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**Breeding bird community of a primaeval temperate forest
(Białowieża National Park, Poland)**

TOMIAŁOJĆ L., WESOŁOWSKI T., WALANKIEWICZ W. 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). *Acta orn.* 20: 241–310.

During 1975–79 bird censuses (covering yearly 260–358 ha of climax forest) were carried out in the Białowieża National Park (eastern Poland) which preserves the remnants of primaeval lowland forests of a mixed deciduous-coniferous type. Improved version of mapping technique has been used. Overall bird densities ranged from 27.4 pairs/10 ha in coniferous to 105.5 p/10 ha in the forest-edge ash-alder stands, with the most frequent values between 50 and 70 (chiefly in oak-hornbeam stands). The densities of most species did not exceed 3 p/10 ha. Density of hole-nesters was surprisingly low (4.6 in coniferous, 22.3 in oak-hornbeam, and up to 36.2 p/10 ha in riverside forest-edge stands); especially tits (*Paridae*) occurred in very scattered populations. The structure of bird assemblages was found to be rather similar among various habitats and stable between years. The analysis of data suggests only a weak correlation between bird densities and the food resources available during the breeding season. Very low breeding densities in BNP are tentatively explained as a result of an undersaturation of habitats by several bird species and, for those that saturate habitats, by low densities being an adaptation to heavy predatory pressure.

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Сообщество птиц гнездящихся в ненарушенном лесу умеренной полосы (Беловежский национальный парк, Польша)

В 1975–79 годах был произведен учет численности птиц на пробных площадках, охватывающих ежегодно 260–358 га, лежащих в климаксовых лесах Беловежского национального парка (восточная Польша). В этом Парке сохранились последние фрагменты первичных низинных смешанных лесов. При учете был применен усовершенствованный картографический метод. Плотность гнездящихся птиц в общем колебалась в пределах от 27.4 пар/10 га в елово-сосновых борах до 105.5 пар/10 га в ольсах ольхово-ясеневых находящихся на опушках. Чаще всего констатированная величина плотности ограничивалась в пределах 50–70 пар (главным образом в дубово-грабовом груде). Плотность большинства видов не превышала 3 пар/10 га. Плотность дуплогнезdnиков была чрезвычайно низка (4.6 в еловососновых борах, 22.3 в груде и до 36.2 пар/10 га в пойменных ольсах на опушках леса), особенно синицы встречались в очень разреженных популяциях. Структура сообществ птиц была довольно сходна между отдельными формациями и стабильна во времени. Связь между обилием доступного корма в период гнездования и плотностью птиц, как показал анализ, была слабая. Очень низкая плотность гнездования предварительно объясняется недостаточной насыщенностью биотопов многими видами, а у видов, которые насыщают биотопы, эволюционным приспособлением, позволяющим им избежать сильного пресса хищников.

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"The forest community
Those woods of Lithuania — who has dared explore
Their depths abysmal, penetrate their midmost core?
A fisher on the beach shall scarcely sound the sea!
The hunter can but skirt our forest-bed — and he
Beholds its outward form and feature, these alone;
To him its inner heart and secret are unknown.
Only report and fable tell what there is found;"

From A. MICKIEWICZ's poem „Pan Tadeusz”,
translated by Oliver ELTON
for Slavonic Year-Book 19(1940): 9.

INTRODUCTION

Most lowland forests of the European and North American temperate zone underwent deep anthropogenic transformations before modern research started. This fact can seriously impair several generalized statements in avian ecology. Inadequate states were frequently compared or secondary situations after man-induced transformations of an unknown degree were accepted as representing natural conditions.

The position of the Białowieża Forest as an object of ecological studies is an exceptional one (FALIŃSKI 1968, TOMIAŁOJÓ *et al.* 1977). Particularly in the Białowieża National Park (BNP) there are the best preserved remnants of primaevial lowland mixed forests. The following traits allow one to consider them as representing a typical European primaevial woodland:

(a) their localization in the very centre of the European lowland, far from the extreme, either oceanic or true continental (Siberian), conditions;

(b) the situation in the middle of the vast European lowland, away from confusing influences of mountainous elevations;

(c) great vastness and compactness of the Białowieża Forest, which surrounds the BNP in the form of 10–20 km broad buffering zone and isolates it from extensive farmland areas;

(d) vast areas of surviving rich deciduous and mixed treestands in BNP, which elsewhere in Europe have undergone transformation into fields, or were replaced by secondary stands after drainage, or finally, reduced to island-like woods extensively influenced by agricultural or urban neighbourhood.

Our studies in BNP were aimed at giving the first comprehensive description (a model) of the close-to-primaevial breeding bird community from a lowland temperate forest in order to: (a) offer a reference point for several other studies in managed woods and forests of Europe, and (b) permit adequate comparisons between undisturbed forest bird communities from other climatic zones and the equivalent temperate ones.

