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Structure of a primaeval forest bird community during 1970s and 1990s (Białowieża National Park, Poland)

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Abstract. Results of mapping censuses carried out in plots situated in three types of old-growth stands (riverine, oak-hornbeam, coniferous) in 1990–1994 are presented and contrasted with data gathered in the same plots in 1970s (Tomiałojć *et al.* 1984). Community composition parameters: number of breeding species (72 *versus* 75), make-up of dominants, and overall assemblage similarity (Renkonen's index 76–87%) remained basically unchanged. Total density did not change in swampy stands but increased by 20–40% in oak-hornbeam and coniferous habitats. These increases were most pronounced in crown and bark insectivores guilds (what could be partially due to three year outbreak of *Geometridae* caterpillars in 1990s), in hole nesters and open nesters in tree crowns. All migratory groups but tropical migrants increased in numbers. The latter group remained numerically stable. Ground nester numbers did not change in dry habitats but they decreased in swampy places, parallel with the decreased hydration of this habitat in 1990s. In coniferous plots, growing number of gaps and expansion of deciduous trees, resulted in enrichment of breeding avifauna and increase in mean number of breeding species there.

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

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INTRODUCTION

The present 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 (e.g. Bezzel 1982, Wiens 1989, Berthold 1990, Perrins *et al.* 1991, Tucker & Heath 1994, Wesołowski 1994). With the current large-scale (even global) changes in the natural environment due to human activities, gathering data from areas affected to the least extent by human disturbance becomes a goal of utmost importance. They should serve as "the control data" enabling one to evaluate to what extent the eventual directional changes occurring in the bird communities across the time-scale result from a direct anthropogenic impact (habitat management, immediate disturbance or transformation), and

to what extent they are reactions to indirect large-scale influences such as the e.g. climate warming, habitat eutrophication or "acidification".

As for now, the bulk of quantitative data on the stability-variability of the bird community structure comes either from the habitats for ages transformed by human activity or being still in the course of maturation or of successional changes of the habitat itself (e.g. Busse 1973, Berthold 1990, Enemar *et al.* 1994).

The old-growth forest stands of the Białowieża National Park (BNP hereafter) offer a place, in which data on the changes of the bird community composition arising without direct human intervention, and in the absence of successional processes, can still be gathered. The data collected here may thus serve as a gauge for the bird community studies made in more transformed woodland habitats.

In our earlier papers (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990, 1994, Wesołowski & Tomiałojć 1995) we have amply documented that it is justified to treat the structure of the bird community from the close-to-primaeval stands of BNP as the one resembling the pristine state.

Both the composition and structure of this bird community were characterised by a considerable stability across the period of 15 years (1975–1989), in spite of substantial changes at the individual species level.

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

— documenting the composition and structure of BNP bird community during early 1990s;

— checking whether any significant differences in its composition and structure between two periods, 1970s (after Tomiałojć *et al.* 1984) and of 1990s (present data) occurred;

— exploring if and how local habitat changes affected community structure;

— checking if earlier conclusions (Tomiałojć & Wesołowski 1994) on stability and trends in this forest bird community composition remain valid for the whole 20-year period of studies.

STUDY AREA

General description

The Białowieża Forest is a remnant of vast European lowland forests once extending over a greater part of the continent. It is situated on the border between Central and Eastern Europe, a 580 km² part of its 1250 km² belongs to Poland; the remaining one to Belarus). The geographical co-ordinates of the Białowieża village are 52°41'N and 23°52'E. Biogeographically the area falls within the mixed forest (deciduous-coniferous) zone containing a significant amount of native Norway spruces *Picea abies* in almost all types of tree-stands. The relief of this lowland Forest is flat — mostly 165–170 m a.s.l. Large stretches of the Polish part remain swampy or boggy, while extensive marshes of the Belarussian part were reclaimed after the Second World War.

The climate is subcontinental: mean annual precipitation 624 (426–857) mm, long-term average

annual temperature +6.6°C, with an average +17.6° in July and –4.3° in January. Snow cover (usually c.0.5 m) lasts up to 90–92 days; morning ground-frosts happen as late as mid-May, during the 1970s even till mid-June. Snow melts between c. 10 March (early spring) and 20 April (exceptionally late). See Faliński (1968, 1986), Okarma *et al.* (1995), Tomiałojć & Wesołowski (1990, 1994), Tomiałojć *et al.* (1984) for details.

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 inhabiting them other plants and animals (Faliński 1968, 1986, 1991, Tomiałojć & Wesołowski 1990, Wesołowski & Tomiałojć 1995).

Since 1921 the most diverse and least disturbed part of the Białowieża Forest has been strictly protected within BNP (47.5 km²). All the 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.

Habitat changes

Apart from internal gap-phase dynamics (formation of gaps by falling old trees, gap regeneration and tree maturation in former gaps) even in these natural old-growth stands, some directional changes were visible. The long-term studies carried out in BNP (Kowalski 1982, Faliński 1986) revealed some trends in the tree species composition. For example, on the verge of this century spruce was expanding, whereas during recent decades this species was strongly retreating. Lime *Tilia cordata*, on the contrary, after more than a hundred-year period of poor regeneration, was expanding during the last sixty years. These changes are mainly of natural character (Kowalski 1982) being dependent mostly on the climate change (perhaps also on the eutrophication of the habitat), and not so much due to cessation of the past lime destruction by game, cattle and man, as it was thought earlier. These processes continued throughout the period of our stud-

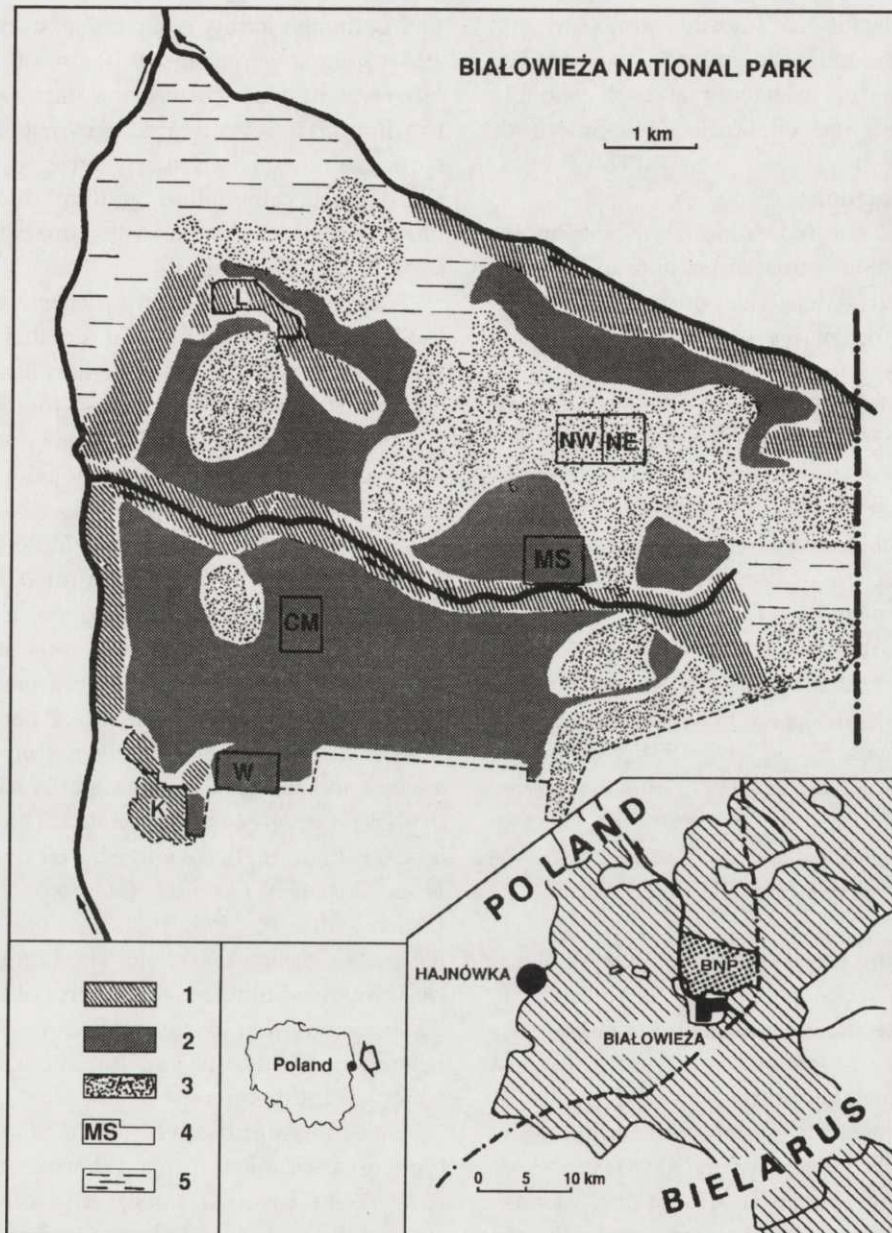


Fig. 1. Distribution of census plots in BNP and the positioning of BNP within the Forest. 1- alder and ash-alder riverine forest, 2- oak-lime-hornbeam forest, 3 — coniferous and mixed coniferous forest, 4 — census plots, 5 — other forest types, mostly swampy dwarf forest.

