Breeding Bird Community of a Primeval Temperate Forest (Białowieża National Park, Poland) at the Beginning of the 21st Century

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Breeding bird community of a primeval temperate forest (Białowieża National Park, Poland) at the beginning of the 21st century

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Abstract. The 2000–2004 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 compared with data gathered in the same plots in the late 1990s. These data supplement earlier observations in the BNP and extend the long-term set of data on the breeding bird numbers there to a 30-year uninterrupted series (1975–2004). Most community parameters, such as the composition of breeding avifauna, the species richness, and the make-up and cumulative share of dominants, have remained basically unchanged. The overall bird density has increased by 8–20% in different plots; in 2001 it reached the highest level within the 30-year study period. The increase was due to parallel increases in numbers of several species, widely differing in their nesting sites, food requirements and migratory habits — during this period 14 of the 26 most numerous species attained their highest numbers in the 30-year study period. Since numbers increased simultaneously in all the plots, the density differences across habitats remained the same, from the highest densities in riverine stands at the forest edge (up to 149 p/10 ha), through oak-hornbeam stands, to the lowest densities in the coniferous stands (54–56 p/10 ha). In most cases the numerical increases could not be attributed to changes in local environmental factors, such as food resources, or to detectable changes in habitat structure. The apparent lack of a relationship between the changes in bird numbers and the local situation suggests that factors acting on a larger scale (beyond 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 the 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, primeval forest, long-term study, species richness, community structure

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INTRODUCTION

To understand the impact of large-scale anthropogenic changes (e.g. deforestation, forest fragmentation, degradation, climate change) on woodland birds, it is necessary to gather data from areas, in which direct human disturbance is kept at the minimum, which could serve as reference sites. Otherwise it would be hardly possible to differentiate between contribution of a direct anthropogenic impact (e.g. habitat management) and that of indirect large-scale influences (e.g. climate change) to the observed changes in the bird communities (Tomiałojć at al. 1984, Wiens 1989, Wesołowski & Tomiałojć 1997, Gatter 2000).

The close-to-primeval stands, protected in the Białowieża National Park (BNP, E Poland) offer such a possibility. This little disturbed forest constitutes one of the best preserved examples of nearly-pristine nemoral forest of the northern temperate zone. Its pristine 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. This postulate has been confirmed by our analyses (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, 1994, 1996, 2004, Wesołowski & Tomiałojć 1995, 1997, Wesołowski et al. 2002).

Observations of bird community dynamics in a natural, undisturbed forest are rare, still scarcer are long-term series of data gathered in such conditions. Apart from the Białowieża project (see below) only two other such long-term programs exist: the LUVRE project in a 9 km^2 of subalpine deciduous forest in Swedish Lapland (37 years, summarised by Enemar et al. 2004) and the Hubbard Brook project, sampling 10–40 ha of eastern deciduous forests of N America (New Hampshire, 30 years, reviewed by Holmes & Sherry 2001).

The breeding bird censuses at BNP were commenced in 1975. Their results were published in regular intervals (Tomiałojć et al. 1984, Tomiałojć & Wesołowski, 1994, 1996, Wesołowski et al. 2002) forming a 25 year (1975–1999) data series. The composition and the structure of the BNP breeding bird community remained considerably stable across this period, in spite of substantial changes at the individual species level and of some slow directional trends.

The present paper extends the data series to a 30 year period. It is aimed at: 1) documenting the composition and structure of BNP bird assemblage during 2000–2004; 2) checking if earlier findings and generalisations on patterns of bird community composition and variability remain valid for the whole 30-year study period.

STUDY AREA

Detailed data on the whole Białowieża Forest (ca. 1500 km^2) and on its central unit constituting in its Polish part the Białowieża National Park (47.5 km^2, since 1996 extended to cover 105 km^2) can be found in earlier publications (Faliński 1968, 1986, 1991, Tomiałojć et al. 1984, Tomiałojć 1991, Wesołowski & Tomiałojć 1995, Tomiałojć & Wesołowski 2004). Here it should 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 primeval 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^2) of the Białowieża Forest has been strictly protected within the BNP. All our observations were made there, within seven permanent census plots (Fig. 1) totally covering 187.5 ha of the never managed old growth stands of natural origin. Vegetation structure of the plots was described in detail in Tomiałojć & Wesołowski (1996). Here only major features of each plot are summarized:

1) Ash-alder riverine forest *Circaeo-Alnetum* — plot K (33 ha) situated at the forest edge (Fig. 1). A fairly open-canopied and very patchy stand, with alder *Alnus glutinosa*, ash *Fraxinus excelsior* and spruce *Picea abies* as dominant trees. It contains 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 the 1970s. The tree stand has become patchier due to new wind-fall gaps.

2) Alder-swamp forest *Carici elongatae-Alnetum* — plot L (25 ha), situated inside the BNP (Fig. 1). The alder carr gradually turns into ash-alder association, both with admixture of spruces. It is characterised by the highest amount of uprooted and dead trees, most luxuriant ground layer, and transparent canopy. During 30 years this tree stand became more heterogeneous due to more intensive gap formation, and became somewhat drier.

3) Oak-lime-hornbeam forest *Tilio-Carpinetum*. The type of forest prevailing in the BNP — the most multilayered association, with highest tree species richness (up to 12 species) and most structurally complex canopy. The amount of dead timber is moderate. During 30 years new gaps were created by falling trees. The proportion of spruce was declining while the share of lime and hornbeam was increasing.

4) 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 MS while lime *Tilia cordata* in plot CM (Wesołowski 1996).

5) 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 sylvestris* with an admixture of birches *Betula* spp. and some oaks

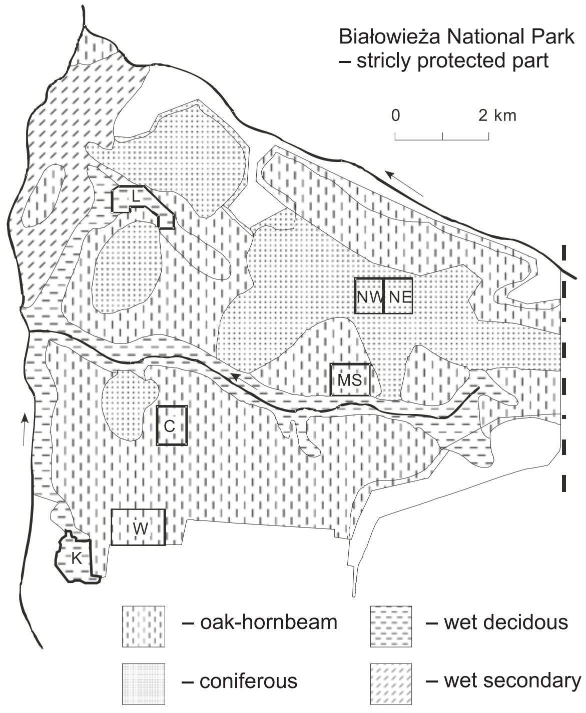

Fig. 1. Distribution of major habitat types and census plots (K, L, W, C, MS, NW, NE) in the strictly protected part of BNP.

Quercus robur are of moderate size and grow very densely. Bush layer underdeveloped. During 30 years some patches have matured, the number of old pines decreased, and numerous new openings due to falling of clumps of dead spruces by wind appeared. The largest gaps were created by tornadoes in 1987 and 2002. Amount of dead timber (mainly broken stumps or logs) already very high in 1998 (ca. 100 snags/ha, Walankiewicz 2002) strongly increased. Young hornbeams, limes, and birches were spreading increasingly in the windfall gaps.

METHODS

Census method

An improved version of the territory mapping technique (a combined mapping) for censusing breeding birds was applied (Tomiałojć 1980). Details of field procedures and field data processing are given in Tomiałojć et al. (1984) and Wesołowski et al. (2002).

