 1970s. Most community parameters, such as composition of breeding avifauna, species richness, make-up and cumulative proportion of dominants, remained basically unchanged. Only the overall bird density has increased considerably, by 13–38% in different plots. This has been due to parallel increases in numbers of several species, widely differing in their nesting sites, food requirements and migratory habits. As numbers increased simultaneously in all the plots, the density differences across habitats remained the same, from highest densities in riverine stands at the forest edge (up to 124 p/10 ha), through oak-hornbeam stands, to lowest in the coniferous stands (48–50 p/10 ha). Despite this differentiation the breeding avifauna in individual plots was quite similar (density similarity index exceeding 50%), indicating that their breeding assemblages constituted samples from a single bird community. In most cases the numerical increases could not be attributed to changes in local environmental factors, such as food resources, weather conditions or changes in habitat structure. Only in the coniferous stands, could habitat changes leading to diversification of their structure (gap formation, increasing number of deciduous trees) have been responsible for increasing species richness and abundance there. The apparent lack of a relationship between changes in bird numbers and the local situation suggests that the factors acting on a larger scale (outside the study area) could have been involved. Despite the directional changes in bird abundance observed in the Białowieża Forest, its breeding bird assemblage, when compared with amplitude of changes recorded over the same period in other areas and habitats, stands out as an example of remarkable stability.

**Key words:** bird community stability, primaeval forest, long-term study, species richness, community structure

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## INTRODUCTION

The current knowledge of the causes of variation in bird numbers indicates that there can be scores of indirect and direct environmental factors of natural and anthropogenic origin involved (review in Newton 1998). Many comprehensive studies have documented this for the European birds, to point out to the recent

books by Berthold (1990), Tucker & Heath (1994), Bauer & Berthold (1996), Hagemeyer & Blair (1997). However, the bulk of quantitative data on the stability-variability of bird community structure comes either from the habitats for ages deeply transformed by human activity or still undergoing successional changes (e.g. Busse 1973, Berthold 1990, Enemar et al. 1994). Interpretation of these results is thus complicated, as it is very

difficult to differentiate between contribution of a direct anthropogenic impact (habitat management, immediate disturbance or transformation) and that of indirect large-scale influences (e.g. climate change, habitat eutrophication or "acidification") to the observed changes in the bird communities (Gatter 2000).

At the time of a large-scale or global anthropogenic impact on the natural environment it is therefore of utmost importance to have some monitoring data from reference areas, in which direct human disturbance is at the minimum. The close-to-primaeval stands, protected in the Białowieża National Park (BNP) fulfil this requirements. The little disturbed forest constitutes one of the best preserved examples of nearly-pristine nemoral forest of the northern temperate zone. Its unique features have been well documented (Faliński 1986, Tomiałojć 1991, Jędrzejewska & Jędrzejewski 1998). The data collected here may, therefore, serve as a gauge for the bird community studies made in more transformed woodland habitats. We have amply documented, in a series of earlier papers (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, 1994, 1996, Wesołowski & Tomiałojć 1995, 1997), that it is justified to treat the BNP breeding bird community as representing the pristine state. Both the composition and the structure of this community were characterised by a considerable stability across the period of 20 years (1975–1994), in spite of substantial changes at the individual species level and of some slow directional trends.

The present paper, being an extension of the earlier ones, is aimed at:

- documenting the composition and structure of BNP bird community during 1995–1999;
- checking if earlier conclusions (Tomiałojć & Wesołowski 1994, 1996, Wesołowski & Tomiałojć 1997) on stability and trends in this forest bird community composition remain valid for the whole 25-year period of studies.

## STUDY AREA

**General description.** Detailed data on the whole Białowieża Forest (almost 1500 km<sup>2</sup>) and on its central unit constituting in its Polish part the Białowieża National Park (47.5 km<sup>2</sup>, since 1996 extended to cover 105 km<sup>2</sup>) can be found in earlier publications (Faliński 1968, 1986, 1991, Tomiałojć et al. 1984, Tomiałojć 1991, Wesołowski & Tomiałojć 1995, Jędrzejewski & Jędrzejewska 1998). Here it

should only be repeated that the Białowieża Forest is a remnant of vast European lowland forests once extending over a greater part of the continent and that the BNP stands are distinguished among temperate forests by some specific features, which are characteristic of rich primaeval forests. These are: multi-storey profile of stands, multi-species tree communities, an impressive age, height and size of trees, large amount of dead timber and uprooted trees, high species richness of other plants and animals inhabiting them (Faliński 1968, 1986, 1991, Tomiałojć & Wesołowski 1990, Wesołowski & Tomiałojć 1995, Jędrzejewska & Jędrzejewski 1998).

Since 1921 the most diverse and least disturbed part (47.5 km<sup>2</sup>) of the Białowieża Forest has been strictly protected within BNP. All our observations were made there, within seven permanent census plots (Fig. 1) established in 1975. Though the direct human influences were excluded, even a 10–20 km wide buffering zone of managed woodland surrounding the reserve could not make it totally immune to some indirect influences such as lowering ground-water level and some degree of the air pollution.

## DESCRIPTIONS OF THE CENSUS PLOTS

All the plots are situated in the never managed old growth stands of natural origin. Detailed descriptions of vegetation composition in the individual plots are given in Tomiałojć & Wesołowski (1996). Here only major features of each plot are summarised.

**Ash-alder riverine forest *Circaeo-Alnetum*** — plot K (33 ha) — Fig. 1. A fairly open-canopied and very patchy stand of alder *Alnus glutinosa*, ash *Fraxinus excelsior* and spruce *Picea abies*, with intrusions of 4 ha younger (c. 80–100 year) alder-birch regeneration and c. 6 ha of dry „islands” of the oak-lime-hornbeam stand (see earlier papers). Herb layer (0.5–1.7 m) very luxuriant. This habitat type is characterised by the highest amount of dead wood; there are about three times more fallen logs than in the oak-hornbeam stands (Wesołowski 1983). The area is less swampy than in pristine times, and has the ground- and pool-water level sunk by c. 10 cm, in comparison to the 1970s, owing to past amelioration works in the neighbouring Narewka rivulet and former meadows. The tree stand has become more patchy due to new wind-fall gaps, and its border with the meadows, formerly sharp, became replaced by a transitional zone of 20-year old alders.

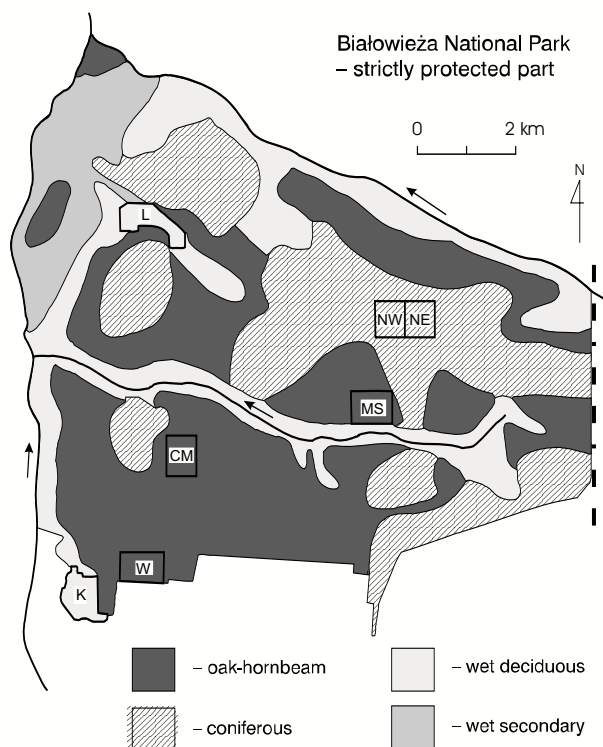


Fig. 1. Distribution of major habitat types and census plots (K, L, W, C, MS, NW, NE) in the strictly protected part of BNP.

**Alder-swamp forest *Carici elongatae-Alnetum*** — plot L (25 ha). Situated inside BNP (Fig. 1) this elongated plot where typical alder carr gradually turns into ash-alder association, both with admixture of spruces, is largely inundated area with tree-roots forming minute dry islands. It is characterised by the highest amount of uprooted and dead trees, most luxuriant, transparent canopy. During 25 years this tree stand became more heterogeneous due to more intensive gap formation, while the water level sunk by some 10 cm.

**Oak-lime-hornbeam forest *Tilio-Carpinetum***. The type of forest association prevailing in BNP, the most multilayered one and with the highest and most complex canopy. It is characterised by the low density of tree trunks, their largest dimensions and the highest diversity of trees (up to 12 species). The amount of dead timber is moderate here. During 25 years some falling trees created some new gaps. The proportion of spruce was declining while the share of lime and hornbeam was increasing.

Three plots in this habitat type — W (25.5 ha), CM (24 ha), MS (30 ha) form a gradient from plot W situated at the forest-edge to MS located three

km deep inside the BNP (Fig. 1). Structurally the plots were fairly similar, but the share of the main tree species varied. Hornbeam *Carpinus betulus* was most abundant tree species in plot W while lime *Tilia cordata* in plot CM. The latter plot had also the greatest share of spruce whereas in plot MS share of spruce was the lowest.

**Pine-bilberry coniferous forest *Peucedano-Pinetum*** — plots NW (25 ha) and NE (25 ha) — Fig. 1. Mixed coniferous-deciduous stands are trophically one of the poorest local habitat types. Trees, mostly spruces and pines *Pinus silvestris* with an admixture of birches *Betula spp.* and some oaks *Quercus robur* are of moderate size and grow very densely. Bush layer underdeveloped, herb layer low, the amount of dead timber (mainly broken stumps or logs) is rather moderate.

During 25 years some patches have matured, the number of old pines decreased, and new openings due to falling of clumps of dead spruces by wind appeared. The largest gaps were created by a tornado in 1987. Young hornbeams and limes were spreading increasingly in the undergrowth.

## METHODS

The censuses were designed so as to produce data adequate for multisided use. The most accurate census method producing close-to-absolute density values was applied (Tomiałojć 1980, Verner 1985) which yielded results comparable between species. The plots were fairly large (24–33 ha), provided with 50×50 m grid system of orientation marks and were situated only in old-growth stands to avoid additional complexities with the re-growth stage. Totally they covered 187.5 ha.

### Census method

An improved version of the mapping technique (a combined mapping) for censusing breeding birds was applied (Tomiałojć 1980). Plot K, as the richest in birds, was subdivided into two parts of c. 16 ha each and censused by two observers, or on the two consecutive mornings. All field work was done by experienced field workers, new participants were admitted only after a period of apprenticeship, and after making sure that they were able to gather field data of adequate quality.

The accuracy of the method was checked by comparing census data with the true bird numbers known for some species from additional, more

careful, estimates based partly or entirely on individually marked birds (Wesołowski 1983, 1985, Wesołowski et al. 1987, Piotrowska & Wesołowski 1989). Most species were registered with a less than 10% field error. However, in the case of some species (*Turdus philomelos*, *Coccothraustes coccothraustes*, *Ficedula albicollis*, probably *Regulus regulus*), methodical papers by Tomiałojć (1980, 1994), Tomiałojć & Lontkowski (1989) and Walankiewicz et al. (1997) showed that their numbers, chiefly in the high density situations, could be underestimated by some 20–33%. Hence, for very careful calculations of the community parameters some arithmetical corrections would be necessary. However, in order to avoid confusion, the data in the tables below contain no such corrections.