[Ryc. 1. Rozmieszczenie powierzchni próbnych w BPN i lokalizacja Parku w obrębie Puszczy Białowieżskiej. 1 — olsy i łęgi jesionowo-olchowe, 2 — grądy, 3 — bory i bory mieszane, 4 — powierzchnie próbne, 5 — inne typy lasu, głównie niskie lasy bagienne.]

ies; especially dramatic was decline of spruce (see below). Additionally to those transformations, main changes noticed in our census plots were as follows:

— Lowered ground-water table in BNP, partly as a result of a recent series of dry years;

— Decline in the canopy volume and forest-stand compactness as a consequence of natural catastrophes, like strong storms (winter 1974, March 1983), heavy wet snow fall (January 1986) and tornado (May 1987, affecting only coniferous plots);

— Spread of deciduous (mostly hornbeam and lime) undergrowth into the mixed and conifer-dominated stands, due to habitat eutrophication in BNP (Rykowski 1995) and/or climate amelioration.

Food-resource fluctuations

Caterpillars of *Geometridae* and *Tortricidae* moths constitute an important source of insect food for birds in the deciduous BNP stands. Their numbers fluctuated widely; the outbreaks of the *Geometridae* caterpillars were especially heavy in 1975, 1982 and chiefly 1992–94, causing in the oak (lime)-hornbeam stands almost complete defoliation of many hornbeams and a serious damage to other deciduous species. In the conifer-dominated and riverine stands, however, only scarce *Geometridae* caterpillars were recorded in deciduous trees. Mosquitoes were usually abundant in all types of stands, reaching plague numbers during humid seasons of 1970s. Earthworm availability depended on weather conditions and soil humidity, which declined during the late 1980s and early 1990s (Tomiałojć *et al.* 1984, Tomiałojć & Wesolowski 1990, 1994, Wesolowski 1983, Wesolowski & Stawarczyk 1991, Tomiałojć 1995).

DESCRIPTIONS OF THE CENSUS PLOTS

Ash-alder riverine forest *Circaeo-Alnetum* — plot K (33 ha). It forms a “forest peninsula” penetrating into the meadows of the Białowieża clearing. The area is less swampy than in pristine times owing to past regulation of the neighbouring Narewka rivulet. It comprises a mosaic of swampy stands, including c. 4 ha patch of the alder-birch regeneration (70–100 years old) after past clear-fellings, but also c. 6 ha of dry “islands” of the oak-lime-hornbeam stand. Main canopy (height 23–26 m, age 120–140, coverage 50 %, many gaps) is composed of alder *Alnus glutinosa*, ash *Fraxinus excelsior*, and some spruce. Young-tree layer and tall bushes are represented by the same tree-species saplings and *Corylus avellana*, *Padus avium*, *Ribes sp.*, *Frangula alnus* (coverage 20–30 %), while very luxuriant herb layer (0.5–1.7 m, coverage 80 %) is composed of *Urtica dioica*, ferns *Dryopteris filix mas*, sedges *Carex sp.*, as well as of *Cirsium oleraceum*, *Caltha palustris*, *Phragmites communis*, *Filipendula ulmaria*, *Cardamine amara* etc. The number of fallen trees is lower than in

plot L, though locally comparable. In comparison with 1970s some lowering (by c. 10 cm) of the ground and open-water table occurred, new gaps were created due to wind-fall of several large trees, especially of mature spruces, and previous sharp forest edge with marshy meadows became more gradual due to secondary growth of alders on neglected marshy meadows in front of the forest wall.

Alder-swamp forest *Carici elongatae-Alnetum* — plot L (25 ha). The swampy plot situated inside BNP is surrounded by the oak-lime-hornbeam and mixed coniferous stands. This elongated plot in its lower part is typical of alder carr, while its upper section gradually turns into ash-alder association, with the increasing number of ashes and the presence of some *Padus avium* bushes. The upper canopy (height 26–28 m, age 100–130 years, coverage 50 %) is formed of alders, ashes and some spruces. It is fairly open due to small and transparent crowns, and numerous snags and gaps after fallen trees. The light easily penetrating to the ground facilitates development of patches of young-trees and bushes (*Frangula alnus*, *Salix caprea*, *Corylus avellana* and *Padus avium*) though these are restricted to dry islets among stagnant water. The luxuriant herb layer (1–1.5 m high, coverage 50–60 %) is composed of ferns *Dryopteris filix mas*, *Carex sp.*, *Iris pseudacorus*, *Caltha palustris*, *Phragmites communis*, *Filipendula ulmaria*, *Cardamine amara* etc. The number of uprooted trees and dead timber is the highest of all plots. During 20-year study this tree stand became somewhat more heterogeneous due to gap formation, while stagnant water level sunk by some 10 cm.

Oak-lime-hornbeam forest *Tilio-Carpinetum* — This type of association forms extensive uniform stands (c. 44 % of the BNP area). The canopy is closed, structurally very diverse, composed of three layers: — upper canopy (above 30 m) of emergent spruces, some oaks *Quercus robur*, limes *Tilia cordata* and ashes, — main canopy (20–30 m) composed of the same trees and maples *Acer platanoides*, elms *Ulmus sp.*, and — lower canopy composed mostly of hornbeams *Carpinus betulus* and younger individuals of other trees. Below develops young-tree layer, formed of limes and hornbeams as well as of few large hazels *Corylus avellana*. Bush layer poorly developed, herb layer fairly low (15–30 cm, higher in gaps) covers c. 85 % with *Aegopodium podagraria*, *Anemone sp.*, *Urtica dioica*,

Allium ursinum etc. Low density of trees (mean 262 ex. per ha) in the very old stands (170–200 years) is typical. The amount of dead timber moderate.

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 share of the main tree species vary. Hornbeam was most abundant tree species in plot W while lime in plot CM. The latter plot had also the greatest share of spruce whereas in plot MS share of spruce was the lowest.

In comparison with 1970s the following changes in the structure of plot W were discernible: more gaps in the main canopy formed by wind-fall, marked retreat of spruce, paralleled by almost total disappearance of spruce regeneration, a stronger pressure of ungulates due to construction of a deer-proof fence along the plot edge, and finally — a gradual development of young aspen, willow and hornbeam regrowth in front of the formerly open edge of the plot.

Plot CM covers to a large extent previous plot CW (75%) but includes also part of former plot CE (25%). This, once very uniform stand, is now more patchy due to gaps after windfall. The retreat of spruce less advanced than in plot W.

Plot MS preserved its uniform character and park-like outlook resulting from steady pressure of herbivores. The main canopy has been punctured by a dozen or so new gaps after wind-fallen large trees, while a few older gaps are being filled up with the regrowth. Amount of spruce, decreased substantially. Once having 10–20 old spruces per ha the stand retained only a half of them, there is no new spruce regeneration.

Pine-bilberry coniferous forest *Peucedano-Pinetum* — plots NW (25 ha) and NE (25 ha). Mixed coniferous-deciduous stands (ca 28 % of the BNP acreage) develop on the sandy elevations and trophically represent one of the poorest local habitat types. Trees are of moderate size and grow very densely (aver. 560 per ha). Main canopy (26–30 m, 130–200 years, coverage 40–70 %) formed of spruces and gradually disappearing old pines *Pinus silvestris*, lower canopy contains additionally birches *Betula sp.*, aspens *Populus tremula* and some oaks, with young spruces. Most fragments resemble *Vaccinium myrtilli-Piceetum* subassociation,

while some smaller patches (mainly in NE plot) are more akin to *Vaccinium myrtilli-Pinetum*. Bush layer underdeveloped, herb layer low, composed of mosses, patches of *Vaccinium sp.*, *Oxalis acetosella*, gaps covered with *Calamagrostis sp.* and *Pteridium aquilinum*.

During 20 years some patches have matured, 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 on May 14th, 1987 when over 2 ha large patches of trees were smashed in each of the plots. 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 sampling was repeated in space (censuses were carried out simultaneously on replicated plots and in three habitats) and in time (all but one plot were studied for 20 years). 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 50x50 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). It differs from international recommendations (I.B.C.C. 1969) in the following points: (a) special attention paid to the contemporary records of simultaneously active birds, (b) significant amount of nest searching, and (c) extended time spent on each plot during single visit (up to 2.0–2.5 hours per 10 ha, starting before the local sun-rise). 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.

The accuracy of the method has been 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, Tomiałojć & Stawarczyk 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 W. Walankiewicz (unpubl. data) showed that their numbers, chiefly in the high density situations, could be underestimated by some 20–30%. Hence, for very careful calculations of the community parameters some arithmetical corrections can be suggested. In order to avoid confusion, however, it should be made clear that all further calculations shown in the tables of this paper do not contain any 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.

All records from field maps were assembled on species maps (in the scale 1:1000) for their evaluation. To assure maximum consistency of evaluation rules (see Morozov 1995) during the whole study, all estimates of cluster/territory numbers on species maps were done by both of us in each case, after negotiating the (usually minor) differences. When elaborating the results 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 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 valid for them visits; 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 (e.g. constituting up to 40% of *Phylloscopus sibilatrix* males in some habitats and years — Wesołowski 1985, 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.

RESULTS

The composition of assemblages of birds found to breed within our census plots during 1990s is shown in the Tab. 1–7.