To analyse year-to-year changes in numbers of a species (or guild) in whole BNP, following Wesołowski & Tomiałojć (1997), we calculated indices of yearly abundance for 26 commonest 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.

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. Following Tomiałojć et al. (1984), we distinguished the following guilds:

1) 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);

2) nesting — three guilds reflecting decreasing 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), and hole (H). There were no nest-boxes in our plots, and hole-nesting birds nested entirely in natural cavities;

3) migration — four guilds: tropical (winter south of Sahara and in tropical Asia — 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).

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, own observations). Additionally, the newly recorded *Turdus pilaris* and *Lanius excubitor* were classified as crown nesters (C), foraging outside the forest (O), migrating short distances (S) — *T. pilaris* or resident in the area (R) — *L. excubitor.*

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. In comparison with 1995–1999 (Wesołowski et al. 2002) the current pentad was slightly milder and drier; in 2000–2004 mean values of weather variables were: annual precipitation 554 mm, annual temperature +8.8°C, July temperature +20.0°C, and January temperature -3.3°C. Snow cover (up to 37 cm) lasted 66–95 days, snow melting occurred between March 8 (2002) and April 11 (2003). The values recorded were nevertheless close to long-term averages — for details see Faliński (1968, 1986), Tomiałojć & Wesołowski (1990, 1994), and Tomiałojć et. al. (1984), Jędrzejewska et al. (1997).

Food-resources. Leaf-eating caterpillars (mostly Geometridae) were counted once each season, in May, always at the same stage of leaf development. Each time 50–120 standard twigs (0.25 m^2) from the lower parts of the hornbeam undercanopy were searched and the caterpillars counted (Tomiałojć et al. 1984, Wesołowski & Rowiński 2006). Additionally caterpillar frass falling from oaks, hornbeams, limes and maples *Acer platanoides* was collected in two interior oak-hornbeam plots (Rowiński 2001, Wesołowski & Rowiński 2006). Other food sources were not closely monitored. An outbreak of spruce bark beetle *Ips typographus* occurred in all stands in 2002–2003. Mosquitoes were usually abundant in all types of stands, but were less numerous than in the plague humid seasons of 1970s. Except of moderate acorn crop in autumn 2001, no mast years were recorded.

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 normality 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 (2000–2004) with the ones from the previous pentad (1995–1999, Wesołowski et al. 2002) 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 1995–2004.

RESULTS

Totally 73 species were found breeding at least once within all the plots in 2000–2004 (Tables 1–7), what amounts to almost two thirds of 111 true forest and forest-edge species known to breed in the Białowieża Forest (Tomiałojć & Wesołowski 2004). Except *Turdus pilaris* and *Lanius excubitor*, breeding for the first time within our plots (plot K, Table 1), all other species had been already found breeding in the earlier periods. In comparison with the late 1990s (Wesołowski et al. 2002), there were on average 1.4 (plot K) to 3.4 (plot W) more species breeding in a single season, but only in two cases (plot L, W) the difference approached significance (t-test, $p = 0.02$ and $p = 0.06$, respectively). As previously, species richness in the forest edge riverine plot K: mean 49.8, total 69 (Tables 1 and 8), and grand total (30 years) — 74 breeding species, was the highest. The oak-hornbeam edge plot W (Table 3) with the mean of 42 species (Table 8) was second richest. The forest interior oak-hornbeam and coniferous plots were used by fewer species; their mean number there amounted to 34–37 (Table 8).

Community composition

Composition of the group of dominants did not change substantially in comparison with the late 1990s (Wesołowski et al. 2002). As before *Fringilla coelebs* and *Erithacus rubecula* were dominants in all plots and in all but one years (Tables 1–7), *Phylloscopus sibilatrix* remained dominant in coniferous habitats (Tables 6 and 7) and less frequently so in the oak-hornbeam stands (Tables 3–5). *Ficedula albicollis* was a regular dominant in the oak-hornbeam (Tables 3–5) and in the ash-alder forests (Tables 1 and 2). *Turdus philomelos* remained frequently dominant in all types of habitats, *Sylvia atricapilla* mostly in swampy stands (Tables 1 and 2), *Coccothraustes coccothraustes* in oak-hornbeam (Tables 3–5), while *Regulus regulus* and *Parus ater* in coniferous forest (Tables 6–7). Frequent domination of *Sturnus vulgaris* in the forest edge plots (Table 1 and 3) and *Phylloscopus collybita* in the riverine areas (Tables 1–2) resembled the situation already observed in the 1970s (Tomiałojć et al. 1984). Evenness did not change from the late 1990s; the cumulative share of dominants amounted to 44–64% (Table 8).

Total bird density. An increasing trend found in the late 1990s continued during the recent pentad, the overall density index reached its highest value