Every year at least ten visits (sometimes 11–12, to compensate for adverse weather conditions) were made between 10 April and 25 June to each plot. Plots were checked by proceeding along marked lines, 100 m apart, though leaving the line for side-penetrations when necessary, and each time choosing a different route across the plot. For the purpose of high inter-plot comparability all plots were visited on a rotational basis by every person conducting the field work (4–7 census-takers). One (sometimes two) visit was performed in the evening for mapping dusk active birds. In such case a 24–30 ha plot was censused after being divided between two observers.

### Data processing

All records from field maps were assembled on species maps (scale 1:1000) for their evaluation. To assure maximum consistency of evaluation rules (see Morozov 1995) all estimates of cluster/territory numbers on species maps were checked by at least three of us. The final estimate was arrived at after negotiating the (usually minor) differences. When processing the data it was taken into account that a higher number of double-registrations of the same individuals resulted from our relatively slow proceeding through the plot. While drawing the „paper territories” around the clusters of records we relied mainly on the presence/absence of contemporary records which helped to avoid apparent tendency in mobile individuals/species to form double clusters in the place of a single large territory (Tomiałojć 1980). As a rule three records were required as a minimum to draw a cluster, with a few exceptions in the case of late arriving, inconspicuous species (e.g. *Muscicapa striata*, *Locustella fluviatilis*), and unsuitable weather conditions during visits valid

for them; then only two records of high territorial significance were assumed to indicate the territory. Many nests found (especially helpful in *Sturnus vulgaris*) and a judgement from bird behaviour were also helpful in deciding on the number of recognised clusters/territories. The territories of bigamists (Wesołowski 1987) or bachelor males were treated as equivalent to those of monogamists.

Compared with the other papers, our species richness estimates may be somewhat higher because they include also those bird territories which were found to occur only partly within the plot boundaries (marked with the sign „+” in the tables). In most cases, they constituted scarce but important elements of a bird assemblage.

Following our earlier approach (Tomiałojć & Wesołowski 1990, 1994, 1996) we use the number of species as the simplest and most basic measure of species richness, and the cumulative share of dominants (species constituting over 5% of community) for expressing the evenness.

The comparisons of bird community structure between plots were done with the application of the index of density similarity calculated according to Sørensen's formula:

$$DS = 2 \frac{\sum_{i=1}^{\min(d_1, d_2)} \min(d_1, d_2)}{D_1 + D_2} \times 100\%$$

where  $d_{1i}$  and  $d_{2i}$  are densities of the  $i$ -th species in the assemblages 1 and 2, and  $D_1$  and  $D_2$  are total densities of assemblages 1 and 2 respectively. The index varies between 0 (no species in common) and 100 (identical densities of all species). The calculations have been based on mutually independent values (densities) instead of on relative ones (dominance = percentage), the latter often slurring over the real differences in abundance of several community components. For our considerations similar density of a species in two habitats is more important than its similar percentage because we could find no support in our data for the idea of a tightly organised bird community (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990), in which the presence of one species would depend on or strongly influence the numbers of the other ones.

To analyse year-to-year changes in numbers of a species (or guild) in whole BNP (in contrast to variation among individual patches), following Wesołowski & Tomiałojć (1997), we calculated indices of yearly abundance for individual species and guilds. This was done as follows: numbers of



breeding territories of a species recorded in all plots censused in a compared year were summed. The same was done for numbers of territories found in the same set of plots in the base year (1977). Then the index of abundance was finally achieved by dividing the sum of territories in the compared year by the 1977 sum, and expressed as a percentage of the 1977 value.

To avoid problems with excessive variability of small samples due to sampling error the indices were calculated only for more numerous species, i.e. those breeding in every season and represented by 10 or more breeding pairs in all the plots in a season. Hence, of 81 species found breeding in the study plots at least one year the indices could be produced only for the 26 most numerous ones. However, they numerically made up over 80% of the BNP breeding bird community (Tomiałojć & Wesołowski 1990, 1997).

Analogously we also calculated indices for the groups (guilds) of birds with common feeding, nesting or migratory habits, as well as for the whole breeding bird community. In those calculations we took into account data on all breeding species, irrespective of their abundance. Subsequently to Tomiałojć et al. (1984), we distinguished the following guilds:

**Foraging** — hierarchical classification — birds foraging outside forest (independently of type of food taken — O) versus within-forest foragers: predators (hunting mainly vertebrates — P), vegetarians (including seed eaters — V), and „insectivores”; the last group was subdivided into ground-feeders (IG), bark-feeders (IB) and crown-feeders (IL).

**Nesting** — three guilds reflecting increasing nest vulnerability: ground (on the ground or in low vegetation up to 1–1.5 m above the ground — G), crown (open or domed nests in high bushes or in trees — C), hole (H). There were no nest-boxes in our plots, and hole-nesting birds nested entirely in natural cavities.

**Migration** — four guilds: tropical (winter south of Sahara — T), short-distance (winter mainly in SW Europe and in the Mediterranean basin — S), resident (winter outside the forest itself but still within the same geographic and climatic region, also nomadic species — R), forest resident (stay whole year in their breeding habitats — RF).

The guilds consist of 8 (IB) to 37 (IL) species. A full list of allocations of individual species to particular guilds is given in Tomiałojć & Wesołowski (1990). Here we followed those earlier allocations in all but two cases, namely

*Sylvia atricapilla* (formerly short-distance) had been moved to the tropical category, whereas *Coccothraustes coccothraustes* (formerly resident) had been displaced to the short-distance group, in light of more recent information (Berthold & Solonen 1997, authors' data).

To calculate an index value for an individual guild in a single season we summed up the total number of pairs of all species ranked with this group recorded breeding in all plots censused in that year and compared them with their number in the same plots in 1977. In cases of species included simultaneously in more than one guild (Tomiałojć & Wesołowski 1990), we parted their numbers and included them proportionally to different categories. For example, as *Parus major* is classified as half ground insectivore and half crown insectivore (Tomiałojć & Wesołowski 1990), thus, the total number of pairs of this species recorded in a given season was divided by two and one half was included into IG and the other half into IL foraging guilds. Because of too small sample size (see above) the index for the predator (P) guild could not be calculated.

## Environmental variables

### Weather conditions

Meteorological data were derived from the local weather station in Białowieża village, situated in the centre of the Białowieża Forest complex, less than 1 km from S edge of BNP (Wesołowski & Stawarczyk 1991, Wesołowski 2001a, data of T. Wesołowski). In 1995–1999 mean values of weather variables were: annual precipitation 637 mm, annual temperature +7.5°C, July temperature +19.7°C, and January temperature −3.7°C. Snow cover (up to 63 cm) lasted 59–138 days, snow melting occurred between March 20 (1995) and April 19 (1996). The values recorded were close to long-term averages — for details see Faliński (1968, 1986), Tomiałojć & Wesołowski (1990, 1994), Tomiałojć et al. (1984), Jędrzejewska et al. (1997). To characterise winter conditions, we used the mean temperature in the period December–March, because it had been shown earlier (Wesołowski 1994) that, due to very strong correlation between different weather factors (number of days with snow, minimum temperatures, temperatures of the coldest months) a single variable was sufficient to describe winter severity in Białowieża.

## Food-resources

Caterpillars constitute an important source of insect food for birds in the deciduous BNP stands (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, 1994, Wesołowski 1983, Wesołowski & Stawarczyk 1991, Tomiałojć 1995, Rowiński & Wesołowski 1999). Leaf-eating caterpillars (mostly *Geometridae* and some *Tortricidae*) were counted once each season, in May, always at the same stage of leaf development. Each time 50–120 standard twigs (0.25 m<sup>2</sup>) from the lower parts of the hornbeam undercanopy were searched and the caterpillars counted (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1994, 1996). The caterpillar numbers fluctuated widely; numbers of *Operophtera brumata* (*Geometridae*) caterpillars on hornbeam were very high in 1995 — 9.1 and much lower (0.4–1.9 caterpillars/twig) in other years. In 1995 they caused visible defoliation of many hornbeams *Carpinus betulus* and other deciduous trees. During 1996–1999 *Ptilophora plumigera* (*Notodontidae*) caterpillars caused partial defoliation of continental maples (Rowiński & Wesołowski 1999). In the conifer-dominated and riverine stands, no strong caterpillar outbreaks were observed, an outbreak of spruce bark beetle *Ips typographus* occurred in all stands in 1995–1997. Mosquitoes were usually abundant in all types of stands, but were less numerous than in the plague humid seasons of 1970s. Mast fruiting of pedunculate oak occurred in 1996 and that of hornbeam in 1997.

## Statistical analysis

All procedures used followed the formulas given in STATISTICA for Windows (Anonymous 1996). Before running parametric statistical procedures all variables had been checked for normalcy and, when necessary, log-transformed to improve the fit. When checking for the existence of long-term numerical trends, to get more meaningful estimates, we combined the current data (1995–1999) with the ones from the previous pentad (1989–1994, Wesołowski & Tomiałojć 1997) to produce a ten-year data set. We therefore could look for the existence of numerical trends in the BNP breeding birds in the decade of 1990s.

## RESULTS

Overall, 74 species were found breeding at least once within all the plots in 1995–1999 (Tables 1–7). That is  $\frac{2}{3}$  of 111 true forest and forest-edge species known to breed in the Białowieża Forest (Tomiałojć & Wesołowski 1990). All those species

had been already breeding in earlier years, 72 of them bred in the plots also in the previous five-year period, and 68 already in the late 1970s. Thus, with minor exceptions, the species composition did not change.

As it was previously, species richness in the forest edge riverine plot K — total 69, mean 48.4 breeding species (Tables 1, 8) was the highest, followed by plot W with the mean of 38.6 species (Table 8). However, due to increase of species richness in the coniferous plots (Tables 6–7), the mean number of species breeding there (34–36) started to exceed their number in the forest interior oak-hornbeam plots (32–33, Table 8). However, the difference was not significant.

## Community composition

Within the current pentad, the DS values of any pair-wise comparison of seasons in the same plot yielded as a rule similarities exceeding 80%, but they could be as low as 68.8% in the extreme cases (plot NE, years 1996 and 1999). Thus, similarities of different oak-hornbeam and riverine plots — DS = 78–91% (Table 9) indicate, that their breeding bird assemblages constituted samples from the same community. Only the coniferous plots harboured somewhat different variant of bird community, but still quite related to the ones found in the deciduous stands (in most cases DS > 50%, Table 9). Overall, the bird assemblages in different plots were currently more similar to one another, than it was in the late 1970s. Within the same plot, similarity of the mean community composition between the latter and the current period was remarkable, the DS values varied between 76.4 (plot K) and 79.6% (plot NE).