Community composition

Pairwise comparisons of relative species abundances in all plots in 1970s and 1990s (for mean values) carried with application of Renkonnen's similarity index demonstrated a remarkable consistency. The RE values ranged from 80.2% (plot K) to 87.1% (plot NE), exceptionally 76% (plot CM). Also composition of the group of dominants did not change substantially. As in 1970s *Fringilla coelebs* and *Erithacus rubecula* were dominants in all years and all plots (Tab. 1–7), *Phylloscopus sibilatrix* remained dominant in dry-land habitats (Tab. 5–7) but less frequently so than in 1970s. *Turdus philomelos*, on the other hand, entered the group of dominants also in swampy forest, thus, became dominant in all habitats. As previously *Sylvia atricapilla* and *Phylloscopus collybita* were dominants in swampy stands (Tab. 1–2), *Coccothraustes coccothraustes* and *Ficedula albicollis* in oak-hornbeam stands (Tab. 3–5) and *Regulus regulus* in coniferous habitat (Tab. 6–7). Appearance of *Parus caeruleus* in the group of dominants in oak-hornbeam plots was a new phenomenon, though.

Also the cumulative share of dominants did not vary considerably between the periods. It amounted to 40–69% in different plots in 1970s and 40–60% in 1990s (Tab. 8–10).

Species diversity

Following our earlier approach (Tomiałojć & Wesolowski 1990, 1994) 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 (Tab. 8–10).

Mean number of breeding species increased by one third in both coniferous plots, from 24–25 in 1970s to 31–32 in 1990s (Tab. 10), whereas it remained stable in other plots or even slightly decreased (plot K, Tab. 8). In spite of this, plot K remained richest in species — up to 50 species could breed there in a single season (Tab. 1). As a result of the enrichment of the coniferous plots, the number of species breeding in them in 1990s levelled with that found in the oak-hornbeam plots in the forest interior (Tab. 9, 10). Plots in swampy habitats and those situated at the forest edge remained, as previously, richest in species (Tab. 8, 9).

Overall, within all our census plots jointly 72 species were found breeding in 1970s whereas 75 species in 1990, i.e. ca 65% of 111 true forest and forest-edge species known to occur in Białowieża Forest (Tomiałojć & Wesolowski 1990). Only three rare species (*Milvus migrans*, *Upupa epops*, *Phylloscopus trochiloides*) ceased to breed in the plots and some other scarce and irregular breeders (*Pernis apivorus*, *Aegolius funereus*, *Asio otus*, *Picus canus*, *Turdus viscivorus*) were recorded to breed there in 1990s. So, only minor changes in the species composition were observed.

Total bird density

In 1990s it was significantly, by 20–40%, higher in all the oak-hornbeam and coniferous plots (Tab. 9–10) but did not change significantly in the swampy areas (Tab. 7). In spite of this, densities in swampy plot K at forest edge remained the highest, with the maximum density recorded there in 1990 — 112.5 p/10 ha (Tab. 1). As previously densities were the lowest in the coniferous plots (Tab. 10) and 60–70% higher in the oak-hornbeam stands (Tab. 9), but the former difference between the oak-hornbeam and swampy habitat

was not visible any more. The increase of density at the forest edge was still visible (plot K and L, Tab. 8 and plot W with other plots in Tab. 9) but less pronounced than in 1970s.

Significant increase in densities in the oak-hornbeam stands in 1990s without parallel increase in the number of species breeding there resulted in a significant increase of the mean species densities (Tab. 9). In the coniferous plots, on the other hand, where both densities and the number of species grew in parallel the mean species values remained similar (Tab. 10).

Assemblage guilds

For a more detailed analysis the bird community has been split into several ecological groups. The division was based on three categories of characters: 1) type and place of food collection, 2) type of nest-site, 3) migratory habits. Data on how the particular species values were allocated to some foraging, nesting or migrating categories are given in the paper by Tomiałojć & Wesolowski (1990).

Foraging guilds

This classification is hierarchical. At first, birds foraging outside or within the forest were separated, then forest-foraging ones divided into predators (hunting mainly vertebrates), vegetarians, and “insectivores”. The last group was subdivided into ground-feeders, bark-feeders and crown-feeders. Several species belong to two foraging guilds. In such cases a part of their density value was included in one guild and another part in another. No special studies on species foraging techniques were conducted, therefore, these divisions must remain tentative.

In 1990s, in comparison with 1970s, birds foraging among leaves of trees or high bushes increased substantially (by 17–36%) in all plots, but plot L (Tab. 8–10). Also the bark foraging birds benefited in all plots except of plot L, their number increased by 42–85%. The changes in numbers of ground foragers were less uniform, their numbers increased in coniferous (almost to 130%) and less so in oak-hornbeam stands (Tab. 9–10), but remained at the same level in swampy stands (Tab. 8).

Among other guilds a consistent increase in all plots of the vegetarian species, a slight tendency to increase

in the predatory species group (but very low numbers overall) and a significant decline in both forest-edge plots (K and W) of the birds foraging outside the forest should be mentioned. The latter result was largely due to a marked decline in the Starling *Sturnus vulgaris* numbers.

Nesting-guilds

These guilds have been distinguished according to criteria of Tomiałojć (1970) and Tomiałojć *et al.* (1984). They attempt to recognise three essentially different degrees of nest vulnerability to a possible destruction by other animals (mainly predators but also by grazing or browsing game species): (a) nests on the ground or in vegetation up to 1–1.5 m above the ground level, depending on the structure of local vegetation (the most endangered group); (b) "arboreal" open or domed nests in high bushes or in trees; (c) nests in tree cavities (the least endangered group). It should be stressed here that there were no nest-boxes in our plots. As in the previous case, some species were partly included in more than one nesting guild.

In comparison with 1970s the ground-nester densities in dry habitats did not change substantially, but they decreased in swampy plots: significantly in plot K (to 73% of the previous value), and to 81% in plot L, though the latter difference was not significant (Tab. 8).

The crown nester densities increased significantly (by 24–43%) in all plots (Tab. 8–10), and hole nester densities showed signs of increase (by 28–73%) in dry habitat plots (Tab. 9–10).

Though those changes generally tended to diminish differences among habitats, yet the differences were not completely blurred. Similarly as in 1970s, hole nesters showed largest variability among plots (over 3.5-fold) and crown nesters were most equally distributed, densities of all the groups were lowest in coniferous plots (Tab. 8–10).

Migratory guilds

Here four groups are distinguished: 1) tropical migrants — species wintering south of Sahara, 2) short-distance migrants — species wintering mainly in SW Europe and in the Mediterranean basin, 3) residents: species wintering outside the forest but within the same geographic and climatic region, and nomadic

species and 4) forest residents: species staying whole year in their breeding habitats.

The least precise is the distinction between some short-distance migrants and residents, as only scarce ringing recoveries for Białowieża birds are available. In comparison to our earliest attempt of classification there are two changes in allocation of particular bird species to the migratory groups, stemming from new, unavailable earlier to us information, namely *Sylvia atricapilla* (formerly included into the short-distance migrants) is moved to the long-distance category, whereas *Coccothraustes coccothraustes* (formerly treated as resident) is classified now as a short-distance migrant. In consequence of these changes, the values of migratory group densities from earlier papers (Tomiałojć *et al.* 1984, Tomiałojć & Wesolowski 1990, 1994) are not directly comparable with the ones presented here. This change of classification has been already announced in our previous paper (Tomiałojć & Wesolowski 1994) but, by mishap, the numerical data shown in the tables there refer to the old classification.

Of four guilds recognised the most pronounced changes occurred in the abundance of both groups of residents. Their averaged densities during the 1990s were significantly often more than 50% higher than during the 1970s (Tab. 8–10). Short-distance migrants also increased, but mostly in dry habitats (Tab. 9–10) and to a lesser extent (20–39%). The long-distance (tropical) migrants showed least change, they stayed at the same level except of plot K in which densities in 1990s were significantly lower than in 1970s (Tab. 8).

DISCUSSION

In the paper describing situation in 1970s we concluded (Tomiałojć *et al.* 1984) that a single bird community inhabited all types of old-growth stands in BNP. Though the riverine, oak-hornbeam and coniferous variants, as well as their forest edge modifications could be distinguished, yet the bulk of breeding species was shared among them. The results from 1990s basically confirm that general conclusion. In spite of substantial increase in the overall bird numbers, qualitative composition of avifauna did not virtually change, breeding assemblages were dominated by the same set of species.

We also demonstrated (Tomiałojć & Wesołowski 1994) that during three consecutive 5-year periods (1975–1989), the basic parameters of the breeding bird community fluctuated fairly slightly, that the structure of this bird community remained fairly stable, in accordance with the theoretical expectations for an undisturbed natural old-growth habitat (Blondel 1979, Noon *et al.* 1985).

As some long-term environmental changes, influencing the structure of the studied habitats (see description of the study area), were discernible, and responses of bird assemblages to them could be slow and gradual, we expected, that by confronting data from two most distant periods (1975–1979 *versus* 1990–1994) the differences might become more conspicuous. This was really so, significant differences in densities of several guilds and in overall bird densities were found (Tab. 8–10), but otherwise bird assemblages remained very similar in such structural aspects as species richness and relative abundance. We conclude therefore, that our earlier statement on a considerable stability of the primaeval bird community composition based on a 15-year study period (Tomiałojć & Wesołowski 1994) remains valid for the whole 20-year period of studies.

As a rule bird densities in the majority of plots changed simultaneously in the same direction. Such pattern of variation, the internal agreement among the results obtained in seven plots (in three habitat types), strongly supports the idea that a single bird community inhabited old-growth stands of BNP (see above). It looks like birds recorded in our plots were actually only samples drawn from a single pool of birds. Thus, it seems that local factors, differentiating individual plots, were probably influencing mostly only their relative attractiveness, controlling what fraction of would-be breeders will settle in them, and to a lesser extent the size of the pool itself.