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 ≥ 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	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**76**	**78**	**80**	**78.5**	**80.5**	23.8	**17.6**
Sturnus vulgaris	**26**	**29**	**56**	**34**	**49.5**	11.8	**8.7**
Erithacus rubecula	**36**	**32.5**	**31.5**	20	**27.5**	8.9	**6.6**
Sylvia atricapilla	**24**	**32**	**28.5**	**27**	**35**	8.9	**6.6**
Ficedula albicollis	**31.5**	**26.5**	**22.5–23.5**	**30–31**	**31.5**	8.7	**6.4**
Phylloscopus collybita	16.5	21.5	**23**	**26–27**	**28.5**	7.0	**5.2**
Turdus philomelos	19.5	22	**22**	13–14	13.5	5.5	4.0
Prunella modularis	13–14	19	14–15	15.5–16.5	18	4.9	3.6
Parus major	18.5	18.5	13.5	14	13.5	4.7	3.5
C. coccothraustes	15–16	**24.5**	14	13.5–14.5	9–10	4.7	3.5
Parus caeruleus	15.5	21.5–22.5	15.5	10.5–11.5	12–14	4.7	3.4
Turdus merula	12.5	14.5	10	13	20.5	4.3	3.2
Phylloscopus sibilatrix	7	9	7	19–20	17–18	3.6	2.7
Troglodytes troglodytes	18	13.5	10.5	9.5	8	3.6	2.7
Muscicapa striata	9.5–10	12–13	10	7	7.5–8.5	2.9	2.1
Regulus regulus	10–11	10.5	8.5–9.5	7–8	4	2.5	1.9
Certhia familiaris	9–10	9.5–10.5	6.5	7	7–8	2.5	1.8
Columba palumbus	6	10	6.5	7.5	9.5	2.4	1.8
Sitta europaea	7	10	6.5	6.5	4.5	2.1	1.5
Parus palustris	7.5	7	4	5.5	5	1.8	1.3
Dendrocopos major	5	11.5	3.5	3.5	5	1.7	1.3
Ficedula hypoleuca	3.5	8	2	3	4	1.2	0.9
Oriolus oriolus	3–3.5	6	4.5	4	2	1.2	0.9
Sylvia borin	4.5–5.5	3–4	4.5	1.5	4–5	1.2	0.9
Dendrocopos medius	3	3.5	2.5	3.5	5	1.1	0.8
Parus ater	1	6	3.5–4.5	2.5	2	0.9	0.7
Regulus ignicapillus	3	0.5	3	3.5	3	0.8	0.6
Hippolais icterina	2	4	1	2.5	3	0.8	0.6
Carduelis carduelis	2	3	2	2	1	0.6	0.4
Aegithalos caudatus	2	2–3	2	1.5	2	0.6	0.4
Carpodacus erythrinus	1.5	1.5	1.5	1.8	3.5	0.6	0.4
Garrulus glandarius	2	1.5	1.5–2	2	2	0.6	0.4
Apus apus	+	1	1	3	3	0.5	0.4
Cuculus canorus	1.5	2	1	1.5	1.5–2	0.5	0.3
Turdus iliacus	2	3	2	-	-	0.4	0.3
Dendrocopos minor	2	1–1.5	0.5	1	2	0.4	0.3
Pyrrhula pyrrhula	2–3	1	2	-	+	0.3	0.3
Dendrocopos leucotos	1	1	0.5	1.5	1	0.3	0.2
Locustella fluviatilis	-	1.5	1	0.5	1	0.2	0.2
Phylloscopus trochilus	-	-	-	2	2	0.2	0.2
Scolopax rusticola	1	+	1	+	1–2	0.2	0.2
Anthus trivialis	1	0.5	1	-	1	0.2	0.2
Tringa ochropus	-	1.5	-	1	1	0.2	0.2
Carduelis spinus	-	1	1	+	1	0.2	0.1
Dryocopus martius	0.5	1	0.5	0.5	0.5	0.2	0.1
Bonasa bonasia	-	0.5–1	-	1	1	0.2	0.1
Luscinia luscinia	-	0.5	1	0.5	-	0.1	0.1
Ficedula parva	1	0.5	0.5	-	-	0.1	0.1
Picus canus	1	0.5	-	0.5	-	0.1	0.1
Buteo buteo	0.5	0.5	-	0.5	+	0.1	0.1
Aquila pomarina	0.5	+	+	-	0.5	0.1	0.1
Parus cristatus	1	-	+	-	-	0.1	
Strix aluco	-	-	0.5	0.5	-	0.1	
Parus montanus	-	-	1	-	-	0.1	
Lanius excubitor	-	-	-	0.5	0.5	0.1	
Turdus pilaris	-	-	-	-	1	0.1	
Corvus corax	-	-	+	-	0.5		
Picoides tridactylus	+	+	+	-	-		
Streptopelia turtur	+	-	-	-	-		
Gallinago gallinago	+	-	-	-	-		
Total (60 species)	429.4	491.8	438.7	414.0	461.0	135.4	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	
	2000	2002	2002	2003	2004	p/10ha	%
Fringilla coelebs	**45**	**45.5**	**50**	**56**	**53.5**	20.0	**19.5**
Erithacus rubecula	**20**	**29.5**	**23.5**	**13.5**	**14–15**	8.1	**7.9**
Ficedula albicollis	**12.5**	**18**	12–13	**19**	**19.5**	6.5	**6.4**
Phylloscopus collybita	10.5	**20**	**16**	12.5	**18.5**	6.2	**6.0**
Sylvia atricapilla	9–10	**15.5**	**14.5**	11.5	**12.5**	5.1	4.9
Turdus philomelos	**13**	12.5	**13**	10.5	10	4.7	4.6
Turdus merula	10.5	10.5	11.5	**12**	12	4.5	4.4
Parus caeruleus	**14**	13–14	8	8.5	8	4.2	4.1
Parus major	11.5–12	10	8	10	10	4.0	3.9
Prunella modularis	6	9	8.5	11	9	3.5	3.4
C. coccothraustes	8.5–9.5	7–8	7	12	3.5	3.1	3.0
Troglodytes troglodytes	7	8.5	7.5–8	9	6.5	3.1	3.0
Phylloscopus sibilatrix	4.5	9	6.5	6	11	3.0	2.9
Regulus regulus	7–8	8	4.5–5.5	6.5	5	2.6	2.5
Ficedula hypoleuca	10.5	5–6	6.5	4.5	2	2.3	2.3
Columba palumbus	4	7	8.5	5	3.5	2.2	2.2
Sitta europaea	7	6	5	5.5	4.5	2.2	2.2
Certhia familiaris	6	4–5	7	4–4.5	5	2.1	2.1
Parus ater	4.5	5.5	6	6	2	1.9	1.9
Dendrocopos major	6	6	3.5	3.5	3.5	1.8	1.8
Muscicapa striata	1	4	4	7–8	4	1.6	1.6
Parus palustris	3.5–4	4	3.5–4.5	3	2	1.3	1.3
Dendrocopos medius	2.5	2	3	2.5	3.5	1.1	1.1
Carduelis spinus	1–2	2–3	2–3	3.5–4.5	1	0.9	0.9
Tringa ochropus	1–2	2–3	3	2	1	0.8	0.8
Cuculus canorus	1–2	3.5	1	2	2	0.8	0.8
Oriolus oriolus	1–1.5	1.5	1–2	2–2.5	2	0.7	0.7
Scolopax rusticola	1	1–2	2	1–2	1–2	0.6	0.6
Garrulus glandarius	-	1	2	2–2.5	1.5	0.5	0.5
Aegithalos caudatus	0.5	2	1	1	1	0.4	0.4
Dendrocopos minor	1.5	0.5	1.5	0.5	1	0.4	0.4
Apus apus	1	1	1–2	-	1	0.4	0.4
Bonasa bonasia	0.5	1	+	2	-	0.3	0.3
Dendrocopos leucotos	0.5	0.5–1	1	0.5	0.8	0.3	0.3
Regulus ignicapillus	1	2	-	-	-	0.2	0.2
Picoides tridactylus	0.5	-	1	1–1.5	+	0.2	0.2
Dryocopus martius	0.5	0.5–1	1	0.5	+	0.2	0.2
Parus cristatus	-	1.5	1	-	-	0.2	0.2
Pyrrhula pyrrhula	+	1.5	-	-	+	0.1	0.1
Ficedula parva	+	-	-	-	1	0.1	0.1
Phylloscopus trochiloides	-	-	-	1	-	0.1	0.1
Phylloscopus trochilus	-	-	-	-	0.5		
Glaucidium passerinum	-	0.5	-	-	-		
Strix aluco	-	-	+	-	-		
Gallinago gallinago	-	-	-	+	-		
Corvus corax	-	+	-	-	-		
Columba oenas	-	-	-	-	+		
Buteo buteo	-	-	+	-	-		
Parus montanus	-	+	-	-	-		
Total (49 species)	239.0	285.7	259.6	260.6	238.2	102.6	100.0

in 30 years (167%) in 2001 (Table 9). In comparison with the late 1990s (Wesołowski et al. 2002), mean densities in all plots were by 8–20% higher (in all plots but NE, the differences approached significance (t test, p = 0.02–0.08), highest in the whole study period.

Despite these increases the rank order of individual plots remained the same. As before, densities in the forest edge plots — K and W were the highest, exceeding 110 p/10 ha (Table 8), with the maximum value 149 p/10 ha recorded in plot K in 2001 (Table 1). Values in the interior deciduous