Composition of the group of dominants did not change substantially in comparison with the early 1990s. As before *Fringilla coelebs* and *Erithacus rubecula* were dominants in all years and all plots (Tables 1–7), *Phylloscopus sibilatrix* remained dominant in coniferous habitats (Tables 6–7) and less frequently so in the oak-hornbeam stands (Tables 3–5). Apart from being regularly among dominants in the oak-hornbeam stands (Tables 3–5) *Ficedula albicollis* became also dominant in the ash-alder forests (Tables 1–2). *Turdus philomelos* remained dominant in all types of habitats, *Sylvia atricapilla* in swampy stands (Tables 1–2), *Coccothraustes coccothraustes* in oak-hornbeam (Tables 3–5) and *Regulus regulus* in coniferous forest (Tables 6–7). Only appearance of *Parus ater* in the group of dominants in the coniferous plots (Tables 6–7) was a new phenomenon. Except for

Table 1. The breeding bird assemblage of the ash-alder forest (plot K, 33 ha). + — breeding, less than 0.5 territory, – — non breeding, bold type — dominant (constituting  $\geq 5\%$  of community). In the species for which number ranges are given, the means were used for all further calculations.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	<b>66.5</b>	<b>69</b>	<b>70</b>	<b>67</b>	<b>82</b>	21.5	<b>19.1</b>
<i>Erithacus rubecula</i>	<b>35–36</b>	<b>26.5</b>	<b>23.5</b>	<b>30</b>	<b>34.5</b>	9.1	<b>8.0</b>
<i>Ficedula albicollis</i>	<b>29.5–30.5</b>	<b>22.5</b>	<b>19.5–20.5</b>	<b>31.5–32.5</b>	<b>34</b>	8.4	<b>7.4</b>
<i>Sturnus vulgaris</i>	10.5	<b>28</b>	<b>19</b>	<b>18</b>	<b>21</b>	5.8	<b>5.2</b>
<i>Sylvia atricapilla</i>	17	17	<b>17.5</b>	<b>21</b>	<b>21</b>	5.7	<b>5.0</b>
<i>C. coccythraustes</i>	13.5	<b>21.5</b>	14	14–15	16.5	4.8	4.3
<i>Turdus philomelos</i>	<b>21</b>	11.5	11.5	16	15.5–16.5	4.6	4.1
<i>Phylloscopus collybita</i>	16–17	15	13	11–12	11.5	4.1	3.6
<i>Parus major</i>	14.5	10	11.5	14	16.5	4.0	3.6
<i>Troglodytes troglodytes</i>	14.5	10.5	11	13	13.5	3.8	3.4
<i>Parus caeruleus</i>	11	13.5	9–11	10.5–12.5	15.5–16.5	3.8	3.3
<i>Prunella modularis</i>	13	11–12	10	11.5	12	3.5	3.1
<i>Sitta europaea</i>	12.5	12	12	9	10	3.4	3.0
<i>Turdus merula</i>	12	10.5	9	11.5	10.5	3.2	2.9
<i>Phylloscopus sibilatrix</i>	15	10.5–11.5	7	12–13	8	3.2	2.9
<i>Regulus regulus</i>	10	10–11	8	7–8	11	2.8	2.5
<i>Certhia familiaris</i>	7–8	8.5	7.5	6.5	9	2.4	2.1
<i>Muscicapa striata</i>	8–9	7	6	10–11	6–7	2.3	2.1
<i>Parus palustris</i>	6	5.5	6.5	5–6	6	1.8	1.6
<i>Dendrocopos major</i>	2	3.5	4.5	3.5	5.5	1.2	1.0
<i>Sylvia borin</i>	7–8	2.5	5	1.5	2.5	1.2	1.0
<i>Ficedula hypoleuca</i>	4	2	4	4	4–5	1.1	1.0
<i>Dendrocopos medius</i>	2.5–3.5	3	4	3.5	3	1.0	0.9
<i>Columba palumbus</i>	3.5	1.5	4	4.5	2–3	1.0	0.9
<i>Oriolus oriolus</i>	2.5	2	4	4	3	0.9	0.8
<i>Carpodacus erythrinus</i>	3	4	2.5–3	0.5	2	0.7	0.7
<i>Hippolais icterina</i>	4.5	3.5	1.5	1	1	0.7	0.6
<i>Regulus ignicapillus</i>	1–2	–	2	2	4	0.6	0.5
<i>Carduelis carduelis</i>	2	2	1	1	3–4	0.6	0.5
<i>Dendrocopos minor</i>	2.5	1.5	1	1.5	2	0.5	0.5
<i>Garrulus glandarius</i>	1.5–2	2	1.5	1.5	1–2	0.5	0.4
<i>Cuculus canorus</i>	1	1	1	2	2.5	0.5	0.4
<i>Anthus trivialis</i>	3	2–3	0.5	0.5	1	0.5	0.4
<i>Pyrrhula pyrrhula</i>	1	2	1	1	1	0.7	0.3
<i>Parus ater</i>	–	1	1	–	4	0.4	0.3
<i>Turdus iliacus</i>	2	1	2	–	–	0.3	0.3
<i>Dendrocopos leucotos</i>	1	1	1	1	1	0.3	0.3
<i>Apus apus</i>	–	1	1	1	2	0.3	0.3
<i>Parus cristatus</i>	1	1	1	–	1	0.2	0.2
<i>Aegithalos caudatus</i>	–	1	1	–	2	0.2	0.2
<i>Locustella fluviatilis</i>	2	0.5	0.5	+	+	0.2	0.2
<i>Jynx torquilla</i>	1	–	–	1	1	0.2	0.2
<i>Picus canus</i>	0.5	+	1	0.5	–	0.1	0.1
<i>Carduelis chloris</i>	1	1	+	–	+	0.1	0.1
<i>Scolopax rusticola</i>	–	1	+	+	1	0.1	0.1
<i>Dryocopus martius</i>	0.5	0.5	+	0.5	0.5	0.1	0.1
<i>Aquila pomarina</i>	0.5	0.5	0.5	0.5	–	0.1	0.1
<i>Ficedula parva</i>	1	–	+	–	1	0.1	0.1
<i>Buteo buteo</i>	0.5	+	0.5	+	+	0.1	0.1
<i>Tringa ochropus</i>	–	–	+	1	+	0.1	0.1
<i>Emberiza citrinella</i>	–	1	–	–	–	0.1	0.1
<i>Carduelis spinus</i>	1	–	–	–	–	0.1	0.1
<i>Strix aluco</i>	0.5	–	–	+	–	–	–
<i>Picoides tridactylus</i>	–	–	+	–	0.5	–	–
<i>Acrocephalus palustris</i>	–	–	0.5	–	–	–	–
<i>Sylvia communis</i>	–	–	+	–	–	–	–
<i>Luscinia luscinia</i>	–	–	–	+	–	–	–
<i>Streptopelia turtur</i>	+	–	–	–	–	–	–
<i>Accipiter nisus</i>	+	–	–	–	–	–	–
Total (69 species)	390.5	365.2	335.5	361.0	409.4	112.8	100.0



Table 2. The breeding bird assemblage of the alder-swamp forest (plot L, 25 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	46	37.5	44.5	42	42.5	17.0	19.5
<i>Erithacus rubecula</i>	21	23.5	16.5–17.5	21–22	18.5	8.1	9.4
<i>Ficedula albicollis</i>	18–19	14.5	15	19–20	19.5	7.0	7.9
<i>Turdus philomelos</i>	13–14	10	9	9.5–10.5	10–11	4.2	4.8
<i>Turdus merula</i>	11	9.5	8–8.5	12	12	4.2	4.8
<i>Phylloscopus collybita</i>	12.5–13.5	9.5–10.5	9	6.5	8	3.7	4.3
<i>Sylvia atricapilla</i>	10	8	8.5	8.5	8.5	3.5	4.0
<i>Parus caeruleus</i>	7	7–8	7	9	11.5	3.4	3.8
<i>C. coccythraustes</i>	5–6	8	7–8	8.5	11.5	3.3	3.7
<i>Parus major</i>	8	5–6	7.5	8	12	3.3	3.7
<i>Troglodytes troglodytes</i>	10	6.5	7	7.5	8.5	3.2	3.6
<i>Sitta europaea</i>	6.5	8.5	8	6	9.5	3.1	3.5
<i>Regulus regulus</i>	8–9	5.5	7	7	11	3.1	3.5
<i>Prunella modularis</i>	7	6.5	8	8–9	7.5	3.0	3.4
<i>Ficedula hypoleuca</i>	5–6	5–6	5	6	8.5	2.4	2.8
<i>Certhia familiaris</i>	5	3.5	4.5	6.5–7	5	2.0	2.3
<i>Phylloscopus sibilatrix</i>	9	2.5	0.5	4	4	1.6	1.8
<i>Parus palustris</i>	2.5	2–3	4	3.5–4	5.5	1.5	1.7
<i>Dendrocopos major</i>	2	3.5	3.5	3.5	3.5–4	1.3	1.5
<i>Muscicapa striata</i>	2	3	5–6	2	3–4	1.3	1.5
<i>Dendrocopos medius</i>	2	2	3	2	2–3	0.9	1.1
<i>Columba palumbus</i>	2.5	1	1	4	2	0.8	0.9
<i>Tringa ochropus</i>	2	1	2	2	2	0.7	0.8
<i>Carduelis spinus</i>	1.5	2	–	2	2	0.6	0.7
<i>Cuculus canorus</i>	1	1	1	1.5	3	0.6	0.7
<i>Garrulus glandarius</i>	1	1	1	3	1	0.6	0.6
<i>Apus apus</i>	1–2	1	+	2	1–2	0.5	0.5
<i>Pyrrhula pyrrhula</i>	+	1	2	0.5	2	0.4	0.5
<i>Parus ater</i>	1	–	–	+	5	0.5	0.5
<i>Oriolus oriolus</i>	–	–	1	3	1	0.4	0.4
<i>Dendrocopos minor</i>	1.5	1–2	+	1	–	0.3	0.4
<i>Dendrocopos leucotos</i>	1	0.5	1	0.5	0.5	0.3	0.3
<i>Scolopax rusticola</i>	+	1	+	+	1	0.2	0.2
<i>Picoides tridactylus</i>	0.5	0.5	1	–	–	0.2	0.2
<i>Dryocopus martius</i>	0.5	–	0.5	+	0.5–1	0.1	0.2
<i>Parus cristatus</i>	0.5	–	–	+	1	0.1	0.1
<i>Aegithalos caudatus</i>	–	–	–	–	1–2	0.1	0.1
<i>F. albicollis</i> x <i>F. hypoleuca</i>	–	–	1	–	–	0.1	0.1
<i>Regulus ignicapillus</i>	1	–	–	–	–	0.1	0.1
<i>Bonasa bonasia</i>	–	–	+	–	0.5		0.1
<i>Ficedula parva</i>	–	–	–	–	0.5		
<i>Gallinago gallinago</i>	–	+	–	–	–		
<i>Nucifraga caryocatactes</i>	–	–	–	+	–		
Total (54 species)	229.2	195.1	201.2	222.5	249.0	87.8	100.0

plot NE, evenness did not change from the early 1990s; the cumulative share of dominants amounted to 42–59% (Table 8).

Total bird density

An increasing trend found in the early 1990s continued during the recent pentad, the overall density index reached its highest value — 147% — in 1999 (Table 10). In comparison with the early 1990s (Tomiałojć & Wesołowski 1996), mean densities in the deciduous plots except MS were by 8–13% higher but mean densities in the coniferous

plots remained unchanged. However, when compared with the 1970s (Tomiałojć et al. 1984), the mean densities in all plots were significantly higher (by 13–38%) in the recent period. These differences, however, did not affect ranking of individual plots. As before, densities in the forest edge plots — K and W were the highest, exceeding 100 p/10 ha, with the maximum value 124.2 p/10 ha recorded in plot K in 1999 (Table 1). Values in the interior deciduous habitats, 82–86 p/10 ha, were intermediate and those in the coniferous plots, 48–50 p/10 ha (Table 8) were the lowest.