The present paper is among the very first ones (see also WESOŁOWSKI 1981, 1983, LEWARTOWSKI and WOLK 1983, PIOTROWSKA and WOLK 1983) which initiate a long series of works dealing with the bird ecology in the Białowieża Forest. Being restricted to an analysis of the data from climax stands of the plant associations dominating in the Białowieża National Park, it leaves aside

such aspects as the bird communities in younger successional stages, in less common plant associations, in transitional zones between main habitats or in managed stands. These tasks, as well as detailed population dynamics problems of some model species, will be the subject of separate papers.

STUDY AREA

The Białowieża Forest (1250 km²; 580 km² belonging to Poland) is situated on the geographical border between central and eastern Europe. The geographical coordinates of Białowieża village (52°41'N and 23°52'E), which is located in a forest clearing (13.7 km²), correspond to the latitudinal position of central England. Biogeographically it falls within the mixed forest (deciduous-coniferous) zone containing a significant amount of native Norway spruces *Picea abies* present in all types of tree-stands.

The Forest represents a relic remnant of vast European lowland forests once extending over a greater part of the continent. Its present unique features result from its considerable size, great compactness and exceptionally good protective measures. Though human presence can be traced back to Neolithic, for ages these forests served mostly as hunting grounds for several sovereigns, thus, being always under some protection. At that time slight direct human interference (local clearing of the forest, single-tree fellings, local fire, hunting, grazing by cattle or by game species bred in excess) occurred also over the area of the present National Park.

Since 1921 the best preserved and most diverse part of the Forest has remained under strict state protection, since 1932 as the Białowieża National Park (BNP), 47.5 km² in size. This area is guarded, with visitors allowed to enter it only under special guidance and then mostly to three of over forty forest compartments. Direct human interference is restricted to the maintenance of rides (lines) dividing the forest into 1066 × 1066 m squares since mid-19th century, removal of fallen logs from a few forest roads, and to strictly controlled activity of scientists. Indirect influences of changes in the neighbourhood, however, cannot be totally prevented and affect BNP in the form of a somewhat lower level of ground-waters, some degree of air pollution from distant urban centres, and some control of the numbers of big game in managed forests surrounding the Park.

Physico-geographic conditions. The relief of the Białowieża Forest area is typical of a glacial ground moraine poor in elevated points. Its altitude varies between 134 and 202 (mostly 165–170) m above sea level. Large stretches of the Polish part remain to be swampy, marshy or covered with small peat-bogs, while extensive marshes of the Byelorussian part have been reclaimed after the Second World War. There are no lakes, except artificial reservoirs recently constructed on the Byelorussian side, 8 km SE from BNP.

This part of the European lowland lies within the zone of subcontinental climate. The oceanic influences are considerable, though continental ones prevail: average annual temperature is 6.6°C, with an average 17.6° in July and minus 4.3° in January. Snow cover (usually c. 0.5 m) lasts for 92 days (max. 140) and morning ground-frosts happen as late as mid-June. Snow melts between c. 10 March (early spring) and 20 April (exceptionally late). Mean annual precipitation is 624 mm (426–857). The synphenological vegetation period in oak-hornbeam stands lasts c. 185 days (FALIŃSKI 1968, 1977). In spring, the bird phenology events show some retardation in comparison to western Poland. *E.g.* first *Fringilla coelebs* and *Turdus merula* appear on 24 March, first *Cuculus canorus* on 22 (15–25) April, *Oriolus oriolus* on 30 April (29 April–5 May); data after DOLBIK (1975) and own unpublished. In the case of *Turdus merula* and *T. philomelos* first fledgelings can be seen in the forest around 18–20 May, those of *Parus major* between 8–18 June and of *Dendrocopos major* 9–18 June.

Vegetation. A pollen analysis indicates that the oak-hornbeam association in the Białowieża Forest started to develop during the Atlantic period 7500–4500 years B.P. (FALIŃSKI 1968), and recently it has been suggested that the increased proportion of hornbeam in central-European forests resulted from early anthropogenic influences (RALSKA-JASIEWICZOWA 1982). Historical period (after 2600 B.P.) brought in a further development of the oak-hornbeam association, with increasing human impact. Like most plant communities, climax stands of BNP are not in equilibrium. Studies by PIGOTT (1975) and KOWALSKI (1982) have revealed the presence of cycles in their tree regeneration. During last fifty years the lime has been strongly expanding in younger generations of BNP stands, while the percentage of spruce, oak, and partly hornbeam, seems to decrease. There are good reasons to suggest (see KOWALSKI 1982) that those cycles are mostly of natural character, dependent on climate changes, and not so much due to a lime destruction in the past by game and man, as suggested by PIGOTT (1975).