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	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**62**	**68.5**	**56**	**60**	**60.5**	24.1	**20.4**
Ficedula albicollis	**34.5**	**29**	**45**	**47**	**38.5**	15.2	**12.9**
Erithacus rubecula	**19**	**21**	**17.5**	**16.5**	**18.5**	7.3	**6.1**
Phylloscopus sibilatrix	11.5	**16.5–17.5**	11	**23.5**	**22**	6.7	**5.6**
C. coccothraustes	**20**	**22**	**16**	**17.5**	8.5–9.5	6.6	**5.6**
Turdus philomelos	**15.5**	**21**	**20**	11	14.5–15	6.5	**5.5**
Sturnus vulgaris	5	15	**17**	**25**	**20**	6.4	**5.4**
Parus major	**13.5–14.5**	**17–18**	11	11.5	9.5	5.0	4.2
Turdus merula	10	10.5	10	12	12	4.3	3.6
Parus caeruleus	11	13.5–14.5	11	8.5–9	9	4.2	3.6
Sylvia atricapilla	4–5	8	7	9.5	13.5	3.3	2.8
Regulus regulus	5	9	5.5	4	3–3.5	2.1	1.8
Certhia familiaris	5.5	5.5	5–6	4–4.5	4.5–5	2.0	1.7
Muscicapa striata	4	5–6	5	6–7	4–5	2.0	1.7
Troglodytes troglodytes	7.5	7	4	3	4	2.0	1.7
Parus palustris	5.5	6	4.5	4	5	2.0	1.7
Columba palumbus	4.5	3.5	4	6	7	2.0	1.7
Dendrocopos major	3–3.5	8	4	3	6.5	1.9	1.6
Sitta europaea	5.5	4	4.5	5	5	1.9	1.6
Dendrocopos medius	2.5	3	4	4.5	4.5	1.5	1.2
Phylloscopus collybita	2.5	2.5	3	2	6.5	1.3	1.1
Prunella modularis	2.5	4	2	2	4	1.1	1.0
Ficedula parva	4.5	3	2.5	2	2	1.1	0.9
Parus ater	2.5	4.5	3	1.5	1	1.0	0.8
Garrulus glandarius	1	2	1.5–2	1.5	2–3	0.7	0.6
Jynx torquilla	2	1	2	2.5	0.5–1	0.6	0.5
Ficedula hypoleuca	2.5	4	0.5	+	1	0.6	0.5
Oriolus oriolus	1	2	1.5	1.5	1	0.5	0.5
Aegithalos caudatus	1	1	2	0.5	2	0.5	0.4
Parus cristatus	2	1.5	1	0.5	1	0.5	0.4
Dendrocopos minor	1	1	1	1	1	0.4	0.3
Regulus ignicapillus	1	+	1–2	1	1	0.4	0.3
Dendrocopos leucotos	0.5	1	1	0.5	0.5–1	0.3	0.2
Picus canus	+	1	1	1	0.5	0.3	0.2
Cuculus canorus	-	1.5	0.5	0.5	1	0.3	0.2
Anthus trivialis	+	+	-	1.5	1.5	0.3	0.2
Pyrrhula pyrrhula	1	-	1	1	-	0.2	0.2
Dryocopus martius	0.5	1	0.5	0.5	0.5	0.2	0.2
Strix aluco	+	0.5	1	0.5	0.5	0.2	0.2
Carduelis chloris	0.5	-	1	-	-	0.1	0.1
Emberiza citrinella	-	0.5	+	+	0.5	0.1	0.1
Hippolais icterina	1	-	-	+	-	0.1	0.1
Picoides tridactylus	-	-	-	+	1	0.1	0.1
Phylloscopus trochilus	-	-	-	-	1	0.1	0.1
Scolopax rusticola	0.5	+	+	+	-	0.1	0.1
Sylvia borin	-	0.5	-	-	-		
Buteo buteo	-	-	-	-	0.5		
Bonasa bonasia	-	-	0.5	-	-		
Carduelis spinus	-	-	-	+	-		
Total (49 species)	278.1	327.8	291.0	304.6	303.3	118.0	100.0

habitats, 98–103 p/10 ha, were intermediate and those in the coniferous plots, 54–56 p/10 ha (Table 8) were the lowest.

Density of the mean species in the deciduous (2.7–2.8 p/10 ha) and coniferous (1.5–1.6 p/10 ha) plots was slightly higher than in the previous pentad, but the difference was significant only in two cases (t-test, plot K, $p = 0.02$, plot NW, $p = 0.05$, Table 8).

Assemblage guilds. The slopes of linear regression (Table 9) demonstrate that all the guilds were

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

Species	Number of pairs					Mean	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**51**	**60.5**	**59**	**54**	**54**	23.2	**24.9**
Ficedula albicollis	**19**	**21**	**29**	**26**	**27.5**	10.2	**10.9**
Erithacus rubecula	**21**	**21.5**	**19**	11	**13**	7.1	**7.6**
C. coccothraustes	**17.5**	**13.5**	11	**13–14**	9–10	5.4	**5.8**
Turdus philomelos	10	**14**	**16**	11	8	4.9	**5.3**
Sylvia atricapilla	4	10	7.5	**13.5**	**13**	4.0	4.3
Phylloscopus sibilatrix	7.5	**14.5**	-	**12**	**15**	4.1	4.4
Parus major	10.5	8.5	**11.5**	9	8	4.0	4.2
Turdus merula	6	7	9	11	7.5	3.4	3.6
Parus caeruleus	**11**	9	6.5–7.5	7	3.5	3.1	3.3
Regulus regulus	6.5	7	5–6	4.5	3.5–4.5	2.3	2.5
Troglodytes troglodytes	7	6	4.5	4	5	2.2	2.4
Certhia familiaris	6	3.5–4.5	4.5–5	6	3–4	2.0	2.2
Columba palumbus	5	3.5–4	4.5	4	3	1.7	1.8
Parus ater	2	6	3	6	1	1.5	1.6
Parus palustris	5	3.5	4.5	4	2	1.6	1.7
Prunella modularis	4.5	3–4	3–4	4	2	1.5	1.6
Sitta europaea	3	3	3	3.5	4	1.4	1.5
Muscicapa striata	1	1	3–4	5	4–5	1.3	1.3
Dendrocopos major	2.8	4–5	3	2.5	3	1.3	1.4
Phylloscopus collybita	-	+	4	3	5.5	1.1	1.1
Dendrocopos medius	2	2.5	3.5	2	2	1.0	1.1
Garrulus glandarius	1	1	1–2	1–2	1.5–2	0.6	0.6
Ficedula parva	1.5	0.5	2	3	-	0.6	0.6
Dendrocopos minor	1	1	1.5	1.5	1	0.5	0.5
Apus apus	1	1–2	1	2–3	-	0.5	0.5
Cuculus canorus	2	1.5	1	1–1.5	0.5	0.5	0.6
Parus cristatus	1	-	1–2	1	1	0.4	0.4
Carduelis spinus	-	1	+	2	-	0.3	0.3
Dryocopus martius	0.5	0.5	0.5	0.5	1	0.3	0.3
Dendrocopos leucotos	+	0.5	0.5	1	0.5	0.2	0.2
Aegithalos caudatus	1	+	1	-	1	0.3	0.3
Oriolus oriolus	1	+	1	1	-	0.3	0.3
Ficedula hypoleuca	-	-	2	-	-	0.2	0.2
Regulus ignicapillus	-	-	1	-	0.5–1	0.1	0.2
Picoides tridactylus	0.5	0.5	+	0.5	-	0.1	0.1
Pyrrhula pyrrhula	-	1	-	-	-	0.1	0.1
Jynx torquilla	-	-	-	1	-	0.1	0.1
Scolopax rusticola	-	-	0.5–1	+	+	0.1	0.1
Picus canus	-	-	-	0.5	+	0.1	0.1
Strix aluco	+	-	-	0.5	-	0.1	0.1
F. albicollis x F. hypoleuca	1	-	-	-	-	0.1	0.1
Bonasa bonasia	-	-	-	-	+		
Accipiter nisus	+	-	-	-	-		
Total (44 species)	214.1	233.6	231.7	234.4	206.3	93.3	100.0

either increasing or fluctuating in 1995–2004. A significant increasing trend in birds collecting invertebrate food among leaves of trees or high bushes (Table 9) paralleled changes in the caterpillar numbers (n caterpillars/hornbeam twig vs. year; regression slope = 0.69, F = 7.39, p = 0.026), what could indicate a causal relationship. The number of caterpillars, though, varied enormously (over 40-fold range), whereas, the numbers of birds varied within narrow limits (ca. 40%). Moreover, the peak numbers of birds occurred in 2001 (Table 9) at 12 caterpillars/twig and not in 2003, when their numbers were highest 68 caterpillars/twig. Abundance of all nesting guilds increased in parallel (Table 9), but in the case of hole- and crown-nesters this constituted part of the long-term trend, whereas numbers of the ground nesters were recovering after the drop in