Table 3. The breeding bird assemblage of the oak-hornbeam-lime forest (plot W, 25.5 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	<b>47.5–48.5</b>	<b>58.5</b>	<b>55</b>	<b>61</b>	<b>59.5</b>	22.1	<b>21.7</b>
<i>Ficedula albicollis</i>	<b>31.5</b>	<b>31</b>	<b>29</b>	<b>33</b>	<b>30</b>	12.1	<b>11.9</b>
<i>C. coccythraustes</i>	<b>17</b>	<b>27</b>	<b>18</b>	<b>19–20</b>	<b>26</b>	8.4	<b>8.2</b>
<i>Erithacus rubecula</i>	<b>19.5</b>	<b>24</b>	<b>16.5</b>	<b>22</b>	<b>21.5–22.5</b>	8.2	<b>8.0</b>
<i>Turdus philomelos</i>	<b>16</b>	<b>16.5</b>	<b>14</b>	<b>15.5</b>	<b>16–17</b>	6.2	<b>6.0</b>
<i>Phylloscopus sibilatrix</i>	<b>21.5</b>	<b>17</b>	6	12	4.5	4.8	4.7
<i>Parus caeruleus</i>	11.5	10.5	6–7	6.5–7.5	11–13	3.7	3.6
<i>Parus major</i>	7.5–8	8.5	8.5	7	<b>14.5</b>	3.6	3.5
<i>Sitta europaea</i>	6	10	11	5	7.5	3.1	3.0
<i>Sylvia atricapilla</i>	7–8	9.5	6.5	5.5	7.5	2.9	2.8
<i>Turdus merula</i>	5–5.5	6	7	7–8	10.5	2.8	2.8
<i>Parus palustris</i>	5	5.5	7	6.5	8.5	2.5	2.5
<i>Regulus regulus</i>	5	5	5.5	5	8.5	2.3	2.2
<i>Troglodytes troglodytes</i>	7–7.5	4	4.5	5.5	6.5	2.2	2.1
<i>Muscicapa striata</i>	4–5	4	5	3–4	5	1.7	1.7
<i>Sturnus vulgaris</i>	3–4	4	7	2	5	1.7	1.7
<i>Certhia familiaris</i>	3	4	5.5	4	5	1.7	1.7
<i>Dendrocopos major</i>	2–2.5	4	5	3	3	1.4	1.3
<i>Ficedula parva</i>	3.5–4	2.5	2–3	2	4–5	1.2	1.2
<i>Columba palumbus</i>	1.5	3	3	3	4.5	1.2	1.1
<i>Phylloscopus collybita</i>	2.5	3.5	2.5	2	2	1.0	1.0
<i>Prunella modularis</i>	3	5	–	3.5	1	1.0	0.9
<i>Dendrocopos medius</i>	2	2.5	3.5	1–1.5	2.5–3	0.9	0.9
<i>Anthus trivialis</i>	2.5	4.5	1	0.5	0.5	0.7	0.7
<i>Garrulus glandarius</i>	1	1	1.5	1.5–2	1.5–2.5	0.6	0.6
<i>Carduelis chloris</i>	1	1	1	1	3	0.5	0.5
<i>Pyrrhula pyrrhula</i>	2	1–2	1	1	–	0.4	0.4
<i>Cuculus canorus</i>	1	1	+	0.5	2	0.4	0.3
<i>Jynx torquilla</i>	0.5	1	–	1	2	0.4	0.3
<i>Oriolus oriolus</i>	0.5	+	1	1	1.5	0.3	0.3
<i>Dendrocopos leucotos</i>	1	0.5	1	1	0.5	0.3	0.3
<i>Regulus ignicapillus</i>	2	–	1	–	1	0.3	0.3
<i>Ficedula hypoleuca</i>	2	1	–	–	–	0.2	0.2
<i>Parus cristatus</i>	0.5	1	1	–	0.5	0.2	0.2
<i>Dendrocopos minor</i>	1	+	1	0.5	+	0.2	0.2
<i>Dryocopus martius</i>	0.5	0.5	0.5	0.5	0.5–1	0.2	0.2
<i>Aegithalos caudatus</i>	–	–	1–1.5	–	1	0.2	0.2
<i>Parus ater</i>	–	–	–	–	2	0.2	0.1
<i>Turdus iliacus</i>	–	1	–	–	–	0.1	0.1
<i>Carduelis spinus</i>	–	1	–	–	–	0.1	0.1
<i>Motacilla alba</i>	–	1	–	–	–	0.1	0.1
<i>Picus canus</i>	–	–	–	+	0.5–1	0.1	0.1
<i>Strix aluco</i>	0.5	+	–	–	–	–	–
<i>Emberiza citrinella</i>	+	–	–	–	0.5	–	–
<i>Hippolais icterina</i>	0.5	–	–	–	–	–	–
<i>Bonasa bonasia</i>	–	–	–	–	0.5	–	–
<i>Sylvia borin</i>	+	–	–	+	–	–	–
<i>Scolopax rusticola</i>	–	–	+	–	+	–	–
<i>Picoides tridactylus</i>	+	–	–	–	+	–	–
<i>Corvus corax</i>	–	–	–	+	–	–	–
<i>Phylloscopus trochilus</i>	–	+	–	–	–	–	–
Total (63 species)	251.6	281.9	240.5	245.3	285.6	102.2	100.0

Some increase in densities in the deciduous stands, without parallel increase in the number of species breeding there, resulted in the significant increase of the density of mean species there, from 2 p/10 ha in the 1970s to 2.3–2.6p/10 ha. This parameter, however, remained stable in the

coniferous plots, where species richness and overall density increased in parallel (Table 8).

### Assemblage guilds

By linearly regressing respective indices of abundance for each guild as a function of time we

Table 4. The breeding bird assemblage of the oak-hornbeam-limeforest (plot CM, 24 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	38.5	46	60	57.5	45	20.6	23.9
<i>Ficedula albicollis</i>	21	23.5	26.5	27.5–28.5	21.5	10.0	11.7
<i>Erithacus rubecula</i>	19.5–20.5	16.5	16	20	17	7.5	8.7
<i>C. coccythraustes</i>	9	20.5	10.5	14.5	15.5	5.8	6.8
<i>Turdus philomelos</i>	8.5	8.5	11	12–13	10.5	4.3	4.9
<i>Parus major</i>	4.5	5.5	10	6	12	3.2	3.6
<i>Parus caeruleus</i>	8–9	8–9	4.5	6–7	8–9	3.0	3.6
<i>Turdus merula</i>	6	6	6	6	11	2.9	3.4
<i>Troglodytes troglodytes</i>	8	5	6.5	6	7.5	2.8	3.2
<i>Sylvia atricapilla</i>	5.5	7.5	6–7	6.5	6.5	2.7	3.2
<i>Phylloscopus sibilatrix</i>	16.5	3.5	–	11	–	2.6	3.1
<i>Sitta europaea</i>	3.5	7.5–8	9.5	3–3.5	5.5	2.5	2.8
<i>Regulus regulus</i>	7	4	6.5	4–6	6	2.4	2.8
<i>Certhia familiaris</i>	4.5	4–4.5	5–5.5	4	5.5	2.0	2.3
<i>Parus palustris</i>	3.5	4.5–5	4.5	3.5–4	5.5	1.8	2.1
<i>Prunella modularis</i>	4–5	7	3	2	4.5	1.8	2.1
<i>Columba palumbus</i>	2	2	3.5	4.5	3.5	1.3	1.5
<i>Muscicapa striata</i>	4	6	4	1	–	1.3	1.5
<i>Phylloscopus collybita</i>	2	3.5	3	1.5	2.5	1.0	1.2
<i>Dendrocopos major</i>	1	2.5	3.5	2	3.5	1.0	1.2
<i>Dendrocopos medius</i>	2	2	2	2–3	2	0.9	1.0
<i>Parus ater</i>	1	1	2	1	3	0.7	0.8
<i>Garrulus glandarius</i>	1	1.5	1.5	1.5	1–2	0.6	0.7
<i>Ficedula parva</i>	1	–	1	3	2	0.6	0.7
<i>Ficedula hypoleuca</i>	2–3	1	+	–	2	0.5	0.6
<i>Cuculus canorus</i>	+	–	1	1	2	0.3	0.4
<i>Pyrrhula pyrrhula</i>	+	1–2	1	+	1	0.3	0.4
<i>Dryocopus martius</i>	0.5	0.5	0.5	0.5	1	0.3	0.3
<i>Dendrocopos minor</i>	+	–	1	1	0.5–1	0.2	0.3
<i>Oriolus oriolus</i>	+	0.5	1	–	1	0.2	0.2
<i>Parus cristatus</i>	–	0.5	–	1	1	0.2	0.2
<i>Apus apus</i>	–	+	1	0.5–1	+	0.2	0.2
<i>Dendrocopos leucotos</i>	+	0.5	0.5	0.5	+	0.1	0.2
<i>Anthus trivialis</i>	1.5	–	–	–	–	0.1	0.2
<i>Sturnus vulgaris</i>	1	–	–	–	–	0.1	0.1
<i>Scolopax rusticola</i>	–	+	–	–	1	0.1	0.1
<i>Aegithalos caudatus</i>	–	–	–	–	1	0.1	0.1
<i>Carduelis spinus</i>	–	–	–	–	1	0.1	0.1
<i>Picoides tridactylus</i>	+	–	–	+	0.5	0.1	0.1
<i>Strix aluco</i>	–	–	–	–	+		
<i>Sylvia borin</i>	–	–	+	–	–		
<i>Buteo buteo</i>	–	–	+	–	–		
<i>Accipiter nisus</i>	–	–	–	+	–		
Total (48 species)	189.1	202.0	213.1	214.6	212.6	85.9	100.0

calculated long-term numerical trends, the regression slopes represented the trends. None of the guilds showed signs of decline in 1990–1999, their numbers either fluctuated or showed significant positive trends (Table 10).

Among foraging guilds the increasing trends were significant in vegetarians and in birds collecting invertebrate food among leaves of trees or high bushes (Table 10). The changes in the latter group did not follow changes in the caterpillar numbers in 1990–1999, which peaked in 1993 and

declined later on (n caterpillars/hornbeam twig vs. year; regression slope = −0.55, F = 3.47, p = 0.1).

An increasing trend found in the hole- and crown-nester densities in the early 1990s continued but the ground-nesters did not show any trend (Table 10). In comparison with 1970s, the mean densities of hole and crown nesters were by 40–50% higher in 1995–1999, whereas those of the ground nesters were slightly (not significantly) lower.