Such local habitat changes as the development of young regrowth in front of the previous old-forest edge could be responsible for the observed declines in numbers of edge species (*Luscinia luscinia*, *Hippolais icterina*, *Locustella fluviatilis*, *Turdus iliacus*, *Emberiza citrinella*) in plots K and W, as well as decline in species richness in plot K. On the other hand, structural changes in the coniferous plots (opening of formerly rather uniform and closed stands due to wind-fall and

spruce die out and increasing share of deciduous trees), enhancing diversification of habitats and making it acceptable place for the “deciduous” species, resulted in large increases of number of species breeding there (Tab. 10).

Changes in numbers in swampy plots K and L slightly deviated from the general increasing tendency. In most parameters analysed, like total bird density, combined density of several (nesting and foraging) guilds, no increase or only an insignificant one, was noticed in those stands. Whether decreased hydration in the recent years made this habitat less attractive to the birds remains to be seen. There are some data showing that it could be really so — in the dry seasons nest predation rates were higher and soil invertebrates less available (Piotrowska & Wesołowski 1989, Tomiałojć 1995). Those factors should be most important for two guilds of birds, namely of ground-insectivores and/or ground-nesters what seems to be the case, indeed (Tab. 8).

Ground-nesters in other habitats did not show any consistent changes but hole- and crown-nester densities in them were much higher in 1990s, densities of the latter group were also higher in swampy stands. Could those differences be accounted for by the observed differences in habitat architecture influencing breeding opportunities of different groups? Rather not, there are no data which would indicate an increase in number of holes, if anything, the observed habitat changes would suggest that their number could rather be lower in 1990s. Moreover, data on the hole availability at BNP (Wesołowski 1989, Walankiewicz 1991) demonstrate that secondary hole-nesters were not limited by shortage of holes, either earlier or in 1990s. Thus, one needs to look for some other possibly influencing factors.

Varying supply of *Geometridae* caterpillars, known to constitute an important food source for breeding birds at BNP (Wesołowski & Tomiałojć 1995) could potentially contribute to that pattern. Caterpillars were more abundant in 1990s than in 1970s, with a three-year period (1992–94) of prolonged caterpillar outbreak. Though it is known that as a rule, numbers of breeding birds at BNP are not adjusted to the current year caterpillar crop, yet it is also known, that changes in numbers of some insectivorous species are positively correlated with caterpillar abundance in the preceding

season (Tomiałojć & Wesołowski 1990, Wesołowski & Stawarczyk 1991, Wesołowski 1994). This mechanism could operate as well in 1990s, indirect effects of caterpillar outbreaks could at least partially account for the observed increase in insectivorous bird numbers.

So far we looked for locally acting causative factors, which could be responsible for the observed between-period differences. There is another possibility, though, namely that the causative factors operated 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. However, this supposition could hardly apply to rise in numbers of residents. A more detailed analysis of a 15yr data set on changes in their numbers (Wesołowski 1994) revealed that numbers of residents breeding in the following spring were rather poorly correlated with severity of the preceding winter and abundance of winter food (tree seeds) then. Hence, in most situations, wintering conditions could not play a decisive role in setting breeding numbers in this group.

Increases in numbers of resident birds were also recorded elsewhere (Berthold 1990, Enemar *et al.* 1994), this was combined with increase in numbers of short-distance migrants and decline in numbers of tropical-migrants. It was suggested that the decline of the latter group was due to the interspecific competition with the former groups (Enemar *et al.* 1994). This conclusion, raises some methodical doubts as it has been based on studies done in habitat underlying successional changes and it is known (Helle & Fuller 1988) that proportion of tropical migrants decreases within the successional series. Even though the tropical migrant decrease did occur in other areas, it would find no support in Białowieża data. Short-distance migrants increased at BNP in accordance with other reports but the tropical migrants numbers remained unchanged, though our earlier analysis carried out for the first 10 years suggested the existence of such downward trend (Tomiałojć & Wesołowski 1990). If real, the disparity of patterns of numerical change in tropical migrants among different areas would speak against the idea of controlling factors acting mainly along migration routes/on the wintering grounds. This question must stay open for a while, before additional comparable data become available, chiefly those collected in other relatively stable natural habitats.

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STRESZCZENIE

[Struktura zespołu ptaków pierwotnego lasu w latach 70. i 90. (Białowieżski Park Narodowy)]

Liczebność ptaków lęgowych oceniano przy użyciu kombinowanej wersji metody kartograficznej na siedmiu stałych powierzchniach próbnych o wielkości 24–33 ha każda (łącznie 187,5 ha), w zbliżonych do pierwotnych siedliskach Białowieżskiego Parku Narodowego. Obserwacje prowadzono w trzech podstawowych typach siedlisk niezaburzonych gospodarką ludzką: w łąkach jesionowo-olszowych, w lasach łąkowych (położonych zarówno na skraju jak i wewnątrz kompleksu leśnego) oraz w borach mieszanych w głębi lasu (ryc. 1). Dane o składzie zgrupowań ptaków na poszczególnych powierzchniach (tab. 1–7) wskazują, że pomimo fluktuacji widocznych na poziomie gatunkowym, pozostawał on w latach 1990–1994 dość ustabilizowany. Porównanie z rezultatami z lat 1975–1979 (Tomiałojć *et al.* 1984) wskazuje, że pomimo obserwowanych zmian struktury lasu (wypadanie świerka) i czynników siedliskowych (obniżenie poziomu wód gruntowych), ogólny skład badanych zbiorowisk ptasich wykazywał znaczną stabilność między okresami (tab. 8–10). Potwierdziły się takie prawidłowości, jak niemal identyczne bogactwo gatunkowe stwierdzone na siedmiu po-

wierzchniach próbnych (odpowiednio 72 i 75 gatunków lęgowych), wysokie (zwykle 80–87 %) podobieństwo składu ilościowego tych samych zbiorowisk ptasich, najniższa różnorodność zespołu i najniższe łączne zagęszczenie występujące w borach, wyższe w grądach, a najwyższe w lęgach. Na powierzchniach przy skraju lasu nadal gnieździło się więcej gatunków i występowało wyższe łączne zagęszczenie ptaków niż na powierzchniach położonych we wnętrzu lasu.

Wykazano jednak także zaistnienie pewnych różnic pomiędzy dwoma porównywanymi okresami. Najwyraźniejszy okazał się ogólny wzrost liczebności ptaków lęgowych, widoczny na wszystkich powierzchniach i w obrębie niemal wszystkich wyróżnionych grup ptaków. Pomimo braku bezpośrednich zmian wprowadzanych przez człowieka do lokalnego środowiska leśnego, w latach dziewięćdziesiątych łączne zagęszczenie ptaków było zdecydowanie większe niż w la-

tach siedemdziesiątych. Częściowo mogło to być wynikiem aż trzyletniego okresu masowego wystąpienia gąsienic *Geometridae* w grądach, co poprzez zwiększenie produktywności ptaków, mogło wpływać na zwiększenie liczebności w kolejnych sezonach (Wesołowski i Tomiałojć 1995). Wzrosty liczebności odnotowano zarówno u gatunków osiadłych jak i gatunków migrujących na krótkie odległości (zimujących w Europie), natomiast migratory tropikalne nie wykazywały objawów spadku liczebności.

Wzrost bogactwa gatunkowego i liczebności ptaków zaistniały w borach mógł być dodatkowo związany ze wzrostem złożoności strukturalnej tamtego środowiska w wyniku sukcesywnego wnikania podrostu drzew liściastych oraz pojawienia się (zwłaszcza na pow. NW) wiatrołomów rychło pokrywających się młodymi liściastymi drzewami.

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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.

[Tabela 1. Zgrupowanie ptaków lęgowych lasu lęgowego (pow. K, 33 ha). "+" — gatunek lęgowy, mniej niż 0.5 terytorium; "-" — nielegowy; wytłuszczone — gatunek dominujący (stanowiący $\geq 5\%$ zgrupowania). W przypadkach dla których podano przedziały wartości, do wszystkich dalszych obliczeń używano wartości środka przedziału.]

Species	Number of pairs					Mean density (p/10 ha)	
	1990	1991	1992	1993	1994		
	1	2	3	4	5	6	7
<i>Fringilla coelebs</i>	71	49	57	62–63	68	18.6	
<i>Erithacus rubecula</i>	31	19	23	27.5	27.5	7.8	
<i>Sturnus vulgaris</i>	26	25	21	22	15	6.6	
<i>Ficedula albicollis</i>	21	11	13–14	21	26	5.6	
<i>Turdus philomelos</i>	22.5	18	17.5	17	17.5	5.6	
<i>Sylvia atricapilla</i>	19–20	11	13.5	17.5	19.5	4.9	
<i>Phylloscopus collybita</i>	15.5	11	13	14	13.5	4.1	
<i>Sitta europaea</i>	12.5	11	11	16	10.5	3.7	
<i>Parus caeruleus</i>	9.5	12–13	14–15	12.5–13.5	10–11	3.6	
<i>Prunella modularis</i>	11	9.5	11.5	11.5	16	3.6	
<i>Troglodytes troglodytes</i>	10	9	15	12	12.5	3.5	
<i>Parus major</i>	11.5	9	11.5	12	11.5	3.4	

Table 1. contd.
[Tabela 1. c.d.]