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	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**75.5**	**70**	**67.5**	**63**	**62**	22.5	**23.1**
Ficedula albicollis	**36**	**40.5**	**41.5**	**40.5**	**38**	13.1	**13.4**
Erithacus rubecula	**27**	**26.5**	**20.5**	**18**	**14.5**	7.1	**7.3**
C. coccothraustes	**22.5–23.5**	**18–19**	**16**	**17–18**	**16**	6.1	**6.2**
Phylloscopus sibilatrix	9.5	**18.5**	9	**17.5–18.5**	**26**	5.4	**5.5**
Parus major	**17.5**	**19**	13.5	10.5–11.5	**14.5**	5.0	**5.2**
Parus caeruleus	**15–16**	**19**	13.5	9.5	8–9	4.4	4.5
Turdus philomelos	10.5–11	13	**20**	9	9.5	4.2	4.2
Turdus merula	11.5	11.5	12.5	12.5	13.5	4.1	4.2
Sylvia atricapilla	8	8	7.5	**14**	**19.5**	3.8	3.9
Sitta europaea	8.5	6.5	6–7	4.5	6.5	2.2	2.2
Troglodytes troglodytes	7.5	8.5	5.5	4.5	4.5	2.0	2.1
Certhia familiaris	7	6.5	5.5	6	4	1.9	2.0
Parus palustris	6.5	6	5.5	2.5	5	1.7	1.7
Columba palumbus	6	3.5	5.5	4	5.5	1.6	1.7
Dendrocopos major	5	7	3	4	4.5	1.6	1.6
Muscicapa striata	2	2–3	4	7.5–8.5	5	1.4	1.5
Dendrocopos medius	4–4.5	2.5	5	3	4.5	1.3	1.3
Parus ater	2	3.5	3.5	4–5	2.5	1.1	1.1
Regulus regulus	4	5.5–6	1	1.5	1	0.9	0.9
Phylloscopus collybita	+	-	3.5	4.5	5.5	0.9	0.9
Ficedula hypoleuca	2.5	2.5	1.5	1.5	2	0.7	0.7
Garrulus glandarius	2–3	1.5	2	1–2	2	0.6	0.6
Ficedula parva	3	3	1	1	0.5	0.6	0.6
Prunella modularis	1	3	1	2	2	0.6	0.6
Oriolus oriolus	2	2	1.5–2	1	1–2	0.6	0.6
Cuculus canorus	1.5	1.5	2	1	1	0.5	0.5
Dendrocopos leucotos	1	1	1	1	1	0.3	0.3
Dendrocopos minor	1	1	+	1	1.5	0.3	0.3
Picus canus	-	1	1	1	1	0.3	0.3
Regulus ignicapillus	-	-	-	1	1	0.1	0.1
Scolopax rusticola	1	+	0.5	-	+	0.1	0.1
Strix aluco	-	1	0.5–1	+	+	0.1	0.1
Aegithalos caudatus	0.5	+	1	-	-	0.1	0.1
Apus apus	-	1	-	+	-	0.1	0.1
Anthus trivialis	-	-	-	-	1	0.1	0.1
Sturnus vulgaris	-	-	-	-	1	0.1	0.1
Carduelis spinus	-	-	-	1	-	0.1	0.1
Pernis apivorus	-	-	-	1	-	0.1	0.1
Pyrrhula pyrrhula	-	1	-	-	-	0.1	0.1
Dryocopus martius	+	+	-	0.5	+	0.1	0.1
Bonasa bonasia	-	-	-	-	0.5		
Corvus corax	+	-	-	+	-		
Buteo buteo	-	+	-	-	-		
Parus cristatus	-	-	+	-	-		
Total (45 species)	303.3	316.7	283.7	274.8	286.8	97.7	100.0

the late 1990s (Wesołowski et al. 2002). In consequence the numbers of crown and hole nesters were ca. 60–70% higher while numbers of ground nesters only ca. 10% higher than in 1970s (Tomiałojć et al. 1984). Numbers of both resident groups did not change in comparison with 1995–1999 while numbers of short distance and tropical migrants significantly increased (Table 9). All the migratory guilds simultaneously reached in 2000–2004 their highest numbers during the whole 30 year study period (Wesołowski & Tomiałojć 1997, Wesołowski et al. 2002). Despite all these changes the structure of the breeding bird community at BNP in the 2000–2004 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

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	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**37.5**	**34.5**	**26**	**35**	**27.5**	12.8	**22.8**
Phylloscopus sibilatrix	**10.5**	**12**	**11**	**10.5**	**16.5**	4.8	**8.6**
Erithacus rubecula	**17.5**	**12.5–13.5**	**12–13**	**8.5**	**8.5**	4.8	**8.5**
Parus ater	**8.5**	**8**	**9**	7	6.5	3.1	**5.5**
Regulus regulus	**11.5–13.5**	**9–10**	4.5–5.5	3	4	2.7	4.8
Phylloscopus collybita	3.5	7	7	**7.5**	6.5	2.5	4.5
Turdus philomelos	5.5–6.5	5.5	9	4	5	2.4	4.2
Prunella modularis	6	5.5	5	4	5	2.0	3.6
Sylvia atricapilla	2.5	4.5	4.5	4	**9**	2.0	3.5
Certhia familiaris	4–5	4	4–5	4–4.5	4.5	1.7	3.1
Ficedula albicollis	6.5	2	3	1	4–5	1.4	2.4
Parus cristatus	3	4.5	2–3	3.5	3	1.3	2.3
Turdus merula	2.5	3.5	3.5	3	3.5	1.3	2.3
Parus major	4	3.5	3	1.5	3	1.2	2.1
Dendrocopos major	3.5–4	4.5	2	2	2	1.1	2.0
Troglodytes troglodytes	4	4	2	1.5	0.5	1.0	1.7
Ficedula hypoleuca	3.5	1–2	3	2	1	0.9	1.6
Muscicapa striata	3	2–3	2–3	2	1	0.9	1.6
Anthus trivialis	1	1.5	2	1.5	3.5	0.8	1.4
Carduelis spinus	1–2	3	-	2–2.5	2	0.7	1.2
Cuculus canorus	1.5	1.5	2	1.5	2	0.7	1.2
Phoenicurus phoenicurus	1.5	1.5	1–2	2	2	0.7	1.2
Pyrrhula pyrrhula	2.5	2.5–3.5	1	+	1.5	0.6	1.2
Columba palumbus	1	2	1	1.5	2	0.6	1.1
Columba oenas	1.5	1.5	1.5	1.5	1	0.6	1.0
Garrulus glandarius	1	1–1.5	1.5	1–1.5	1.5	0.5	0.9
Parus montanus	1	1.5	1	1	1	0.4	0.8
C. coccothraustes	2–3	1	-	1	-	0.4	0.6
Bonasa bonasia	1–1.5	1.5	1	-	0.5–1	0.4	0.6
Picoides tridactylus	0.5–1	1	1	1	0.5	0.3	0.6
Oriolus oriolus	0.5	1	0.5–1	1	0.5–1	0.3	0.6
Sitta europaea	1	1	1	-	1	0.3	0.6
Parus caeruleus	1	1	1	-	1	0.3	0.6
Dryocopus martius	0.5	1	0.5–1	0.5	0.5	0.3	0.5
Glaucidium passerinum	1	-	+	0.5	-	0.1	0.2
Parus palustris	1	-	+	-	-	0.1	0.2
F. albicollis x F. hypoleuca	-	1	-	-	-	0.1	0.1
Turdus viscivorus	-	+	-	+	0.5	0.1	0.1
Scolopax rusticola	+	-	+	-	-		
Loxia curvirostra	+	+	-	-	-		
Dendrocopos leucotos	-	+	+	-	-		
Aegithalos caudatus	-	-	-	+	-		
Dendrocopos medius	+	-	-	-	-		
Buteo buteo	+	-	-	-	-		
Corvus corax	-	-	-	-	+		
Total (45 species)	161.7	155.1	132.4	121.1	133.1	56.3	100.0

the most numerous foraging, nesting and migratory guilds, respectively.