Among migratory guilds, the significant increase was recorded only in the short-distance

Table 5. The breeding bird assemblage of the oak-hornbeam-lime forest (plot MS, 30 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	<b>43</b>	<b>54.5</b>	<b>64</b>	<b>59</b>	<b>58</b>	18.6	<b>22.7</b>
<i>Ficedula albicollis</i>	<b>30.5</b>	<b>32</b>	<b>25–26</b>	<b>32.5</b>	<b>31.5</b>	10.1	<b>12.4</b>
<i>Erithacus rubecula</i>	<b>24.5–25.5</b>	<b>20.5</b>	<b>18.5</b>	<b>19.5</b>	<b>22</b>	7.0	<b>8.7</b>
<i>C. coccythraustes</i>	<b>12</b>	<b>25.5</b>	<b>15</b>	<b>17</b>	<b>15</b>	5.6	<b>6.9</b>
<i>Parus caeruleus</i>	8.5–9.5	12	9.5	10.5	<b>15.5</b>	3.8	4.6
<i>Parus major</i>	8.5	9	<b>12.5</b>	11	<b>14.5</b>	3.7	4.5
<i>Turdus philomelos</i>	10	9	<b>12.5</b>	10	11	3.5	4.3
<i>Sitta europaea</i>	8	10.5	<b>13</b>	9	10	3.4	4.1
<i>Phylloscopus sibilatrix</i>	<b>19</b>	4	0.5	<b>15</b>	8.5	3.1	3.9
<i>Turdus merula</i>	7.5	8.5	8.5	6	9	2.6	3.2
<i>Sylvia atricapilla</i>	6.5	8	7	6–7	4.5	2.2	2.7
<i>Parus palustris</i>	5.5	5.5	7.5	6.5	7.5	2.2	2.7
<i>Troglodytes troglodytes</i>	7.5	6.5	4.5	6	7.5	2.1	2.6
<i>Certhia familiaris</i>	3.5–4	4.5	5.5	6	4.5–5.5	1.7	2.0
<i>Regulus regulus</i>	4	4.5	3–4	3.5	5–6	1.4	1.7
<i>Dendrocopos medius</i>	3	3–5	4	4	3–4	1.2	1.5
<i>Ficedula hypoleuca</i>	5	4	4	2–2.5	3	1.2	1.5
<i>Dendrocopos major</i>	0.5	4.5	5	3.5	3–3.5	1.1	1.4
<i>Muscicapa striata</i>	2	3	5	3	3	1.1	1.3
<i>Ficedula parva</i>	1	2	2	5–7	2.5	0.9	1.1
<i>Columba palumbus</i>	1	1	3	3.5	4.5	0.9	1.0
<i>Phylloscopus collybita</i>	3.5	4.5	3	0.5	0.5	0.8	1.0
<i>Garrulus glandarius</i>	1	1	2	2	2	0.5	0.7
<i>Anthus trivialis</i>	3.5	3	1	–	–	0.5	0.6
<i>Cuculus canorus</i>	0.5–1	1	1	1	2.5	0.4	0.5
<i>Prunella modularis</i>	2	2	+	1	–	0.3	0.4
<i>Dendrocopos leucotos</i>	1	1	1	1	1	0.3	0.4
<i>Oriolus oriolus</i>	1	0.5	0.5	–	3	0.3	0.4
<i>Aegithalos caudatus</i>	–	–	1	–	2	0.2	0.2
<i>Dendrocopos minor</i>	0.5	1	0.5	–	0.5	0.2	0.2
<i>Dryocopus martius</i>	0.5	+	0.5	0.5	+	0.1	0.1
<i>Pyrrhula pyrrhula</i>	–	1	+	–	–	0.1	0.1
<i>Strix aluco</i>	–	–	–	+	1	0.1	0.1
<i>Apus apus</i>	–	–	–	–	1	0.1	0.1
<i>Regulus ignicapillus</i>	–	–	–	–	1	0.1	0.1
<i>Parus cristatus</i>	–	–	–	–	1	0.1	0.1
<i>Scolopax rusticola</i>	–	0.5–1	–	–	+	0.1	0.1
<i>Pernis apivorus</i>	–	0.5–1	–	–	–	0.1	0.1
<i>Corvus corax</i>	–	–	+	–	+		
<i>Buteo buteo</i>	+	–	–	–	–		
<i>Picoides tridactylus</i>	–	–	–	–	+		
<i>Parus ater</i>	–	–	–	–	+		
Total (49 species)	226.1	249.6	241.3	246.4	260.8	81.6	100.0

migrants (Table 10). Their densities reached the highest level in 1995–1999 (Table 8), when they were by 20–40% higher than in the 1970s (Tomiałojć et al. 1984). The (non-significant) increasing tendency in the long-distance migrants, being rather recovery after earlier decline (Wesołowski & Tomiałojć 1997), resulted in the mean 1995–1999 densities not higher than in 1970s (Tomiałojć et al. 1984). Mean winter temperatures in the 1990s did not tend to increase, rather the opposite (mean

year; regression slope =  $-0.37$ ,  $F = 1.27$ ,  $p = 0.29$ ). Actually the winter 1995/1996 was the most severe in 25 years. This harsh winter, however, did not cause any visible drop in numbers of either group of residents (Table 10). The numbers of residents did not increase in the 1990s (Table 10), yet due to the increases during 1980s, their densities in 1995–1999 (Table 8) were significantly, often more than 50%, higher than in the 1970s (Tomiałojć et al. 1984).

Despite all these changes the structure of the breeding bird community at BNP in the 1995–1999

Table 6. The breeding bird assemblage of the pine-bilberry coniferous forest (plot NW, 25 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	27	22.5	35.5	30.5	28	11.5	24.0
<i>Erithacus rubecula</i>	14	13	9.5	17	13	5.3	11.2
<i>Regulus regulus</i>	11.5–12.5	4.5–5.5	8.5–9.5	6.5	11.5	3.5	7.3
<i>Phylloscopus sibilatrix</i>	10.5	7	6	11	8	3.4	7.1
<i>Parus ater</i>	6	6.5	7.5	5	8	2.6	5.5
<i>Turdus philomelos</i>	3.5	3.5	3.5	7.5	6.5	2.0	4.0
<i>Certhia familiaris</i>	4.5	4	5	3.5	5.5	1.8	3.8
<i>Ficedula hypoleuca</i>	5	5	4	5–6	2	1.7	3.7
<i>Phylloscopus collybita</i>	5.5	5	2	4	4.5	1.7	3.6
<i>Parus cristatus</i>	4–5	1.5	4–5	3.5	4.5	1.5	3.0
<i>Prunella modularis</i>	2.5	3.5	3	2	5	1.3	2.7
<i>Troglodytes troglodytes</i>	4	1	3.5	4	3.5	1.3	2.6
<i>Ficedula albicollis</i>	2	3	3–4	2–3	2	1.0	2.2
<i>Turdus merula</i>	1	2.5	3	3	1.5	0.9	1.9
<i>Dendrocopos major</i>	1.5	1.5	2.5	2	2	0.8	1.6
<i>Parus major</i>	1	–	2.5	1	5.5	0.8	1.6
<i>Pyrrhula pyrrhula</i>	2	2	1	1–2	2	0.7	1.4
<i>Sylvia atricapilla</i>	0.5	1	1	2	3	0.6	1.2
<i>Columba palumbus</i>	1–2	2	+	2	1.5	0.6	1.2
<i>Anthus trivialis</i>	+	1–1.5	1	2.5	2	0.5	1.1
<i>Muscicapa striata</i>	0.5	2.5	2	+	1	0.5	1.1
<i>Garrulus glandarius</i>	1	1	1.5	2	1	0.5	1.1
<i>Carduelis spinus</i>	1	2–3	1	1	0.5	0.5	1.1
<i>Dryocopus martius</i>	1	1	1	1	0.5	0.4	0.8
<i>Cuculus canorus</i>	0.5	1	0.5	1	1.5	0.4	0.7
<i>Sitta europaea</i>	1	–	1.5	1	1	0.4	0.7
<i>Columba oenas</i>	0.5	1	1	–	1.5	0.3	0.7
<i>Picoides tridactylus</i>	0.5	0.5–1	1	0.5	1	0.3	0.6
<i>Parus palustris</i>	+	+	1	1.5	0.5	0.3	0.5
<i>Parus caeruleus</i>	1	–	+	1	–	0.2	0.3
<i>Oriolus oriolus</i>	–	+	1	0.5	0.5	0.2	0.3
<i>Loxia curvirostra</i>	1	–	–	1	–	0.2	0.3
<i>Glaucidium passerinum</i>	–	–	–	0.5	1	0.1	0.2
<i>C. coccythraustes</i>	+	–	+	+	1	0.1	0.2
<i>Ficedula parva</i>	+	–	–	–	1	0.1	0.2
<i>Parus montanus</i>	–	–	–	–	1	0.1	0.2
<i>Phoenicurus phoenicurus</i>	0.5	–	–	+	–	–	0.1
<i>Phylloscopus trochilus</i>	0.5	–	–	–	–	–	0.1
<i>Nucifraga caryocatactes</i>	–	–	–	0.5	–	–	0.1
<i>Scolopax rusticola</i>	–	+	+	+	+	–	0.1
<i>Dendrocopos leucotos</i>	–	–	–	+	–	–	–
<i>Bonasa bonasia</i>	–	–	–	–	+	–	–
Total (45 species)	117.9	100.8	119.4	128.5	132.7	47.9	100.0

remained very similar to that in the 1970s (Tomiałojć et al. 1984). Invertebrate eaters, collecting food from leaves of trees and bushes, crown nesting birds, as well as short-distance migrants constituted still slightly over 50% of the foraging, nesting and migratory guilds, respectively.

Individual species

Of 26 species, for which the regression analysis could be run, none showed signs of any significant

decline during 1990–1999. Numbers of most species fluctuated, but three species (*Ficedula albicollis*, *Turdus merula* and *Parus palustris*) showed significant positive trends, and in four additional species (*Dendrocopos major*, *Ficedula hypoleuca*, *Sylvia atricapilla*, *Coccothraustes coccothraustes*) the positive tendencies approached significance (Table 11). This picture a constituted continuation of patterns recorded already in 1985–1994, when almost half of species showed increasing trends



Table 7. The breeding bird assemblage of the pine–bilberry coniferous forest (plot NE, 25 ha). For explanations see Table 1.