	1	2	3	4	5	6	7
<i>C. coccythraustes</i>		16	6.5	10-11	10.5-11.5	9-10	3.2
<i>Phylloscopus sibilatrix</i>		1	11.5	11	11.5	17.5	3.2
<i>Turdus merula</i>		10	9.5	10.5	8	10	2.9
<i>Regulus regulus</i>		10-11	6	10.5	6	10	2.6
<i>Certhia familiaris</i>		8	8-9	9.5	8	7.5	2.5
<i>Muscicapa striata</i>		8	9	4-5	7	5-6	2.1
<i>Parus palustris</i>		6.5	6.5	7-8	5	7	2.0
<i>Ficedula hypoleuca</i>		4	3-4	3-4	5	5	1.3
<i>Dendrocopos major</i>		5	3	2-3	4.5	4.5	1.2
<i>Columba palumbus</i>		4	4	4.5	2.5	2-3	1.1
<i>Dendrocopos medius</i>		3.5	3.5-4.5	3	2.5-3	3-4	1.0
<i>Sylvia borin</i>		4	1	4	4.5	2.5	1.0
<i>Oriolus oriolus</i>		3-4	2	2	4	2-3	0.8
<i>Carduelis carduelis</i>		2.5	3	2	5	1	0.8
<i>Carpodacus erythrinus</i>		4	2	1.5	2.5	1.5	0.7
<i>Dendrocopos minor</i>		2	3	2	1-2	2.5	0.7
<i>Hippolais icterina</i>		1	3-4	1.5	1.5-2.5	1.5	0.6
<i>Garrulus glandarius</i>		2	1-2	1	1	2	0.5
<i>Apus apus</i>		+	3-4	1-2	1	+	0.4
<i>Anthus trivialis</i>		1	-	1	2.5	1.5	0.4
<i>Carduelis chloris</i>		2	1	1	-	2	0.4
<i>Cuculus canorus</i>		1	1	1-2	1	1-2	0.4
<i>Regulus ignicapillus</i>		1	-	1	2	1.5	0.3
<i>Buteo buteo</i>		1	1	1	1	1	0.3
<i>Turdus iliacus</i>		-	1	0.5	2	1	0.3
<i>Dendrocopos leucotos</i>		1	1	0.5	1	1	0.3
<i>Pyrrhula pyrrhula</i>		1	2	-	-	1	0.2
<i>Parus cristatus</i>		1	1	2	-	-	0.2
<i>Carduelis spinus</i>		-	2-3	+	1	-	0.2
<i>Locustella fluviatilis</i>		1	2	-	-	-	0.2
<i>Picoides tridactylus</i>		0.5	1	-	1	0.5	0.2
<i>Aegithalos caudatus</i>		0.5	1	+	1	-	0.2
<i>Picus canus</i>		-	1	-	1	0.5	0.2
<i>Ficedula parva</i>		1	-	-	1	-	0.1
<i>Jynx torquilla</i>		-	-	1	-	1	0.1
<i>Corvus corone</i>		-	2	-	-	-	0.1
<i>Luscinia luscinia</i>		+	1	+	-	0.5	0.1
<i>Dryocopus martius</i>		+	0.5-1	+	-	0.5	0.1
<i>Scolopax rusticola</i>		+	-	-	+	1	0.1
<i>Streptopelia turtur</i>		1	-	-	-	-	0.1
<i>Parus ater</i>		-	-	1	-	-	0.1
<i>Tringa ochropus</i>		1	-	-	-	-	0.1
<i>Loxia curvirostra</i>		-	-	-	1	-	0.1
<i>Aquila pomarina</i>		+	0.5	+	+	+	0.1
<i>Strix aluco</i>		-	+	+	-	-	
<i>Acrocephalus palustris</i>		-	-	-	-	+	
<i>Accipiter nisus</i>		-	-	-	+	-	
<i>Nucifraga caryocatactes</i>		+	-	-	-	-	
Total (60 species)		371.1	306.4	326.1	354.6	358.8	105.1

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

[Tabela 2. Zgrupowanie ptaków lęgowych olsu (pow. L, 25 ha). Pozostałe objaśnienia patrz tab. 1.]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	35.5–36.5	35	40	37	43.5	15.3
<i>Erithacus rubecula</i>	21–22	13.5	13	15	23	6.9
<i>Phylloscopus collybita</i>	11.5	7.5	11	14	14	4.6
<i>Ficedula albicollis</i>	10	9	6.5–7.5	13	8	3.8
<i>Turdus philomelos</i>	8.5	9	8.5	9–10	11.5	3.8
<i>Sitta europaea</i>	10	8.5	7.5	10	8.5	3.6
<i>Parus caeruleus</i>	8	8–9	14	8	5–7	3.6
<i>Sylvia atricapilla</i>	10–11	7.5	10–11	6.5	9	3.5
<i>Turdus merula</i>	8.5	8	8.5	7	9	3.3
<i>Prunella modularis</i>	10.5	5	7	9	8	3.2
<i>Parus major</i>	7.5	5.5	9	8.5	8–9	3.1
<i>Troglodytes troglodytes</i>	6	6.5	6.5	7	7	2.6
<i>Ficedula hypoleuca</i>	5	8	6.5	5–6	4–5	2.4
<i>Regulus regulus</i>	8.5	3–3.5	6.5	5.5	4	2.2
<i>Certhia familiaris</i>	6	6–7	6.5	4	4.5	2.2
<i>Phylloscopus sibilatrix</i>	+	7	6.5	5.5	7	2.0
<i>C. coccythraustes</i>	8	4–4.5	2	3	4	1.7
<i>Parus palustris</i>	4	2	1.5	3.5	3	1.1
<i>Muscicapa striata</i>	1	2–3	3–4	1	4	1.0
<i>Dendrocopos medius</i>	2.5	1.5–2	3	2	2	0.9
<i>Dendrocopos major</i>	2	1	0.5	4.5	3	0.9
<i>Columba palumbus</i>	2	2–2.5	1.5	2	2	0.8
<i>Tringa ochropus</i>	2	1–2	2–2.5	1–2	2	0.7
<i>Apus apus</i>	1–2	1	2	1–2	1	0.6
<i>Garrulus glandarius</i>	1–2	1.5–2	1–1.5	1	1	0.5
<i>Cuculus canorus</i>	0.5–1	1.5–2	1.5	1.5	1	0.5
<i>Carduelis spinus</i>	–	4	1–2	–	+	0.4
<i>Dendrocopos minor</i>	2	1–2	1	+	1	0.4
<i>Oriolus oriolus</i>	1	2	–	1	+	0.3
<i>Scolopax rusticola</i>	0.5–1	+	1	1	1	0.3
<i>Dendrocopos leucotos</i>	1	0.5–1	0.5	0.5	1	0.3
<i>Bonasa bonasia</i>	1.5	1	1	+	+	0.3
<i>Pyrrhula pyrrhula</i>	1	–	–	2	–	0.2
<i>Picoides tridactylus</i>	1	1	+	–	+	0.2
<i>Dryocopus martius</i>	+	1	0.5	+	0.5	0.2
<i>Aegithalos caudatus</i>	2	+	–	–	–	0.2
<i>Sylvia borin</i>	2	–	–	–	–	0.2
<i>F. albicollis x hypoleuca</i>	–	1	–	–	–	0.1
<i>Parus ater</i>	–	–	1	–	–	0.1
<i>Buteo buteo</i>	0.5	–	–	+	–	
<i>Strix aluco</i>	–	+	–	+	–	
<i>Glaucidium passerinum</i>	–	–	–	+	–	
<i>Columba oenas</i>	–	–	–	–	+	
<i>Regulus ignicapillus</i>	+	–	–	–	–	
Total (43 species)	206.3	180.5	193.6	191.6	203.0	78.0

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

[Tabela 3. Zgrupowanie ptaków lęgowych grądu (pow. W, 25.5 ha). Pozostałe objaśnienia patrz tab. 1]