Individual species. Of the 26 species, for which the regression analysis could be run, only two (*Ficedula hypoleuca* and *Sitta europaea*) showed significant decline during 1995–2004 (Table 10). In both cases, though, this decline was only relative, i.e. their numbers dropped after a period of numerical increase to the level already recorded at BNP in the 1970s (Tomiałojć et al. 1984). Overall, the increasing trends prevailed (nine species significantly increased, Table 10) and 14 species reached the highest numbers ever recorded at BNP in 2000–2004. This picture largely constituted continuation of patterns recorded already in 1985–1994, when almost half of species showed increasing trends (Wesołowski & Tomiałojć 1997).

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	
	2000	2001	2002	2003	2004	p/10ha	%
Fringilla coelebs	**37**	**35.5**	**36**	**37.5**	**32.5**	14.3	**26.5**
Phylloscopus sibilatrix	**13**	**14**	**12**	**11**	**15.5**	5.2	**9.7**
Erithacus rubecula	**15.5**	**13**	**13**	**6**	5–6	4.2	**7.9**
Parus ater	**9**	**7.5–8.5**	**9**	**8**	**9**	3.4	**6.4**
Regulus regulus	**10**	**12**	**7.5**	**6**	4	3.2	**5.9**
Turdus philomelos	9.5	6.5	8.5	5	4	2.7	**5.0**
Phylloscopus collybita	3	5	6	5	6	2.0	3.7
Certhia familiaris	4	4.5	5	4–4.5	4.5	1.8	3.3
Prunella modularis	4–5	4.5	3	4	4.5	1.6	3.0
Parus cristatus	3	5	4	4	4	1.6	3.0
Turdus merula	4	3	4	4	3.5	1.5	2.7
Sylvia atricapilla	2.5	2	3	3.5	4	1.2	2.2
Parus major	3	3	3.5	+	3	1.0	1.9
Dendrocopos major	2.5	3.5	2.5	1–2	2–2.5	1.0	1.8
Columba palumbus	2.5	2.5	3	1	1.5	0.8	1.6
Troglodytes troglodytes	4.5	3.5	1.5	-	1	0.8	1.6
Ficedula albicollis	1.5	-	2	1	4	0.7	1.3
Pyrrhula pyrrhula	2.5	3.5	-	1–2	1	0.7	1.3
Carduelis spinus	2	2–3	1–2	1–2	-	0.6	1.1
Muscicapa striata	-	2–3	2–3	2	-	0.6	1.0
Ficedula hypoleuca	3.5	1	1	-	1	0.5	1.0
Anthus trivialis	1.5	1.5	1.5	0.5	1.5	0.5	1.0
Cuculus canorus	-	1.5	1	1.5	1.5	0.4	0.8
Garrulus glandarius	1	1	1	1.5	1	0.4	0.8
Parus montanus	1	1.5	1	+	1.5	0.4	0.8
Parus caeruleus	1.5	2	-	-	1.5	0.4	0.7
Ficedula parva	1	1	1	1	0.5	0.4	0.7
Oriolus oriolus	1	+	1–2	1	-	0.3	0.5
Loxia curvirostra	1	1	-	1	-	0.2	0.4
Bonasa bonasia	-	1.5	+	+	1	0.2	0.4
Columba oenas	0.5	+	0.5	0.5	0.5	0.2	0.3
Dryocopus martius	0.5	+	0.5	0.5	0.5	0.2	0.3
Phoenicurus phoenicurus	0.5	-	-	-	1.5	0.2	0.3
C. coccothraustes	-	+	-	+	1.5	0.1	0.3
Glaucidium passerinum	-	-	1	0.5	-	0.1	0.2
Picoides tridactylus	0.5	+	+	-	0.5	0.1	0.2
Accipiter nisus	-	-	0.5	-	0.5	0.1	0.1
Sitta europaea	-	-	-	-	1	0.1	0.1
Turdus viscivorus	-	-	-	-	1	0.1	0.1
Scolopax rusticola	-	-	+	-	+		
Corvus corax	-	+	-	+	-		
Aegolius funereus	-	-	-	-	+		
Apus apus	-	+	-	-	-		
Dendrocopos leucotos	-	+	-	-	-		
Dendrocopos medius	+	-	-	-	-		
Buteo buteo	+	-	-	-	-		
Aegitalos caudatus	-	+	-	-	-		
Total (47 species)	147.2	146.9	138.3	115.3	126.5	53.9	100.0

DISCUSSION

Field work and data analysis were done by largely the same team of experienced workers, using the same census and analytical techniques (see Methods). Therefore, the data are fully comparable between the periods, if any substantial differences between the figures from two periods appeared, they were due to the real changes in birds' numbers and not to the observer's factor. The current results largely confirm the patterns found in the 25 year data set (Wesołowski et al. 2002, Tomiałojć & Wesołowski 2004). Composition of the breeding bird community in primeval old-growth stands in the BNP remained fairly stable. The breeding bird assemblage was only weakly dependent on the habitat structure; all types of old-growth stands in the BNP were (with few exceptions) inhabited by the same species of birds. As before the species richness and overall density

Table 8. Main structural parameters of bird assemblages of different BNP stands in 2000–2004. Mean values ± standard deviations in individual plots, densities in pairs/10 ha.

	Ash-alder plots		Oak-hornbeam plots			Coniferous plots	
	K (edge)	L	W (edge)	CM	MS	NE	NW
Total assemblage							
Number of species (NS)	49.8 ± 1.3	38.6 ± 1.5	42.0 ± 1.2	35.2 ± 1.3	35.4 ± 1.8	34.2 ± 2.2	36.6 ± 2.4
Overall density (OD)	135.4 ± 9.2	102.6 ± 7.8	118.0 ± 7.2	93.2 ± 5.3	97.7 ± 5.6	53.9 ± 5.5	56.3 ± 6.8
Density of mean species (DMS)	2.7 ± 0.1	2.7 ± 0.2	2.8 ± 0.2	2.6 ± 0.1	2.8 ± 0.2	1.6 ± 0.2	1.5 ± 0.1
Cumulative share of dominants (%)	50.6 ± 6.7	44.5 ± 7.4	58.6 ± 3.6	57.3 ± 4.3	63.6 ± 3.5	57.3 ± 7.5	52.5 ± 4.5
Densities of foraging groups							
Forage outside forest (O)	11.7 ± 3.4	0.6 ± 0.3	6.1 ± 2.4	0.7 ± 0.5	0.6 ± 0.2	0.2 ± 0.0	0.4 ± 0.0
Predators (P)	0.4 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.3 ± 0.1	0.4 ± 0.1	0.4 ± 0.2	0.3 ± 0.2
Vegetarians (V)	11.6 ± 1.8	10.5 ± 1.9	12.1 ± 1.0	10.7 ± 1.1	11.0 ± 1.1	5.9 ± 1.2	5.8 ± 1.5
Ground insectivores (IG)	38.6 ± 4.3	30.7 ± 3.4	27.7 ± 2.6	24.4 ± 2.6	24.0 ± 2.4	13.3 ± 3.2	14.8 ± 2.2
Bark insectivores (IB)	6.8 ± 1.5	6.9 ± 0.9	6.8 ± 0.6	5.7 ± 0.4	6.3 ± 0.7	2.6 ± 0.3	3.2 ± 0.4
Crown insectivores (IL)	66.3 ± 4.3	53.7 ± 4.2	64.8 ± 3.5	51.6 ± 3.0	55.5 ± 2.7	31.5 ± 1.9	31.7 ± 3.3
Densities of nesting groups							
Ground nesters (G)	36.4 ± 3.2	27.0 ± 4.4	20.2 ± 3.8	17.4 ± 2.7	17.7 ± 2.7	14.6 ± 2.0	16.5 ± 1.7
Crown nesters (C)	52.8 ± 4.3	42.8 ± 3.8	50.8 ± 4.1	44.5 ± 3.4	42.9 ± 2.8	25.8 ± 2.3	23.4 ± 3.7
Hole nesters (H)	45.8 ± 3.7	32.0 ± 3.8	46.8 ± 3.6	30.8 ± 3.1	36.6 ± 4.1	13.1 ± 2.3	15.6 ± 2.8
Densities of migratory groups							
Tropical migrants (T)	31.2 ± 3.9	21.4 ± 2.6	30.9 ± 4.6	21.7 ± 4.5	26.2 ± 4.1	10.0 ± 1.2	12.4 ± 2.2
Short-distance migrants (S)	78.4 ± 5.1	56.3 ± 4.3	61.9 ± 4.0	50.7 ± 4.1	49.4 ± 4.1	28.3 ± 3.5	28.3 ± 3.6
Resident in region (R)	13.2 ± 1.3	12.4 ± 1.3	13.1 ± 1.1	10.5 ± 1.8	10.6 ± 0.7	5.9 ± 0.7	7.3 ± 3.0
True forest residents (RF)	10.2 ± 1.7	10.8 ± 1.8	10.5 ± 0.9	9.2 ± 1.4	9.1 ± 1.0	7.9 ± 0.8	8.1 ± 1.0