Species	Number of pairs					Mean	
	1995	1996	1997	1998	1999	p/10ha	%
<i>Fringilla coelebs</i>	<b>27.5</b>	<b>23</b>	<b>41</b>	<b>37</b>	<b>37.5</b>	13.3	<b>27.0</b>
<i>Erithacus rubecula</i>	<b>12.5</b>	<b>14.5</b>	<b>12</b>	<b>13</b>	<b>16.5</b>	5.5	<b>11.2</b>
<i>Phylloscopus sibilatrix</i>	<b>14</b>	<b>11</b>	<b>4</b>	<b>11.5</b>	<b>17</b>	4.6	<b>9.1</b>
<i>Regulus regulus</i>	<b>16–17</b>	<b>6.5</b>	<b>7</b>	<b>7.5–8.5</b>	<b>13</b>	4.1	<b>8.2</b>
<i>Parus ater</i>	4–4.5	5	<b>7.5</b>	3.5	7.5	2.2	4.5
<i>Certhia familiaris</i>	5	3.5–4.5	5–6	4.5	4.5–5.5	1.9	3.9
<i>Parus cristatus</i>	5	2–3	3	4	4.5	1.5	3.1
<i>Turdus philomelos</i>	2.5	3.5	1.5	4.5	7	1.5	2.9
<i>Phylloscopus collybita</i>	3	3	2	2.5	5	1.2	2.4
<i>Ficedula albicollis</i>	1	5	0.5	5	3	1.2	2.4
<i>Prunella modularis</i>	1	3.5	3	1	6	1.2	2.2
<i>Ficedula hypoleuca</i>	1.5	1	3	4	1–2	0.9	1.8
<i>Pyrrhula pyrrhula</i>	1	3	2	2	3	0.9	1.8
<i>Turdus merula</i>	1	1	2	1.5	4.5–5	0.8	1.5
<i>Troglodytes troglodytes</i>	1.5	1.5	1.5	2	3	0.8	1.5
<i>Parus major</i>	2	–	1.5	1	6	0.8	1.5
<i>Muscicapa striata</i>	2	4	1	+	1	0.6	1.4
<i>Dendrocopos major</i>	0.5	1.5	2	2	2	0.6	1.3
<i>Anthus trivialis</i>	1.5	1	1.5	1.5	2–3	0.6	1.3
<i>C. coccythraustes</i>	–	–	2	2	2–3	0.5	1.0
<i>Cuculus canorus</i>	1	0.5	1	2	1.5	0.5	1.0
<i>Columba palumbus</i>	1	1	1	1	2	0.5	0.9
<i>Garrulus glandarius</i>	2	+	0.5	1.5	2	0.5	0.9
<i>Carduelis spinus</i>	–	2–3	1	1	0.5	0.4	0.9
<i>Ficedula parva</i>	1	0.5	1	1	2	0.4	0.8
<i>Sylvia atricapilla</i>	1.5	1	+	+	3	0.5	0.8
<i>Sitta europaea</i>	1	1	+	–	3	0.4	0.7
<i>Dryocopus martius</i>	0.5	0.5	1	0.5	0.5–1	0.3	0.5
<i>Parus palustris</i>	+	–	1	0.5	2	0.3	0.5
<i>Glaucidium passerinum</i>	1	1	–	0.5	–	0.2	0.4
<i>Oriolus oriolus</i>	+	–	+	0.5	2	0.2	0.4
<i>Picoides tridactylus</i>	0.5	–	0.5	0.5	0.5	0.2	0.3
<i>Parus caeruleus</i>	1	–	+	–	1	0.2	0.3
<i>Bonasa bonasia</i>	0.5	1	–	+	+	0.1	0.3
<i>Accipiter nisus</i>	–	–	1	+	–	0.1	0.2
<i>Phylloscopus trochilus</i>	0.5	0.5	–	–	–	0.1	0.2
<i>Phoenicurus phoenicurus</i>	–	+	–	–	1	0.1	0.1
<i>Parus montanus</i>	–	–	–	–	1	0.1	0.1
<i>Columba oenas</i>	0.5	–	+	–	+	0.1	0.1
<i>Nucifraga caryocatactes</i>	–	–	–	0.5	–		0.1
<i>Scolopax rusticola</i>	+	–	+	+	+		0.1
<i>Loxia curvirostra</i>	+	–	–	+	+		
<i>Dendrocopos leucotos</i>	–	+	–	–	+		
<i>Sylvia borin</i>	–	–	+	–	–		
<i>Turdus viscivorus</i>	+	–	–	–	–		
<i>Dendrocopos medius</i>	–	–	–	–	+		
<i>Aegolius funereus</i>	–	–	+	–	–		
Total (51 species)	115.8	104.3	112.3	120.6	171.1	49.9	100.0

(Wesołowski & Tomiałojć 1997). Cumulating these increasing tendencies across two periods resulted in no fewer than 14 species reaching their highest ever recorded in BNP numbers in 1995–1999.

## DISCUSSION

Tomiałojć et al. (1984) analysing the 1970s data concluded that a single breeding bird community

Table 8. Main structural parameters of bird assemblages of different BNP stands in 1995–1999. Mean values (pairs/10 ha) ± SD.

	Ash-alder plots		Oak-hornbeam plots		Coniferous plots		
	K (edge)	L	W (edge)	CM	MS	NE	NW
Total assemblage							
Number of species (NS)	48.4 ± 2.3	35.4 ± 1.5	38.6 ± 2.9	33.4 ± 1.8	32.4 ± 3.3	34.0 ± 3.2	36.2 ± 3.3
Overall density (OD)	112.8 ± 8.6	87.8 ± 8.7	102.4 ± 8.4	85.9 ± 4.5	81.6 ± 4.2	47.9 ± 4.9	49.9 ± 10.6
Density of mean species (DMS)	2.3 ± 0.2	2.5 ± 0.2	2.6 ± 0.1	2.6 ± 0.2	2.5 ± 0.2	1.4 ± 0.1	1.4 ± 0.2
Cumulative share of dominants (%) (CSD)	44.7 ± 3.2	42.2 ± 7.2	59.7 ± 2.8	56.2 ± 6.4	59.0 ± 5.0	54.1 ± 4.7	56.1 ± 5.1
Densities of foraging groups							
Forage outside forest (O)	6.9 ± 1.8	0.5 ± 0.3	2.3 ± 0.9	0.3 ± 0.2	0.2 ± 0.2	0.2 ± 0.1	0.1 ± 0.1
Predators (P)	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.2	0.3 ± 0.2	0.5 ± 0.1
Vegetarians (V)	9.7 ± 0.6	8.4 ± 1.1	12.4 ± 1.8	10.2 ± 1.9	9.2 ± 1.7	4.8 ± 0.3	5.2 ± 1.1
Ground insectivores (IG)	32.9 ± 4.2	27.6 ± 2.1	25.9 ± 3.0	23.4 ± 1.6	20.5 ± 1.3	12.7 ± 2.4	12.1 ± 3.7
Bark insectivores (IB)	7.5 ± 0.6	6.8 ± 0.3	6.4 ± 1.5	5.9 ± 1.3	6.6 ± 1.1	3.1 ± 0.5	3.0 ± 0.6
Crown insectivores (IL)	55.5 ± 5.1	44.2 ± 6.1	55.1 ± 4.2	45.9 ± 2.2	44.8 ± 2.9	26.7 ± 2.8	29.0 ± 6.1
Densities of nesting groups							
Ground nesters (G)	29.0 ± 3.8	20.7 ± 2.6	18.3 ± 4.7	16.1 ± 3.5	13.9 ± 3.6	12.5 ± 2.1	12.9 ± 4.0
Crown nesters (C)	45.2 ± 3.0	36.8 ± 3.5	48.3 ± 5.2	40.3 ± 5.0	35.7 ± 4.7	21.0 ± 2.4	23.7 ± 4.8
Hole nesters (H)	38.1 ± 4.2	29.6 ± 4.5	35.4 ± 3.4	29.2 ± 3.0	31.6 ± 2.6	14.1 ± 1.8	12.8 ± 2.9
Densities of migratory groups							
Tropical migrants (T)	26.2 ± 3.6	18.1 ± 2.7	24.9 ± 4.1	18.5 ± 3.0	20.0 ± 2.9	8.5 ± 0.9	9.7 ± 3.2
Short-distance migrants (S)	62.5 ± 4.0	47.9 ± 3.0	55.1 ± 5.2	48.1 ± 3.9	41.6 ± 2.8	24.9 ± 2.5	25.3 ± 5.5
Resident in region (R)	13.7 ± 1.9	12.7 ± 2.8	12.7 ± 2.8	10.6 ± 2.1	10.6 ± 2.1	7.1 ± 1.6	7.6 ± 2.4
True forest residents (RF)	10.4 ± 1.3	9.1 ± 2.0	9.7 ± 2.2	8.8 ± 1.9	9.4 ± 1.4	7.5 ± 1.5	7.3 ± 1.6

Table 9. Density similarities (DS, according to Soerensen’s formula) of bird assemblages (1995–1999 means) from different forest types in BNP.

Riverine		Oak-hornbeam			Coniferous		Plot
K	L	W	CM	MS	NW	NE	
x	82.7	81.7	82.4	79.5	50.8	51.3	K
	X	77.7	84.9	81.6	59.3	58.8	L
		x	88.1	86.5	40.6	54.6	W
			x	90.6	57.5	59.3	CM
				x	56.4	57.8	MS
					x	89.9	NW
						x	NE

inhabited all types of old-growth stands in BNP. There were distinguishable riverine, oak-hornbeam and coniferous variants, as well as their forest edge modifications, yet the bulk of breeding species was shared among them. Further observations (Tomiałojć & Wesołowski 1994, 1996, 1999, Wesołowski & Tomiałojć 1997) showed that the breeding bird community in primeval oldgrowth stands in BNP remained fairly stable, as theoretically expected for the primeval “climax” habitats. Yet, some minor

environmental changes, influencing the structure of BNP habitats, have occurred during the 25 year period. Detectable responses of bird community to those changes appeared according to our earlier results to be slight and apparently gradual. This is why we expected, that by confronting data from two most distant in time periods (1975–1979 versus 1995–1999) the differences may become more conspicuous. However, despite the substantial increase in the overall bird numbers, the qualitative composition of avifauna did not virtually change, and the breeding assemblage was dominated by the same set of species. Actually, as shown by the DS values exceeding 75%, the breeding assemblages in the riverine and oak-hornbeam stands in the late 1990s became even more similar than in the late 1970s. On the other hand, colonisation of coniferous stands by several “deciduous” species, resulted in the increasing species richness there, but this process was not accompanied by parallel increase of breeding densities in the coniferous forest. The net result of these changes was a slight decline in overall DS values between the deciduous and coniferous stands in the late 1990s. These small changes notwithstanding, our earlier genera-

Table 10. Patterns of year-to-year variation in the percentage indices of abundance of individual guilds and of the total breeding bird community and results of regression analysis of the patterns of numerical change in 1990–1999. Procedures — see “Methods”. In bold type — slopes differing significantly from zero (at  $p < 0.05$ , t test, two-tailed).

Ecological group	Index					Regression		
	1995	1996	1997	1998	1999	Slope	F	P
Foraging								
Outside (O)	40.9	69.3	53.2	44.6	66.6	0.34	1.01	0.34
Veget. (V)	122.7	164.6	152.6	156.5	166.9	<b>0.72</b>	8.30	0.02
Ground (IG)	129.7	119.5	111.6	124.1	138.6	0.53	3.18	0.11
Bark (IB)	126.4	142.8	167.3	128.2	153.0	-0.18	0.27	0.62
Crown (IL)	140.5	130.6	129.5	140.1	155.6	<b>0.74</b>	9.86	0.01
Nesting								
Ground (G)	120.4	101.2	77.1	96.8	98.1	0.12	0.12	0.73
Crown (C)	134.2	140.3	147.7	150.3	164.0	<b>0.78</b>	12.07	< 0.01
Hole (H)	134.3	138.8	142.3	140.3	170.8	<b>0.75</b>	9.97	0.01
Migration								
Tropical (T)	129.3	109.6	93.0	121.9	115.7	0.52	3.01	0.12
Short-dist. (S)	125.2	131.5	128.1	134.2	143.0	<b>0.74</b>	9.77	0.01
Resident (R)	150.6	144.7	147.2	142.8	208.5	0.15	0.17	0.69
Forest resid. (RF)	132.2	138.4	167.5	127.8	183.3	0.07	0.04	0.83
All birds	129.7	127.9	124.9	131.3	146.9	<b>0.76</b>	10.68	0.01

Table 11. Patterns of year-to-year variation in the percentage indices of abundance of 26 most numerous breeding species and results of regression analysis of the patterns of numerical change in 1990–1999. Procedures — see “Methods”. In bold type — slopes differing significantly from zero (at  $p < 0.05$ , t test, two-tailed).