Table 3. Contd. [Tabela 3. c.d.]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	49	52	42	49.5	54.5	19.4
<i>Ficedula albicollis</i>	23	17	27-28	36	27-28	10.3
<i>Erithacus rubecula</i>	21	15	13.5-14.5	19.5	22.5	7.2
<i>Turdus philomelos</i>	14-15	13	14-15	17.5	20.5	6.3
<i>C. coccythraustes</i>	17	13.5	13-14	17	16.5	6.1
<i>Phylloscopus sibilatrix</i>	1	16	16.5	18	17.5	5.4
<i>Parus caeruleus</i>	9	12	16	10	7	4.2
<i>Parus major</i>	6	9.5-10.5	12	10	7-8	3.6
<i>Sylvia atricapilla</i>	7-8	10	5	6.5	9	3.0
<i>Sitta europaea</i>	7	9	7	7	5.5	2.8
<i>Turdus merula</i>	5	6	8.5	6.5	6	2.5
<i>Muscicapa striata</i>	4	3-4	5.5	10	6.5-7.5	2.4
<i>Troglodytes troglodytes</i>	6.5	6.5	6.5	4.5-5	5	2.3
<i>Regulus regulus</i>	5.5	3.5-4	5	5	6	2.0
<i>Parus palustris</i>	5	5	4.5	5	5-5.5	1.9
<i>Certhia familiaris</i>	5	5	4-5	4-5	4-5	1.8
<i>Sturnus vulgaris</i>	2	2	2	6.5	5	1.4
<i>Prunella modularis</i>	1	2	1	5	7.5	1.3
<i>Dendrocopos major</i>	2.5	2	2.5	3.5	3.5	1.1
<i>Columba palumbus</i>	2	4	2.5	2.5	2	1.0
<i>Ficedula parva</i>	1.5	3.5-4	3	2	2	1.0
<i>Dendrocopos medius</i>	2.5	2.5	3.5	1	2	0.9
<i>Anthus trivialis</i>	0.5	0.5	2	4.5	2.5-3.5	0.8
<i>Phylloscopus collybita</i>	2	1.5-2	2	2	2.5	0.8
<i>Ficedula hypoleuca</i>	1.5	2	1	2	1	0.6
<i>Garrulus glandarius</i>	2	1	2	1	1	0.5
<i>Carduelis chloris</i>	3	2	0.5-1	1	-	0.5
<i>Oriolus oriolus</i>	1	2	1-2	1	1	0.5
<i>Dendrocopos leucotos</i>	1	0.5-1	0.5	0.5-1	1	0.3
<i>Parus cristatus</i>	0.5-1	1	1	1	-	0.3
<i>Dryocopus martius</i>	1	0.5	0.5	0.5	1	0.3
<i>Dendrocopos minor</i>	1	-	-	1.5	0.5-1	0.3
<i>Emberiza citrinella</i>	-	0.5	2	0.5	+	0.2
<i>Cuculus canorus</i>	-	1	1	1	+	0.2
<i>Pyrrhula pyrrhula</i>	-	0.5	+	-	2	0.2
<i>Strix aluco</i>	0.5	0.5-1	1	-	-	0.2
<i>Jynx torquilla</i>	0.5	-	1	0.5	-	0.2
<i>Regulus ignicapillus</i>	1	-	-	-	1	0.2
<i>Carpodacus erythrinus</i>	+	-	-	1	-	0.1
<i>Hippolais icterina</i>	0.5	-	0.5	-	-	0.1
<i>Streptopelia turtur</i>	-	1	-	-	-	0.1
<i>Parus ater</i>	-	-	-	1	-	0.1
<i>Phylloscopus trochilus</i>	-	0.5	0.5	-	-	0.1
<i>Aegithalos caudatus</i>	-	-	-	-	0.5-1	0.1
<i>Sylvia borin</i>	-	-	0.5	+	+	0.1
<i>Buteo buteo</i>	0.5	+	+	-	-	0.1
<i>Picoides tridactylus</i>	+	-	-	0.5	-	-
<i>Carduelis carduelis</i>	0.5	-	-	-	-	-
<i>Corvus corax</i>	+	-	-	-	+	-
<i>Scolopax rusticola</i>	-	-	+	-	-	-
<i>Bonasa bonasia</i>	-	+	-	-	-	-
<i>Accipiter nisus</i>	-	-	-	+	-	-
<i>Anas platyrhynchos</i>	+	-	-	-	-	-
<i>Motacilla alba</i>	-	-	-	-	+	-
Total (54 species)	215.2	229.5	235.5	267.2	259.3	94.6

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

[Tabela 4. Zgrupowanie ptaków lęgowych grądu (pow. CM, 24 ha). Pozostałe objaśnienia patrz tab. 1.]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	53	44	44	45.5	47.5	19.5
<i>Erithacus rubecula</i>	17	16	16	21.5	20.5	7.6
<i>Ficedula albicollis</i>	17	11	13	24.5	24-25	7.5
<i>Turdus philomelos</i>	12.5	7	9	12-13	9	4.2
<i>C. coccythraustes</i>	12	6.5	7.5-8.5	9.5-10.5	11	4.0
<i>Parus caeruleus</i>	9.5	6.5	11	9	7	3.6
<i>Sitta europaea</i>	8	9.5	5-5.5	8.5	5.5	3.1
<i>Parus major</i>	9.5	5.5	6	6	6.5	2.8
<i>Phylloscopus sibilatrix</i>	-	12.5	6.5	7	4	2.5
<i>Regulus regulus</i>	7	4.5	4.5	8	5	2.4
<i>Troglodytes troglodytes</i>	5	5.5	5.5	6.5	5.5	2.3
<i>Sylvia atricapilla</i>	4	4	5	7	6.5	2.2
<i>Turdus merula</i>	4.5	3	6.5	4.5	5	2.0
<i>Prunella modularis</i>	5.5	4	4	6	3.5-4.5	2.0
<i>Certhia familiaris</i>	5	4.5	4.5	4.5	4	1.9
<i>Parus palustris</i>	4.5	3.5-4	3-3.5	4.5	3	1.6
<i>Muscicapa striata</i>	4-5	1	2-3	4.5	3	1.3
<i>Columba palumbus</i>	4.5	3	3.5	1.5	2	1.2
<i>Dendrocopos medius</i>	2.5	1	2	0.5-1	1.5	0.6
<i>Ficedula parva</i>	2.5	2	2	-	1	0.6
<i>Phylloscopus collybita</i>	2.5	0.5	+	2	2	0.6
<i>Dendrocopos major</i>	1	+	0.5	2-2.5	2.5-3	0.6
<i>Garrulus glandarius</i>	1	1	0.5	1	1	0.4
<i>Ficedula hypoleuca</i>	1	-	1	2	0.5	0.4
<i>Parus ater</i>	1	-	1	1	1	0.3
<i>Oriolus oriolus</i>	+	1.5	1	-	1	0.3
<i>Pyrrhula pyrrhula</i>	1	1	-	1	-	0.3
<i>Strix aluco</i>	1	+	0.5	+	1	0.2
<i>Cuculus canorus</i>	0.5-1	0.5	0.5	+	0.5	0.2
<i>Apus apus</i>	+	-	1	-	1	0.2
<i>Dendrocopos minor</i>	-	1	0.5	0.5	-	0.2
<i>Sturnus vulgaris</i>	-	-	-	-	2	0.2
<i>Dendrocopos leucotos</i>	0.5	+	0.5	0.5	+	0.1
<i>Parus cristatus</i>	-	-	1	0.5	+	0.1
<i>Picoides tridactylus</i>	0.5	0.5	+	0.5	-	0.1
<i>Dryocopus martius</i>	+	-	+	0.5	0.5	0.1
<i>Aegithalos caudatus</i>	1	-	-	-	-	0.1
<i>F. albicollis x hypoleuca</i>	-	-	-	-	1	0.1
<i>Sylvia borin</i>	1	-	-	-	-	0.1
<i>Bonasa bonasia</i>	0.5	-	-	-	-	
<i>Scolopax rusticola</i>	-	-	+	-	-	
<i>Buteo buteo</i>	-	-	-	+	-	
Total (41 species)	201.1	161.1	170.5	204.4	191	77.8

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

[Tabela 5. Zgrupowanie ptaków lęgowych grądu (pow. MS, 30 ha). Pozostałe objaśnienia patrz tab. 1]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	59	55	55.5	56	67.5	19.5
<i>Ficedula albicollis</i>	22	21	22.5	30	36.5	8.8
<i>Erithacus rubecula</i>	20.5	13.5	13-14	19	23	6.0
<i>Parus caeruleus</i>	14	14-15	32	15.5	9-10	5.7
<i>C. coccythraustes</i>	17	19	14-15	9.5	17-18	5.2
<i>Phylloscopus sibilatrix</i>	-	18	20	18-19	12	4.6
<i>Parus major</i>	9.5	14	21.5	9.5	11.5-12.5	4.4
<i>Sitta europaea</i>	14	15.5	12	9.5	9	4.0
<i>Turdus philomelos</i>	10	10	8.5	11-12	9-10	3.3
<i>Turdus merula</i>	6	8.5	8	10.5	10	2.9
<i>Sylvia atricapilla</i>	3	4-4.5	4-5	7	12	2.1
<i>Troglodytes troglodytes</i>	4.5	5	7	5.5-6	7	2.0
<i>Certhia familiaris</i>	5	6-6.5	6.5	5-6	4-5	1.9
<i>Parus palustris</i>	6	5.5	5.5	5	5.5	1.8
<i>Muscicapa striata</i>	3	2-3	7.5	9	3-4	1.7
<i>Dendrocopos medius</i>	4-5	5	4	2	4	1.3
<i>Ficedula hypoleuca</i>	1	2	2.5	6.5	6	1.2
<i>Regulus regulus</i>	2	2-3	5.5	3	4	1.1
<i>Dendrocopos major</i>	4	3	1.5-2	2.5	4	1.0
<i>Anthus trivialis</i>	-	0.5	2	5.5	5.5-6.5	0.9
<i>Columba palumbus</i>	4	2	2	3	2.5-3	0.9
<i>Oriolus oriolus</i>	-	4	1-2	1	1	0.5
<i>Garrulus glandarius</i>	2.5	2	+	1.5	1	0.5
<i>Ficedula parva</i>	1	5	+	-	0.5	0.4
<i>Prunella modularis</i>	+	1	-	2	3	0.4
<i>Dendrocopos minor</i>	1	1	1-2	1	1	0.4
<i>Cuculus canorus</i>	0.5	0.5	1.5	1.5	1	0.3
<i>Dendrocopos leucotos</i>	1	1	0.5	1	1	0.3
<i>Phylloscopus collybita</i>	+	-	-	1.5	2	0.2
<i>Strix aluco</i>	-	1	0.5	1	1	0.2
<i>Aegithalos caudatus</i>	-	-	1.5	-	-	0.1
<i>Pyrrhula pyrrhula</i>	-	-	-	-	1	0.1
<i>Dryocopus martius</i>	+	+	+	0.5	-	0.1
<i>Pernis apivorus</i>	-	0.5	-	-	+	
<i>Columba oenas</i>	-	-	-	0.5	-	
<i>Corvus corax</i>	+	-	-	-	+	
<i>Carduelis spinus</i>	-	-	+	-	-	
<i>Accipiter nisus</i>	+	-	-	-	-	
<i>Picoides tridactylus</i>	+	-	-	-	-	
Total (39 species)	215.6	243.7	264.2	255.8	278.5	84.6