Table 9. 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 1995–2004. Procedures — see "Methods". In bold type — slopes differing significantly from zero (at p < 0.05, t test, two-tailed).

Ecological group	Index					Regression		
	2000	2001	2002	2003	2004	Slope	F	p
Foraging								
Outside (O)	64.0	88.2	125.7	113.3	125.6	**0.89**	29.45	<0.01
Predators (P)	99.8	116.1	160.4	142.0	125.0	0.63	5.15	0.05
Vegetarians (V)	180.6	200.3	161.0	171.6	152.2	0.46	2.09	0.19
Ground (IG)	146.6	151.0	134.1	127.4	135.1	0.40	1.48	0.26
Bark (IB)	146.2	156.6	144.6	121.1	131.9	-0.18	0.28	0.61
Crown (IL)	158.7	177.5	158.1	163.8	164.1	**0.81**	15.62	<0.01
Nesting								
Ground (G)	107.7	131.5	109.6	115.7	136.5	0.55	3.38	0.10
Crown (C)	169.1	181.0	167.4	163.5	152.3	**0.66**	6.25	0.04
Hole (H)	171.0	183.2	171.8	157.0	159.8	**0.68**	6.84	0.03
Migration								
Tropical migrants(T)	118.2	140.3	127.3	149.9	160.9	**0.74**	9.44	0.02
Short-dist. migrants(S)	154.5	164.2	159.2	145.9	147.0	**0.76**	10.84	0.01
Resident (R)	203.5	238.5	161.1	146.2	143.4	0.25	0.52	0.49
Forest residents (RF)	163.1	173.7	162.9	148.0	142.9	0.01	0.01	0.82
All birds	151.3	167.1	151.3	147.2	149.8	**0.75**	10.54	0.01

was changing along a habitat gradient from the highest in the riverine forest at the forest edge to the lowest in the coniferous stands in the forest interior. No major shift in proportion of different guilds occurred, either. The crown insectivores, crown nesters, and short-distance migrants constituted the most numerous foraging, nesting and migratory guilds, respectively.

Though numbers of *Ficedula hypoleuca* and *Sitta europaea* dropped from a very high level in 1990s to a lower level characteristic of the 1970s (Tomiałojć et al. 1984), the parallel increases in numbers of several other bird species, reaching their highest ever numbers in 2000–2004, constituted the most pronounced difference between the two periods. As a consequence of these

Table 10. 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 1995-2004. Procedures — see "Methods". In bold type — slopes differing significantly from zero (at p < 0.05, t test, two-tailed).

Species	Index					Regression		
	2000	2001	2002	2003	2004	Slope	F	p
Columba palumbus	252.2	280.4	287.0	252.2	278.3	**0.92**	44.67	<0.01
Dendrocopos major	269.0	428.6	204.8	190.5	254.8	0.42	1.7	0.23
Dendrocopos medius	121.6	114.4	144.1	131.4	165.3	**0.70**	7.7	0.02
Anthus trivialis	30.0	30.0	37.5	29.2	70.8	-0.54	3.22	0.11
Troglodytes troglodytes	163.2	150.0	105.1	92.6	86.8	-0.43	1.86	0.20
Prunella modularis	211.1	269.4	208.3	238.9	247.2	**0.67**	6.51	0.03
Erithacus rubecula	133.9	134.8	118.0	80.3	87.6	-0.45	2.02	0.19
Turdus merula	193.2	205.1	205.1	228.8	245.8	**0.96**	94.69	<0.01
Turdus philomelos	181.2	203.2	233.3	137.6	139.2	0.25	0.53	0.49
Sylvia atricapilla	150.7	219.2	198.6	227.4	291.8	**0.91**	37.89	<0.01
Phylloscopus sibilatrix	71.3	105.6	63.5	112.9	138.8	0.42	1.71	0.23
Phylloscopus collybita	83.0	129.0	143.7	140.2	177.0	**0.73**	8.95	0.02
Regulus regulus	172.3	190.0	118.5	101.5	77.7	-0.51	2.87	0.13
Muscicapa striata	152.6	224.3	231.6	279.4	198.5	0.43	1.82	0.22
Ficedula parva	116.8	84.2	73.7	73.7	42.1	-0.20	3.36	0.58
Ficedula albicollis	185.0	179.1	203.9	215.7	213.7	**0.79**	13.29	0.01
Ficedula hypoleuca	288.9	250.0	183.3	123.3	122.2	**-0.70**	7.71	0.02
Parus palustris	158.1	143.2	122.2	102.7	102.7	-0.42	1.72	0.23
Parus caeruleus	247.3	286.5	199.3	159.3	158.4	0.15	0.19	0.67
Parus major	264.2	266.7	213.3	190.3	205.0	0.50	2.65	0.14
Sitta europaea	130.1	124.0	107.7	101.6	107.7	**-0.77**	11.6	0.01
Certhia familiaris	125.0	114.7	114.0	105.9	99.3	0.23	0.43	0.53
Sturnus vulgaris	55.4	78.6	130.4	105.4	125.9	**0.88**	26.69	<0.01
Fringilla coelebs	169.5	173.3	165.3	169.5	163.6	**0.75**	10.1	0.01
Carduelis spinus	43.5	87.0	44.3	95.2	34.8	0.37	1.26	0.30
C. coccothraustes	194.0	193.1	141.9	167.6	108.6	0.27	0.65	0.44

increases, the overall breeding bird density raised to highest ever level in 2000–2004, there were ca. 60% more birds breeding at the BNP then, than in the 1970s (Tomiałojć et al. 1984). As these changes were not accompanied by large scale parallel trends improving the habitat structure and/or environmental conditions (see below), it seems that the carrying capacity of local habitats did not improve, and the additional birds were mostly filling previously undersaturated habitats. This in retrospection confirms the claim of Tomiałojć et al. (1984) that the low densities recorded in the BNP old growth stands were frequently due to undersaturation, due to insufficient number of birds to occupy all the available space.

The numerical increases constituted to a large extent continuation of the long-term trends detectable already in te earlier periods (Wesołowski et al. 2002). The observed directional changes in habitat structure, such as gap formation due to windfalls (most extensive in the coniferous habitat), and declining amount of spruce in the oak-hornbeam stands could be beneficial to species dependent on gaps, like *Phylloscopus collybita* (Piotrowska & Wesołowski 1989), *Prunella modularis*, *Sylvia atricapilla* or *Anthus trivialis* (Fuller 2000a). The numbers of former species did increase, while numbers of *Anthus trivialis* showed a declining tendency. For the bulk of other species, those relying on spruce or mature trees in general, the observed habitat changes would rather mean deterioration, not improvement in the habitat quality. The spruce dependent *Regulus regulus* as expected tended to decline, but numbers of hole-nesters were increasing, despite the number of trees with holes was reduced in gaps, and despite decreases in numbers of *Ficedula hypoleuca* and *Sitta europaea* (partially also *Parus palustris*). The declines of the latter species could suggest that they were losing in a strong interspecific competition for restricted supply of holes. This, however, was not the case. The holes were all the time superabundant (Wesołowski 2001, 2002, 2003, 2006, Wesołowski and Rowiński 2004).