The present BNP stands are distinguished among temperate forests by some features often attributed to subtropical seasonal forest, although they are rather characteristic of all rich primaeval forests, but have been lost by temperate ones in the course of management. These are:

— Unusual height of stands. The maximum measurements for several Białowieża stands are as follows (FALIŃSKI 1968, 1977): Norway spruce *Picea abies* — 55 m high, pine *Pinus silvestris* — 45 m, pedunculate oak *Quercus robur*, small-leaved lime *Tilia cordata* and ash *Fraxinus excelsior* — up to 42–43 m, aspen *Populus tremula* — 40 m, alder *Alnus glutinosa* and hornbeam *Carpinus betulus* — 32–33 m.

— Multi-storey profile of stands. Especially those of oak-hornbeam forest can be subdivided into 5–6 layers. The emergents of tropical forest find here

their equivalents in giant spruces rising 10–15 m above the main canopy. — Relatively diverse tree community. Białowieża stands harbour 26 species of trees and 55 shrub species. The oak-hornbeam stands alone may be composed of a dozen or so tree species. They are also very diversified as regards the age and size of trees. Several stands as a whole are over 200 years old, with many trees being 250–400 years old.

— Large amount of dead timber and uprooted trees. The BNP stands contain a lot of dead standing stems, stumps, freshly uprooted trees and old fallen logs. There are many discs of flat root systems (called in Polish as “vykhrot”) belonging to fallen trees. They rise vertically up to 7 m, and represent a special unit intermediate between the ground and the tree-layers. All those structures, especially abundant in riverside swampy forests, provide preferable feeding, nesting and hiding places for many birds. They are absent or very scarce in the surrounding managed forest.

Food resources for birds. Unfortunately, to date there are only scarce quantitative data on the numbers or biomass of invertebrates in the BNP habitats. *E.g.* BOROWSKI and DEHNEL (1952) tried to estimate the seasonal dynamics in the numbers of some ground insects, by capturing them in traps. These data are, however, hardly comparable to any from other European forests. For this reason, we are forced to rely only on our own rough comparative estimates made during our travels over the Europe. Judging from them it is our strong impression that the invertebrate biomass in the Białowieża deciduous or mixed forests belongs to the highest ones.

The most conspicuous and abundant insect group in the oak-hornbeam forest are *Lepidoptera* caterpillars, belonging mainly to two families: diverse and more abundant *Geometridae* (mostly *Hibernia defoliaria*, *Operophtera brumata*, *O. boreata*), and less abundant *Tortricidae* (*Tortrix viridana*). The outbreaks of *Geometridae* caterpillars were especially heavy in 1975 and 1979, causing almost total defoliation of several hornbeams and serious damage to other deciduous species. At that time a “rain” of their droppings falling to the ground could be heard as a permanent sound. The abundance of caterpillars was monitored by checking hornbeam twigs from lower parts of the undercanopy. It should be added that *Geometridae* and *Tortricidae* larvae only very scarcely occur in other types of BNP forests in spite of the presence of deciduous trees.

Another very important group — *Diptera* — seems to be equally abundant and important to birds in BNP. Its abundance can be estimated only descriptively. *E.g.* 23 *Culicidae* species occur in the Forest in fluctuating, though usually very high numbers, not unlike those from Amazonian forests (after E. O. WILLIS visiting Białowieża), making the work inside the forest impossible without repellents. *E.g.* one can kill up to 20 of them, sometimes 40, with one hand stroke. *Tabanidae* are the other serious nuisance; during warm Junes (1975, 1979) they used to occur in mid-day hours in numbers almost drowning

bird voices. The same can be said about some unidentified fly-like dipterans of coniferous stands.

To this list *Ephemeroptera*, *Trichoptera*, *Neuroptera* and *Plecoptera* can be added, insects occurring in large numbers in wet ash-alder stands during June, as well as masses of *Succinea* snails omnipresent in swampy forests. It seems that in spite of the absence of *Geometridae*, the total biomass of insects and spiders (*Arachnida*) in wet riverside forests exceeds that of the oak-hornbeam ones, being more diverse and available to birds for a longer period.

The spruce dominated coniferous stands constitute the poorest, tropically, type of habitats studied. Only single caterpillars of *Geometridae* were recorded on their deciduous trees. On the other hand, in 1979 a conspicuous outbreak of some small *Noctuidae* butterflies was recorded here. The numbers of flies, mosquitoes and *Tabanidae* are also rather considerable in this habitat.