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

[Tabela 6. Zgrupowanie ptaków lęgowych boru (pow. NW, 25 ha). Pozostałe objaśnienia patrz tab. 1.]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	24.5	25.5	30	46.5	41	13.4
<i>Phylloscopus sibilatrix</i>	2	11.5	18	14.5	12.5	4.7
<i>Erethacus rubecula</i>	9.5	9.5	11.5-12.5	12	15	4.6
<i>Regulus regulus</i>	17.5	4.5	15.5	9.5	4.5-5.5	4.2
<i>Turdus philomelos</i>	6	7.5	7.5	11	5	3.0
<i>Parus ater</i>	5	5	6	4	4-5	2.0
<i>Certhia familiaris</i>	5	4.5	4.5	4.5	3	1.7
<i>Phylloscopus collybita</i>	2.5	2.5	4.5	6	4	1.6
<i>Parus cristatus</i>	5	2.5-3	4	3.5-4.5	3-4	1.5
<i>Prunella modularis</i>	4.5	3.5	3	4	1.5	1.3
<i>Troglodytes troglodytes</i>	4.5	2	4	2	2.5	1.2
<i>C. coccythraustes</i>	-	1-2	4-5	2	1-2	0.8
<i>Turdus merula</i>	-	2.5	3	0.5-1	2	0.7
<i>Pyrrhula pyrrhula</i>	2	1	1-1.5	2	2	0.7
<i>Ficedula hypoleuca</i>	1	-	1	2-3	3	0.6
<i>Garrulus glandarius</i>	1	1.5	1-2	1	1.5-2	0.5
<i>Sylvia atricapilla</i>	1.5	1	1	1.5	1.5	0.5
<i>Ficedula albicollis</i>	1	-	-	2-3	3	0.5
<i>Dendrocopos major</i>	2	0.5	+	1.5	2	0.5
<i>Carduelis spinus</i>	-	1	3	1	1	0.5
<i>Parus major</i>	1.5	+	1-2	1.5	1-1.5	0.5
<i>Bonasa bonasia</i>	1.5	1	1	1	-	0.4
<i>Picoides tridactylus</i>	1	1	0.5	1	1	0.4
<i>Columba palumbus</i>	1	+	1	1	1	0.3
<i>Cuculus canorus</i>	1	1	1	0.5	0.5	0.3
<i>Columba oenas</i>	0.5	0.5	0.5	1.5	1	0.3
<i>Sitta europaea</i>	1.5	0.5	-	-	2	0.3
<i>Parus caeruleus</i>	-	+	2.5	-	1	0.3
<i>Anthus trivialis</i>	1	-	-	0.5	2	0.3
<i>Muscicapa striata</i>	-	0.5	-	1-2	1	0.2
<i>Dryocopus martius</i>	1	0.5	0.5	0.5	0.5	0.2
<i>Ficedula parva</i>	-	-	2	0.5	-	0.2
<i>Ph. phoenicurus</i>	0.5	0.5	-	0.5	0.5-1	0.2
<i>Scolopax rusticola</i>	-	+	1	-	1	0.2
<i>Aegithalos caudatus</i>	1	-	1	-	-	0.2
<i>Glucidium passerinum</i>	0.5	-	-	1	-	0.1
<i>Loxia curvirostra</i>	-	-	1	0.5	-	0.1
<i>Parus palustris</i>	+	-	0.5	+	0.5	0.1
<i>Oriolus oriolus</i>	1	-	-	-	-	0.1
<i>Asio otus</i>	0.5	-	-	-	-	
<i>Parus montanus</i>	-	+	-	-	-	
<i>Dendrocopos leucotos</i>	-	-	+	-	-	
Total (42 species)	108.1	93.8	138.5	144.6	128.9	49.1

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

[Tabela 7. Zgrupowanie ptaków lęgowych boru (pow. NE, 25 ha). Pozostałe objaśnienia patrz tab. 1]

Species	Number of pairs					Mean density (p/10 ha)
	1990	1991	1992	1993	1994	
<i>Fringilla coelebs</i>	24	25.5	37.5	36.5	39	13.0
<i>Phylloscopus sibilatrix</i>	4	16	21	20	16	6.2
<i>Erithacus rubecula</i>	17	7	10.5	12.5-13.5	16	5.1
<i>Regulus regulus</i>	18	6-7	10.5-11.5	12.5	9	4.6
<i>Turdus philomelos</i>	3	5-6	9.5	6-7	5	2.4
<i>Certhia familiaris</i>	6	7	6	3.5	4	2.1
<i>Parus cristatus</i>	5	3.5	6-7	3	3-5	1.8
<i>Parus ater</i>	4	3-4	4	3	5.5	1.6
<i>Phylloscopus collybita</i>	3.5	2.5	3	5.5	2	1.3
<i>Troglodytes troglodytes</i>	3.5	4.5	2.5	2	1.5	1.1
<i>Prunella modularis</i>	1.5	2.5	2	3	1.5	0.8
<i>Turdus merula</i>	2	2	2	1.5	2	0.8
<i>Ficedula parva</i>	-	1	3	2-3	2	0.7
<i>Pyrrhula pyrrhula</i>	1	2	1	2	1	0.6
<i>Parus major</i>	1.5	-	2.5	1.5	1-2	0.5
<i>Anthus trivialis</i>	1	1.5	1	0.5	2	0.5
<i>C. coccythraustes</i>	+	-	2	3	-	0.4
<i>Carduelis spinus</i>	1	1	2	1-2	-	0.4
<i>Garrulus glandarius</i>	1	1.5	0.5-1.5	1	1	0.4
<i>Sylvia atricapilla</i>	1	1	2	1	0.5	0.4
<i>Sitta europaea</i>	1.5	-	-	+	3	0.4
<i>Muscicapa striata</i>	1.5-2	1-1.5	1-2	-	-	0.4
<i>Columba palumbus</i>	1	1	0.5	1	1	0.4
<i>Bonasa bonasia</i>	0.5	+	1	2	0.5	0.3
<i>Columba oenas</i>	-	-	1	1	1.5	0.3
<i>Dryocopus martius</i>	1	0.5	0.5	0.5	0.5	0.2
<i>Dendrocopos major</i>	-	-	-	1.5	1	0.2
<i>Parus caeruleus</i>	+	+	1	+	1	0.2
<i>Picoides tridactylus</i>	+	1.5	0.5	+	-	0.2
<i>Cuculus canorus</i>	0.5	-	0.5	+	1	0.2
<i>Ficedula hypoleuca</i>	1	-	-	1	-	0.2
<i>Ph. phoenicurus</i>	0.5	-	-	1	-	0.1
<i>Glaucidium passerinum</i>	0.5	1	-	-	-	0.1
<i>Scolopax rusticola</i>	-	+	1	-	-	0.1
<i>Nucifraga caryocatactes</i>	+	1	-	-	-	0.1
<i>Parus montanus</i>	1	-	-	-	-	0.1
<i>Accipiter nisus</i>	0.5	-	-	0.5	-	0.1
<i>Loxia curvirostra</i>	-	-	-	1	-	0.1
<i>Turdus viscivorus</i>	-	1	-	-	-	0.1
<i>Apus apus</i>	-	-	1	-	-	0.1
<i>Ficedula albicollis</i>	-	-	-	-	1	0.1
<i>F. albicollis x hypoleuca</i>	-	-	-	-	1	0.1
<i>Parus palustris</i>	-	-	0.5	-	-	-
<i>Asio otus</i>	0.3	-	-	-	-	-
<i>Oriolus oriolus</i>	-	+	-	-	-	-
<i>Strix aluco</i>	-	+	-	-	-	-
<i>Aegolius funereus</i>	+	-	-	-	-	-
Total (46 species)	108.6	101.8	139	133.4	125	49.3

Table 8. Main structural parameters of bird assemblages of riverine BNP stands in the two study periods. Mean values and standard deviations are shown; densities are given in pairs/10 ha. Means differing significantly between the periods (at $p < 0.05$, t test, two-tailed) are shown in bold type. Data for 1975–79 calculated from materials published in Tomiałojć *et al.* (1984).

[Tabela 8. Podstawowe parametry struktury zgrupowań ptaków podmokłych lasów BPN w dwóch okresach badań. Podano przeciętne wartości zagęszczeń (p/10 ha) i ich odchylenia standardowe. Różniące się istotnie wartości średnie ($p < 0.05$, test t , dwustronny) wytuszczono. Wartości dla lat 1975–79 wyliczono z danych w Tomiałojć *et al.* (1984). NS — liczba gatunków, OD — łączne zagęszczenie, DMS — zagęszczenie przeciętnego gatunku, CSD — łączny udział dominantów. Grupy żerowiskowe: O — żerują poza lasem, P — drapieżne, V — roślinożerne, IG — bezkręgowce z dna lasu, IB — 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 — zimują w regionie, RF — zimują w lesie. Definicje poszczególnych grup patrz tekst.]