Species	Index					Regression		
	1995	1996	1997	1998	1999	Slope	F	p
<i>Columba palumbus</i>	113.0	100.0	135.7	195.7	178.3	0.29	0.71	0.42
<i>Dendrocopos major</i>	93.3	200.0	247.6	185.7	219.0	0.61	4.87	0.06
<i>Dendrocopos medius</i>	101.7	114.4	139.8	112.7	117.4	-0.03	0.01	0.94
<i>Anthus trivialis</i>	100.8	102.5	41.7	41.7	50.0	0.12	0.11	0.75
<i>Troglodytes troglodytes</i>	155.3	102.9	113.2	133.8	147.1	0.29	0.73	0.42
<i>Prunella modularis</i>	183.3	216.7	150.6	163.9	200.0	0.04	0.01	0.92
<i>Erithacus rubecula</i>	126.6	118.9	97.0	122.7	123.2	0.46	2.08	0.94
<i>Turdus merula</i>	148.5	149.2	148.5	161.0	200.8	<b>0.76</b>	11.24	0.01
<i>Turdus philomelos</i>	161.3	134.4	135.5	163.4	167.7	-0.21	0.37	0.56
<i>Sylvia atricapilla</i>	132.9	142.5	129.0	137.3	147.9	0.57	3.91	0.08
<i>Phylloscopus sibilatrix</i>	118.5	62.9	27.0	86.5	56.2	-0.11	0.10	0.76
<i>Phylloscopus collybita</i>	105.7	102.3	79.3	65.5	78.2	-0.01	<0.01	0.97
<i>Regulus regulus</i>	193.8	126.2	143.1	130.8	204.6	-0.01	<0.01	0.97
<i>Muscicapa striata</i>	172.8	216.9	209.6	148.5	147.1	-0.06	0.03	0.87
<i>Ficedula parva</i>	83.2	52.6	69.5	126.3	142.1	0.30	0.78	0.40
<i>Ficedula albicollis</i>	175.8	171.9	156.9	199.3	185.0	<b>0.83</b>	17.57	<0.01
<i>Ficedula hypoleuca</i>	283.3	216.7	223.3	242.2	238.9	0.59	4.27	0.07
<i>Parus palustris</i>	122.7	129.2	170.3	151.9	191.9	<b>0.69</b>	7.22	0.03
<i>Parus caeruleus</i>	174.4	185.1	134.2	161.9	229.5	-0.08	0.05	0.83
<i>Parus major</i>	154.3	128.3	180.0	160.0	270.0	0.34	1.04	0.33
<i>Sitta europaea</i>	156.5	202.4	224.0	135.4	189.0	-0.41	1.65	0.24
<i>Certhia familiaris</i>	97.9	96.5	114.1	103.8	117.6	-0.32	0.92	0.37
<i>Sturnus vulgaris</i>	26.8	57.1	46.4	35.7	46.4	-0.18	0.28	0.61
<i>Fringilla coelebs</i>	130.9	137.3	163.4	156.3	155.6	0.62	4.87	0.06
<i>Carduelis spinus</i>	30.4	69.6	17.4	34.8	34.8	-0.08	0.06	0.82
<i>C. coccythraustes</i>	126.6	227.3	148.8	168.7	195.1	0.59	4.35	0.07

lisation, that all types of old-growth stands in BNP are inhabited by a single breeding bird community still holds true. Moreover, Fuller (2000) showed that even windfall gaps (up to several ha) in BNP were inhabited by the subset of species of this oldgrowth assemblage. No new species, regularly inhabiting clearcuts and young tree stands in the managed parts of the Białowieża Forest occurred in treefall gaps within its primeval stands. These results clearly demonstrate that in BNP, relationships between vegetation structure and composition of breeding bird assemblage are not very close.

Numbers of several bird species, as well as, the overall breeding bird density, were increasing in BNP in the late 1990s. These trends were visible, even though the data were collected in the never-managed, "climax" old-growth stands, in which one would rather expect to find fluctuations around some mean values. Some directional changes in habitat structure, such as formation of new gaps due to windfalls (most extensive in the coniferous stands), and declining amount of spruce in the oak-hornbeam stands were detectable as well. These habitat changes could be beneficial to species dependent on gaps, like *Phylloscopus collybita* (Piotrowska & Wesołowski 1989), *Anthus trivialis* or *Prunella modularis* (Fuller 2000). However, their numbers did not increase. For the majority of other species, those relying on spruce or mature trees in general, the observed habitat changes would mean a deterioration, not improvement in the quality. In spite of widespread spruce retreat, the spruce dependent *Regulus regulus* did not show any decline, and numbers of hole-nesters tended to increase, though the number of trees with holes was reduced in gaps. Apparently their numbers grew not because of habitat changes, but in spite of them. Only increases of species richness and overall density in the coniferous stands could be accounted for by local habitat factors — their structural complexity gradually increased, due to the increasing share of deciduous trees, and appearance of new treefall gaps in these originally closed stands.

Wesołowski & Tomiałojć (1997) suggested that the increase in numbers of foliage insectivores in the early 1990s could be at least partially attributed to the indirect effect of the then occurring outbreak of *Operophtera brumata* caterpillars. However, the numbers of the foliage insectivores continued to increase also in 1995–1999, despite very low numbers of *Operophtera*

caterpillars. Equally, the increasing numbers of hole-nesters in the 1990s could not be accounted for by the increasing hole supply. There are no data which would indicate an increase and the observed habitat changes would rather suggest some decline in hole availability. Moreover, data at hand demonstrate that secondary hole-nesters were limited by shortage of holes neither earlier (Wesołowski 1989, Walankiewicz 1991) nor in the 1990s (Wesołowski 2001b). Similarly, the severe winter of 1995/96 had no decimating effect on the numbers of resident birds. Thus, one needs to look for some other possibly influencing factors.

The failure to relate the patterns of numerical change in BNP to variation in local environmental conditions, could partially be due to our inability to measure all relevant variables and the synergistic effect on birds productivity/mortality in the forest. For example, despite the very low numbers of *Operophtera brumata* caterpillars in 1995–1999, no symptoms of acute food shortage were noticed, as the birds could apparently switch to the alternative source — abundant *Ptilophora plumigera* caterpillars on continental maples (Rowiński & Wesołowski 1999). One should keep also in mind, that the causative factors could operate at much larger geographical scale, that numbers of birds at BNP were set by processes taking place on the wintering grounds, far away from Białowieża (Tomiałojć & Wesołowski 1996). This supposition could hardly apply to the permanent residents, spending their whole lives in the forest, but would be more substantiated in the case of tropical migrants, which spend most of the year outside the forest.

The parallel increases observed in species differing in their food requirements, nest sites, and migratory patterns suggest rather that a number of different causal factors had to be involved, as it would be difficult to find a single factor (set of factors) which could account for all those increases. Similar individualistic patterns of numerical change were also found in the British woodland birds (Noble & Siriwardena 2001).

So far we underlined the directional changes in bird abundance observed in BNP. But it should be stressed the magnitude of all these changes (no distinct change in species composition and community structure, 50% increase in the overall density) was rather meagre, when compared with amplitude of changes recorded over the same period in other habitats, for example vast changes in farmland bird communities in western Europe (Marchant & Gregory 1994, Saris et al. 1994,

Schifferli 2001) or to the extensive changes of bird communities of the Vistula floodplain (Bukaciński et al. 1994). Against such background the BNP breeding bird community stands out as an example of remarkable stability.

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## REFERENCES

- Anonymous 1996. Statistica for Windows. StatSoft, Inc., Tulsa.
- Bauer H.-G., Berthold P. 1996. Die Brutvögel Mitteleuropas: Bestand und Gefährdung. AULA-Verlag, Wiesbaden.
- Berthold P. 1990. Die Vogelwelt Mitteleuropas: Entstehung der Diversität, gegenwärtige Veränderungen und Aspekte der künftigen Entwicklung. Verh. Dtsch. Zool. Ges. 83: 227–244.
- Berthold P., Solonen T. 1997. *Sylvia atricapilla* Blackcap. In: Hagemeyer W. J. M., Blair M. J. (eds). The EBCC Atlas of European Breeding Birds. T & AD Poyser, London, pp 601–602.
- Bukaciński D., Cygan J. P., Keller M., Piotrowska M., Wójciak J. 1994. [Numbers and distribution of waterfowl nesting in the Vistula middle course-fluctuations in 1973–1993]. Notatki Ornitol. 35: 5–47.
- Busse P. 1973. [Dynamics of numbers in some migrants caught at Polish Baltic coast 1961–1970]. Notatki Ornitol. 14: 1–38.
- Enemar A., Cavallin B., Nyholm E., Rudebeck I., Thorner A. M. 1994. Dynamics of a passerine bird community in a small deciduous wood, S Sweden, during 40 years. Ornis Svec. 4: 65–104.
- Faliński J. B. 1968 (ed.). Park narodowy w Puszczy Białowieskiej. PWN, Warszawa.
- Faliński J. B. 1986. Vegetation dynamics in temperate forests (Ecological studies in Białowieża Forest). W. Junk Pbl., Dordrecht.
- Faliński J. B. 1991. Le Parc national de Białowieża et le système intégral des espaces protégés en Pologne. Rev. For. Fr. 43: 190–206.
- Fuller R. J. 2000. Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Białowieża forest, Poland. Condor 102: 267–274.
- Gatter W. 2000. Vogelzug und Vogelbestände in Mitteleuropa. AULA-Verlag, Wiesbaden.
- Hagemeyer W. J. M., Blair M. J. 1997. The EBCC Atlas of European Breeding Birds. T & AD Poyser, London.
- Jędrzejewska B., Jędrzejewski W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer, Berlin.
- Jędrzejewska B., Jędrzejewski W., Bunevich A. N., Miłkowski L., Krasieński Z. A. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol. 42: 399–451.
- Marchant J. H., Gregory R. D. 1994. Recent population changes among seed-eating passerines in the United Kingdom. In: Hagemeyer E. J. M., Verstrael T. J. (eds). Bird Numbers 1992 — Distribution, monitoring and ecological aspects. Proc.12 Intern. Conf. IBCC and EOC. Statistics Netherlands and SOVON 1: 87–95.
- Morozov N. S. 1995. Inter-analyst variation in the combined version of the mapping method: the role of experience. Acta Ornithol. 29: 89–99.
- Newton I. 1998. Population limitation in birds. Academic Press, London.
- Noble D., Siriwardena D. 2001. Population trends in woodland birds in the UK. Abstracts of the 15th International Conference of the EBCC, Nyíregyháza, Hungary 45.
- Piotrowska M., Wesołowski T. 1989. The breeding ecology and behaviour of the chiffchaff *Phylloscopus collybita* in primeval and managed stands of Białowieża Forest (Poland). Acta Ornithol. 25: 25–76.
- Rowiński P., Wesołowski T. 1999. Timing of Marsh Tit (*Parus palustris*) and Nuthatch (*Sitta europaea*) breeding in relation to their caterpillar food in primeval conditions — preliminary data. The Ring 21: 126.
- Saris S., van Dijk A. J., Hustings M. F. H., Lensink R., van Scharenburg C. W. M. 1994. Breeding birds in the changing agricultural environment in The Netherlands in the 20th century. In: Hagemeyer E. J. M., Verstrael T. J. (eds). Bird Numbers 1992 — Distribution, monitoring and ecological aspects. Proc.12 Intern. Conf. IBCC and EOC. Statistics Netherlands and SOVON 1: 75–85.
- Schifferli L. 2001. Birds breeding in a changing farmland. Acta Ornithol. 36: 35–51.
- Tomiałojć L. 1980. The combined version of the mapping method. In: Oelke H. (ed.): Vogelerfassung und Naturschutz. Proc. VI Intern. Conf. Bird Census Work, Göttingen. 92–106.
- Tomiałojć L. 1991. Characteristics of old growth in the Białowieża Forest, Poland. Natural Areas J. 11: 7–18.
- Tomiałojć L. 1994. Accuracy of the mapping technique estimates for the Hawfinch — preliminary results. In: Hagemeyer E. J. M., Verstrael T. J. (eds). Bird Numbers 1992 — Distribution, monitoring and ecological aspects. Proc.12 Intern. Conf. IBCC and EOC. Statistics Netherlands and SOVON 2: 145–147.
- Tomiałojć L. 1995. Breeding ecology of the Blackbird *Turdus merula* studied in the primeval forest of Białowieża (Poland). Part 2. Reproduction and mortality. Acta Ornithol. 29: 101–121.
- Tomiałojć L., Lontkowski J. 1989. A technique for censusing territorial song thrushes *Turdus philomelos*. Ann. Zool. Fenn. 26: 235–243.
- Tomiałojć L., Wesołowski T. 1990. Bird communities of the primeval temperate forest of Białowieża, Poland. In: Keast A. (ed.). Biogeography and ecology of forest bird communities. The Hague, pp. 141–165.