The increase in numbers of foliage insectivores in the early 1990s could be partially attributed an effect of the outbreak of *Operophtera brumata* caterpillars Wesołowski & Tomiałojć (1997). However, the numbers of the foliage insectivores continued to increase up to a peak in 2001 despite very low to low numbers of *Operophtera* caterpillars, and surprisingly did not increase in 2002–2004 when the highest caterpillar peak in 30 years occurred. These results indicate that variation in numbers of insectivores at BNP is not controlled by fluctuating caterpillar abundance, that alternative invertebrate prey (Rowiński 2001, Wesołowski et al. 2002, Wesołowski 2003) is usually available in adequate quantities. The same situation was found in Swedish Lapland, where only one species *Fringilla montifringilla* tracked outbreaks of *Epirrita autumnata* caterpillars while numbers of the remaining insectivores appeared unaffected by the changing caterpillar supply (Enemar et al. 2004). The Hubbard Brook data show a totally different picture. There the breeding birds seem to face food shortages most of the time, only from time interrupted by short-term insect outbreaks (review in Holmes & Sherry 2001).

The lack of relationship between the numerical changes in BNP and variation in local environmental conditions, could be possibly explained by our inability to determine all important factors (see alternative prey, above) influencing bird productivity/mortality in the forest. Additionally some factors could operate at much larger spatial scale that numbers of birds at BNP could be set by processes taking place outside the study area, ranging in space from the managed part of the Białowieża Forest to the distant tropical wintering grounds. This supposition could hardly apply to the permanent residents (their numbers mostly did not increase, Table 9) but would be more substantiated in the case of migrants, which spend most of the year outside the forest (both short-distance and tropical migrants strongly increased, Table 9). Simultaneous declines of *Anthus trivialis* at BNP, in Germany (Flade & Schwarz 2004) and in Britain (Fuller et al. 2005) could suggest existence of widespread problems in the African wintering areas. On the other hand, geographically discordant pattern of change in *Muscicapa striata*, with strong declines in Britain (Fuller et al. 2005), tendency to increase in Germany (Flade & Schwarz 2004) and very high breeding numbers at the BNP indicate that the set of limiting factors differ across the species breeding/wintering range. It remains to be seen, though, what are the spatial limits of these differently affected "subpopulations".

The parallel changes observed in species with very different food requirements, nest sites, and migratory patterns suggest that a number of different causal factors had to be involved, as it would be difficult to find a single factor (set of factors) to account for all these changes. Analyses of possible causes of birds' numerical change in Lapland (Enemar et al. 2004), Hubbard Brook (Holmes & Sherry 2001), Germany (Flade & Schwartz 2004, Gatter & Schütt 2004), and the British Isles (Fuller et al. 2005) revealed similar individualistic patterns.

Though the numbers of birds at the BNP were changing directionally over 30 years, the magnitude of all these changes (no distinct change in species composition and community structure, ca. 60% increase in the overall density) was rather meager, when compared with the amplitude of changes recorded over the same period in other habitats, for example vast changes in farmland bird communities in western Europe (Saris et al. 1994, Fuller 2000b, Schifferli 2001). It was also very small in comparison with the amplitude of changes in numbers of rodents (> 40x), defoliating caterpillars (2000x) or tree seed crop (> 900x) at BNP (Wesołowski & Tomiałojć 1997, Jędrzejewska & Jędrzejewski 1998, Wesołowski & Rowiński 2006). Against such background the BNP breeding bird community stands out as an example of remarkable stability.

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STRESZCZENIE

[Zgrupowanie ptaków lęgowych pierwotnego lasu Białowieskiego Parku Narodowego na początku XXI wieku]

Praca przedstawia wyniki cenzusów ptaków lęgowych prowadzonych w latach 2000–2004 na stałych powierzchniach próbnych w ściśle chronionej części Białowieskiego Parku Narodowego (BPN) i porównuje je z rezultatami uzyskanymi tamże w latach 1975–1999 (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1995, 1996, Wesołowski et al. 2002). Wykorzystując trzydziestoletnią serię

danych (1975–2004) sprawdzono również, w jakim stopniu wcześniejsze wnioski autorów zachowały swą aktualność. Liczenia prowadzono na siedmiu powierzchniach próbnych (łącznie 187.5 ha), obejmujących trzy podstawowe typy pierwotnego lasu: łęgi, grądy i bory mieszane (Fig. 1). Stosowano tę samą odmianę metody kartograficznej, jak w poprzednio prowadzonych na tym terenie liczeniach (Tomiałojć et al. 1984).

Większość analizowanych parametrów takich jak skład gatunkowy, bogactwo gatunkowe (łącznie w tym pięcioleciu stwierdzono gnieżdżenie 73 gatunków) i struktura dominacji awifauny okazały się zbieżne z otrzymanymi w latach poprzednich (Tab. 1–8). Nadal utrzymywały się, zaobserwowane już wcześniej tendencje do wzrostu liczebności wielu gatunków, 14 spośród 26 najliczniejszych gatunków osiągnęło w badanym okresie swoje najwyższe liczebności w ciągu 30 lat (Tab. 10). Łącznym efektem tych zmian był wzrost całkowitego zagęszczenia ptaków o 8–20% na poszczególnych powierzchniach (Tab. 8). W 2001 odnotowano najwyższe z dotąd stwierdzonych łączne zagęszczenie zgrupowania ptaków (Tab. 9). Ponieważ liczebność wzrastała jednocześnie we wszystkich typach lasów, utrzymywały się różnice zagęszczeń między siedliskami. Nadal najniższym łącznym zagęszczeniem charakteryzowały się bory (54–56 p/10 ha), wyższe wartości obserwowano w grądach, a najwyższe zagęszczenia (do 149 p/10 ha, Tab. 1) i najwyższe bogactwo gatunków stwierdzano w łęgu na skraju lasu. W większości przypadków te zmiany ilościowe nie były powiązane z zauważalnymi zmianami lokalnych czynników siedliskowych, takich jak zasoby pokarmu, czy zmiany struktury roślinności. Ten brak związku z lokalnymi warunkami wskazuje na to, że czynniki działające w większej skali przestrzennej (wykraczające poza badany obszar) mogły mieć duży wpływ na obserwowane trendy liczebności.

Łączne wyniki z trzydziestolecia, pomimo stwierdzenia pewnych zmian, zarówno w warunkach środowiskowych, jak i w liczebności różnych grup ekologicznych (Tab. 9) oraz poszczególnych gatunków ptaków (Tab. 10), potwierdziły znaczną stabilność składu badanego zbiorowiska ptaków pierwotnego lasu. Ta względna stabilność wyraźnie kontrastuje z głębokimi zmianami, jakie zaszły w tym samym czasie na innych obszarach Europy, w siedliskach o prostszej strukturze i/lub poddanych silnym wpływom antropogenicznym.

ERRATUM

In the paper by Witt K., Mischke A., Luniak M. "A comparison of common breeding bird populations In Hamburg, Berlin and Warsaw" (Acta Ornithol. 40: 139-146, 2005) there should be as follows:
– the title of the abstract (page 139) should be the same as the main title of the paper i.e. “A comparison of common breeding bird populations In Hamburg, Berlin and Warsaw”.
– in Table 3 (page 143) the density of *Parus major* in Berlin should be 41 (not 1) and *Parus palustris* (not *Parus atricapillus*) should be indicated.