		Plot K (edge)				Plot L			
		1975–79		1990–94		1976–77		1990–94	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total assemblage	Number of species (NS)	50.2	0.8	47.6	1.5	35.0	1.4	36.0	1.6
	Overall density (OD)	100.0	4.9	104.0	8.0	72.8	11.4	78.0	4.0
	Density of mean species (DMS)	2.0	0.2	2.2	0.2	2.1	0.4	2.2	0.1
	Cumulative share of dominants (%) — (CSD)	39.7	3.7	40.2	6.4	51.2	9.5	41.6	8.3
Densities of foraging groups	Forage outside forest (O)	13.0	3.3	8.0	1.8	0.0	0.0	0.6	0.1
	Predators (P)	0.2	0.1	0.5	0.1	0.2	0.1	0.3	0.1
	Vegetarians (V)	5.8	0.6	8.5	1.0	5.0	0.0	6.9	0.7
	Ground insectivores (IG)	33.0	1.4	30.7	3.4	24.4	5.2	24.8	3.4
	Bark insectivores (IB)	5.4	0.5	8.1	0.5	6.8	0.6	7.4	0.8
	Crown insectivores (IL)	42.7	1.8	48.2	4.9	36.4	5.6	38.1	1.7
Densities of nesting groups	Ground nesters (G)	35.5	2.3	26.8	3.4	26.3	6.3	21.2	2.6
	Crown nesters (C)	32.5	2.1	41.2	4.7	24.7	2.2	30.7	1.9
	Hole nesters (H)	31.7	4.9	35.7	1.7	21.5	3.3	25.7	1.4
Densities of migratory groups	Tropical migrants (T)	29.5	3.2	21.9	3.4	17.3	4.4	15.0	1.1
	Short-distance migrants (S)	53.4	3.5	57.7	6.2	37.9	5.8	42.5	5.0
	Resident in region (R)	9.8	1.8	13.5	0.2	9.0	0.9	11.0	1.7
	True forest residents (RF)	7.5	1.0	10.9	0.6	8.6	0.4	9.5	1.6

Table 9. Main structural parameters of bird assemblages of oak-linden-hornbeam BNP stands in the two study periods. Mean values and standard deviations are shown; densities are given in pairs/10 ha. Means differing significantly between the periods (at $p < 0.05$, t -test, two-tailed) are shown in bold type. Data for 1975–79 calculated from materials published in Tomiałojć *et al.* (1984).

[Tabela 9. Podstawowe parametry struktury zgrupowań ptaków w grądach BPN w dwóch okresach badań. Podano przeciętne wartości zagęszczeń (p/10 ha) i ich odchylenia standardowe. Różniące się istotnie wartości średnie ($p < 0.05$, test t , dwustronny) wytuszczono. Wartości dla lat 1975–79 wyliczono z danych w Tomiałojć *et al.* (1984). NS — liczba gatunków, OD — łączne zagęszczenie, DMS — zagęszczenie przeciętnego gatunku, CSD — łączny udział dominantów. Grupy żerowiskowe: O — żerują poza lasem, P — drapieżne, V — roślinożerne, IG — bezkręgowce z dna lasu, IB — 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 — zimują w regionie, RF — zimują w lesie. Definicje poszczególnych grup patrz tekst.]

		Plot W				Plot CM				Plot MS			
		1975–79		1990–94		1975–79		1990–94		1975–79		1990–94	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total	Number of species (NS)	39.8	2.4	40.0	1.6	30.8	3.6	33.4	2.1	29.4	3.1	31.2	1.1
assemblage	Overall density (OD)	76.1	8.1	94.6	8.4	62.4	6.5	77.4	7.9	61.2	4.7	83.8	7.9
	Density of mean species (DMS)	2.0	0.2	2.4	0.3	2.0	0.1	2.3	0.2	2.0	0.3	2.7	0.2
	Cumulative share of dominants (%) — (CSD)	60.7	3.8	60.9	3.3	62.5	5.0	54.6	2.5	62.3	4.9	62.4	8.6
Densities of foraging groups	Forage outside forest (O)	4.8	2.1	2.2	0.6	0.1	0.2	0.4	0.4	0.2	0.2	0.2	0.1
	Predators (P)	0.5	0.3	0.5	0.3	0.2	0.2	0.4	0.2	0.4	0.2	0.4	0.2
	Vegetarians (V)	7.4	0.8	9.8	0.8	6.2	0.6	8.5	1.2	6.0	0.7	9.2	1.2
	Ground insectivores (IG)	19.5	1.8	24.7	3.0	17.2	2.6	21.5	2.5	16.5	1.8	20.0	3.4
	Bark insectivores (IB)	3.8	0.9	6.3	0.3	4.0	0.8	5.7	0.7	4.0	0.7	7.4	1.1
	Crown insectivores (IL)	40.3	3.1	51.2	6.1	34.6	3.5	40.8	4.3	34.2	2.0	46.6	6.8
Densities of nesting groups	Ground nesters (G)	18.9	2.0	19.1	4.2	16.5	2.7	14.8	2.0	16.6	1.3	14.5	4.7
	Crown nesters (C)	33.2	2.8	42.6	3.2	28.6	2.2	36.1	4.3	25.1	3.0	35.9	2.4
	Hole nesters (H)	23.7	5.5	32.7	3.9	16.7	3.6	26.3	4.1	19.4	2.6	33.2	3.3
Densities of migratory groups	Tropical migrants (T)	22.0	3.3	24.7	6.0	15.6	2.8	15.3	2.8	18.7	2.0	20.6	6.6
	Short-distance migrants (S)	40.2	3.2	48.4	5.5	35.2	2.9	43.4	4.5	30.9	2.5	40.4	4.2
	Resident in region (R)	8.2	1.2	12.5	2.0	6.0	1.9	10.0	1.7	4.1	1.5	12.9	4.2
	True forest residents (RF)	5.6	1.3	9.0	0.6	5.6	1.6	8.5	1.3	5.4	0.8	10.0	1.4

Table 10. Main structural parameters of bird assemblages of coniferous BNP stands in the two study periods. Mean values and standard deviations are shown; densities are given in pairs/10 ha. Means differing significantly between the periods (at $p < 0.05$, t -test, two-tailed) are shown in bold. Data for 1975–79 calculated from materials published in Tomiałojć *et al.* (1984).

[Tabela 10. Podstawowe parametry struktury zgrupowań ptaków w borach BPN w dwóch okresach badań. Podano przeciętne wartości zagęszczeń (p/10 ha) i ich odchylenia standardowe. Różniące się istotnie wartości średnie ($p < 0.05$, test t , dwustronny) wytuszczono. Wartości dla lat 1975–79 wyliczono z danych w Tomiałojć *et al.* (1984). NS — liczba gatunków, OD — łączne zagęszczenie, DMS — zagęszczenie przeciętnego gatunku, CSD — łączny udział dominantów. Grupy żerowiskowe: O — żerują poza lasem, P — drapieżne, V — roślinożerne, IG — bezkręgowce z dna lasu, IB — 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 — zimują w regionie, RF — zimują w lesie. Definicje poszczególnych grup patrz tekst.]

		Plot NE				Plot NW			
		1975–79		1990–94		1975–79		1990–94	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total	Number of species (NS)	25.8	3.7	31.4	2.7	24.2	1.6	32.6	1.1
assemblage	Overall density (OD)	38.5	6.2	48.6	6.4	34.7	5.2	49.1	8.5
	Density of mean species (DMS)	1.5	0.2	1.6	0.3	1.4	0.2	1.5	0.2
	Cumulative share of dominants (%) — (CSD)	61.7	4.2	63.2	2.6	69.5	5.3	58.8	5.4
	Densities of foraging groups								
	Forage outside forest (O)	0.2	0.2	0.3	0.3	0.1	0.1	0.2	0.1
	Predators (P)	0.3	0.3	0.4	0.3	0.2	0.1	0.4	0.2
	Vegetarians (V)	4.0	1.1	5.0	1.4	3.2	0.6	5.5	1.3
	Ground insectivores (IG)	9.9	0.8	12.1	1.0	9.5	1.6	12.5	1.5
	Bark insectivores (IB)	1.8	0.3	2.9	0.6	1.6	0.3	2.8	0.5
	Crown insectivores (IL)	22.4	4.6	27.9	5.0	20.1	3.8	27.7	5.9
Densities of nesting groups	Ground nesters (G)	12.3	2.9	14.2	2.5	10.6	2.1	13.2	2.8
	Crown nesters (C)	18.1	2.9	24.3	3.9	17.3	2.5	24.8	5.1
	Hole nesters (H)	7.8	1.4	10.0	1.8	6.6	1.4	10.8	2.0
Densities of migratory groups	Tropical migrants (T)	8.7	2.3	8.8	3.1	6.8	1.6	7.6	2.8
	Short-distance migrants (S)	20.7	2.2	25.7	4.1	19.7	2.1	27.4	5.7
	Resident in region (R)	4.1	1.5	7.2	1.9	3.8	0.9	7.2	2.9
	True forest residents (RF)	5.0	1.0	6.9	1.2	4.4	1.4	6.9	1.1