## STRESZCZENIE

- Tomiałojć L., Wesołowski T. 1994. Die Stabilität der Vogelgemeinschaft in einem Urwald der gemäßigten Zone: Ergebnisse einer 15jährigen Studie aus dem Nationalpark von Białowieża (Polen). *Ornithol. Beob.* 91: 73–110.
- Tomiałojć L., Wesołowski T. 1996. Structure of a primaeval forest bird community during 1970s and 1990s (Białowieża National Park, Poland). *Acta Ornithol.* 31: 133–154.
- Tomiałojć L., Wesołowski T., Walankiewicz W. 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). *Acta Ornithol.* 20: 241–310.
- Tucker G., Heath M. F. 1994. *Birds in Europe. Their conservation status.* BirdLife International, Cambridge.
- Verner J. 1985. Assessment of counting techniques. *Current Ornithol.* 2: 247–302.
- Walankiewicz W. 1991. Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primaeval deciduous forest? *Natural Areas J.* 11: 203–212.
- Walankiewicz W., Czeszczewik D., Mitrus C., Szymura A. 1997. How the territory mapping technique reflects yearly fluctuations in the Collared Flycatcher *Ficedula albicollis* numbers? *Acta Ornithol.* 32: 201–207.
- Wesołowski T. 1983. The breeding ecology of Wrens *Troglodytes troglodytes* under primaeval and secondary conditions. *Ibis* 125: 499–515.
- Wesołowski T. 1985. The breeding ecology of the Wood Warbler *Phylloscopus sibilatrix* in primaeval forest. *Ornis Scand.* 16: 49–60.
- Wesołowski T. 1987. Polygyny in three temperate forest Passerines (with a critical reevaluation of hypotheses for the evolution of polygyny). *Acta Ornithol.* 23: 273–302.
- Wesołowski T. 1989. Nest sites of hole-nesters in a primaeval temperate forest (Białowieża National Park, Poland). *Acta Ornithol.* 25: 321–351.
- Wesołowski T. 1994. Variation in the numbers of resident birds in a primaeval temperate forest: are winter weather, seed crop, caterpillars and interspecific competition involved? In: Hagemeyer E. J. M., Verstrael T. J. (eds). *Bird Numbers 1992 — Distribution, monitoring and ecological aspects.* Proc.12 Intern. Conf. IBCC and EOC. Statistics Netherlands and SOVON 203–211.
- Wesołowski T. 2001a. Host-parasite interactions in natural holes: marsh tits (*Parus palustris*) and blow flies (*Protocalliphora falcozi*). *J. Zool.* 255: 495–503.
- Wesołowski T. 2001b. Ground checks — an efficient and reliable method to monitor holes' fate. *Ornis Fennica* 78: 193–197.
- Wesołowski T., Stawarczyk T. 1991. Survival and population dynamics of Nuthatches *Sitta europaea* breeding in natural cavities in a primaeval temperate forest. *Ornis Scand.* 22: 143–154.
- Wesołowski T., Tomiałojć L. 1995. Ornithologische Untersuchungen im Urwald von Białowieża — eine Übersicht. *Ornithol. Beob.* 92: 111–146.
- Wesołowski T., Tomiałojć L. 1997. Breeding bird dynamics in a primaeval temperate forest: Long-term trends in Białowieża National Park (Poland). *Ecography* 20: 432–453.
- Wesołowski T., Tomiałojć L., Stawarczyk T. 1987. Why low numbers of *Parus major* in Białowieża Forest — removal experiments. *Acta Ornithol.* 23: 303–316.

## [Zgrupowanie ptaków lęgowych pierwotnego lasu Białowieskiego Parku Narodowego pod koniec XX wieku]

W pracy przedstawiono wyniki liczeń ptaków lęgowych prowadzonych w latach 1995–1999 na stałych powierzchniach próbnych w ściśle chronionej części Białowieskiego Parku Narodowego (BPN) oraz porównano je z rezultatami uzyskanymi tam wcześniej (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1995, 1996). Na podstawie danych z całego ostatniego ćwierćwiecza sprawdzono też, w jakim stopniu wcześniejsze wnioski autorów zachowały swą aktualność. Liczenia były prowadzone na siedmiu powierzchniach próbnych (łącznie 187.5 ha), obejmujących trzy podstawowe typy prawie pierwotnego lasu: łęgi, grądy i bór mieszany (Fig. 1). Stosowano tę samą odmianę metody kartograficznej, jak w poprzednio prowadzonych na tym terenie liczeniach (Tomiałojć et al. 1984).

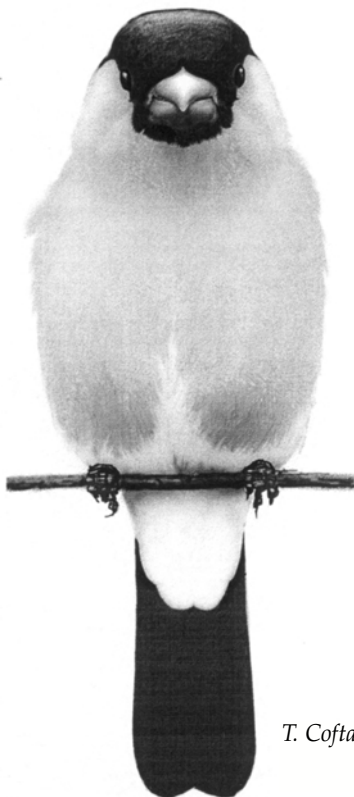
Wyniki ilościowe z drugiej połowy lat 1990. (Tab. 1–8) okazały się zbieżne z otrzymanymi w latach poprzednich. Potwierdziły się też takie prawidłowości, jak wysokie bogactwo gatunkowe (łącznie 74 gatunki lęgowe na wszystkich powierzchniach), wysokie podobieństwo składu ilościowego zgrupowań ptasich różnych typów lasu (wskaźnik DS przekraczający 50%, Tab. 9), wskazujące że wszystkie typy dojrzałego lasu zasiedlało jedno zgrupowanie ptaków lęgowych. Występowanie najniższej różnorodności gatunkowej zespołu i najniższego łącznego zagęszczenia stwierdzono — zarówno w końcu lat 1990. jak i 1970. — w borach, wyższe wartości otrzymano dla grądów, a najwyższe dla w łęgów (Tab. 8). Powierzchnie położone przy skraju lasu nadal oznaczają się wyższą różnorodnością gatunkową i wyższym (choć mniej wyraźnie) całkowitym zagęszczeniem ptaków. Łączne wyniki z 25-lecia potwierdziły znaczną stabilność składu badanego zbiorowiska ptaków pierwotnego lasu, pomimo stwierdzenia pewnych zmian, tak w warunkach środowiskowych, jak i w liczebności różnych grup ekologicznych (Tab. 10) i poszczególnych gatunków ptaków (Tab. 11). Ta względna stabilność składu zbiorowiska ptaków lęgowych bardzo silnie kontrastuje z głębokimi zmianami, jakie odnotowano na innych obszarach Europy, w siedliskach o prostszej strukturze i/lub poddanych silnym wpływom antropogenicznym.

Potwierdzono także utrzymywanie się pewnych różnic zauważonych już pomiędzy latami

1970. a wczesnymi latami 1990. (Tomiałojć & Wesołowski 1996). W latach 1995–1999 jeszcze wyraźniej zaznaczył się ogólny wzrost liczebności (i zagęszczenia) ptaków lęgowych, widoczny na wszystkich powierzchniach i w obrębie niemal wszystkich badanych ekologicznych grup ptaków. Pomimo braku bezpośrednich zmian antropogenicznych, łączne zagęszczenia ptaków w latach 1990. były na różnych powierzchniach o 13–38% wyższe niż w latach 1970. Nie znalazło potwierdzenia wcześniejsze przypuszczenie, jakoby o wzroście liczebności ptaków w grądach zadecydowało czteroletnie (1992–1995) masowe wystąpienie gąsienic *Geometridae* (Wesołowski & Tomiałojć 1995, Tomiałojć & Wesołowski 1996). Pomimo kilku-, a potem nawet kilkunastokrotnego obniżenia się liczebności tych gąsienic, liczebność ptaków w latach 1996–1999 utrzymała się na wysokim poziomie lub wzrosła. Jedynie stwierdzony trwały i znaczny wzrost bogactwa gatunkowego ptaków w borach był związany ze wzrostem złożoności strukturalnej (i zapewne wzrostem troficzności) tego środowiska, w wyniku pojawienia się wiatrolomów szybko pokrywających się młodymi liściastymi drzewami. Zmiany liczebności ptaków w innych siedliskach BPN zachodziły w znacznym stopniu niezależnie od obserwowanych zmian

struktury jego drzewostanów. Potwierdzają to także wyniki badań Fullera (2000) nad ugrupowaniem ptaków luk i wyłomów w drzewostanach BPN. Taki charakter zmian wskazuje na brak postulowanych wcześniej, ścisłych zależności składu awifauny lęgowej od struktury roślinności. Ponadto względna niezależność zmian liczebności ptaków od zmian warunków siedliskowych wskazuje na możliwy wpływ czynników działających w skali większej niż obszar BPN.

Objaśnienia symboli w Tab. 8. Podstawowe parametry struktury zgrupowań ptaków w różnych typach siedlisk BPN w latach 1995–1999. Podano przeciętne wartości zagęszczeń (p/10 ha) i ich odchylenia standardowe. NS — liczba gatunków, OD — łączne zagęszczenie, DMS — zagęszczenie przeciętnego gatunku, CSD — łączny udział dominantów. Grupy żerowiskowe: O — żerujące poza lasem, P — drapieżne, V — roślinożerne, IG — bezkręgowce z dna lasu, IB — łowiące bezkręgowce z kory, IL — bezkręgowce z koron. Grupy gniazdowe: G — naziemne, H — dziuplaki, C — w koronach. Grupy migracyjne: T — migranty dalekodystansowe, S — migranty krótkodystansowe, R — zimujące w regionie, RF — zimują w lesie. Definicje poszczególnych grup — patrz tekst do rycin.



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