Diversity of predators on birds. The richness and abundance of this group in the Białowieża Forest, in spite of some past extinctions (*Ursus arctos*, *Felis silvestris*, *Falco peregrinus*, *Strix nebulosa*, perhaps *Pteromys volans**), remains very high and contrasts with the present state of the predatory fauna in the majority of European managed forests and woods. Here there are still over 30 species of important predators on birds and/or bird nests (most important predators underlined): *Martes martes*, *Mustela nivalis*, *M. erminea*, *M. putorius*, *M. vison*, *Meles meles*, *Lutra lutra*, *Vulpes vulpes*, *Canis lupus*, *Lynx lynx*, domestic cat, *Nyctereutes procyonoides* (new and common predator), *Sus scrofa* (common), *Sciurus vulgaris*, *Glis glis*, *Eliomys quercinus*, *Accipiter gentilis*, *A. nisus*, *Hieraetus pennatus*, *Aquila pomarina*, *Buteo buteo* and *Pernis apivorus* (both hunting below forest canopy), *Falco subbuteo*, *Strix aluco*, *Glaucidium passerinum*, *Corvus corax*, *Garrulus glandarius*, *Nucifraga caryocatactes*, as well as very scarce or irregularly breeding species like *Circaetus gallicus*, *Aquila chrysaetos*, *Bubo bubo*, *Aegolius funereus*, and *Corvus cornix*, even when one neglects smaller rodents, insectivores or few and scarce snakes. *Sus scrofa* has appeared to be an important nest predator of ground-nesting birds (WESOŁOWSKI 1980), while the impact of *Gliridae* mammals on hole-nesters has been evidenced several times (DALMEE *et al.*, 1972, LÖHRL 1977, POMARNACKI 1976, WALANKIEWICZ and WOŁK unpubl.).

Theoretically it is possible for medium-sized predators, which are most important for birds, to be secondarily more abundant now than in the primaeval times, due to the lack of large predators. The presence of big predators, however, in the Białowieża Forest (*Canis lupus*, *Lynx lynx*, *Aquila*, *Bubo bubo*), makes this possibility very unlikely there.

*The past occurrence of *Gulo gulo* and *Martes zibellina* in the Białowieża Forest quoted earlier (TOMIAŁOJĆ *et al.* 1977) after older sources by most theriologists is considered uncertain (PUCEK and RACZYŃSKI 1983, pers. comm.).

METHODS

Because of the unique value of BNP forests our intention was to collect the most accurate possible quantitative data suitable for a multisided future use. This we attempted to achieve by:

- carrying out studies simultaneously in several plots and several habitats to avoid one-sample judgements;
- carrying out studies during (2) 3–5 years on each plot to reduce the effect of year-to-year fluctuations;
- applying most accurate census method producing absolute density values (TOMIAŁOJĆ 1980 b) which are comparable even between species;
- studying relatively large plots to reduce chance error and the overestimation of densities.

Census method

All the plots studied in BNP (Fig. 1) have been provided with a grid system of marks (plastic tapes around the tree stems) which have been laid down every 50 m after making accurate measurements. Additionally, every 100 m there was a timber pole driven into the ground in order to make the repetition of studies possible even after many years. The poles have been carefully preserved from decaying.

An improved version of the mapping technique (a combined mapping) for censusing breeding birds has been applied (TOMIAŁOJĆ 1980b). It differs from the 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) prolonged duration of a single visit to the plot (up to 6 hours per 25 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, usually the same morning.

The accuracy of the method applied has been checked by comparing census data with the actual bird numbers known for some species from additional, more careful, estimates based among other things on individual marking (WESOŁOWSKI 1980, 1983). Most species seem to have been registered in our censuses with a close-to-hundred per cent accuracy. In methodical paper (TOMIAŁOJĆ 1980b) it was estimated that *Turdus philomelos* numbers were too low by some 28% and those of *Parus caeruleus* and *Regulus regulus* by some 20–25%. However, later field tests (unpublished data) have shown that previous test yielded too pessimistic results, being performed during the exceptionally warm and dry season 1979, which had a negative effect on the song activity of turdids and regulids, at least. Hence, we believe that also for those species our results remain within the limits of a 10% error. Other tests (TOMIAŁOJĆ 1980b) and



Photo 1. Surroundings of the main gate to the BNP — a winter aspect. The structure of oak-hornbeam stand can be seen from outside.

<http://rcin.org.pl>
Photo by J. Herczyński



Photo 2. Searching for nests in a “vykhrot”.

Photo by J. Walencik



<http://rcin.org.pl>
Photo 3. Early spring in an ash-alder riverside forest.

Photo by J. Hereźniak



Photo 4. Ash-alder stand in June.

Photo by J. Walencik



Photo 5. Size and structure of trees in an oak-hornbeam stand — a fragment typical of some parts of plot W.

<http://rcin.org.pl>
Photo by J. Hereźniak

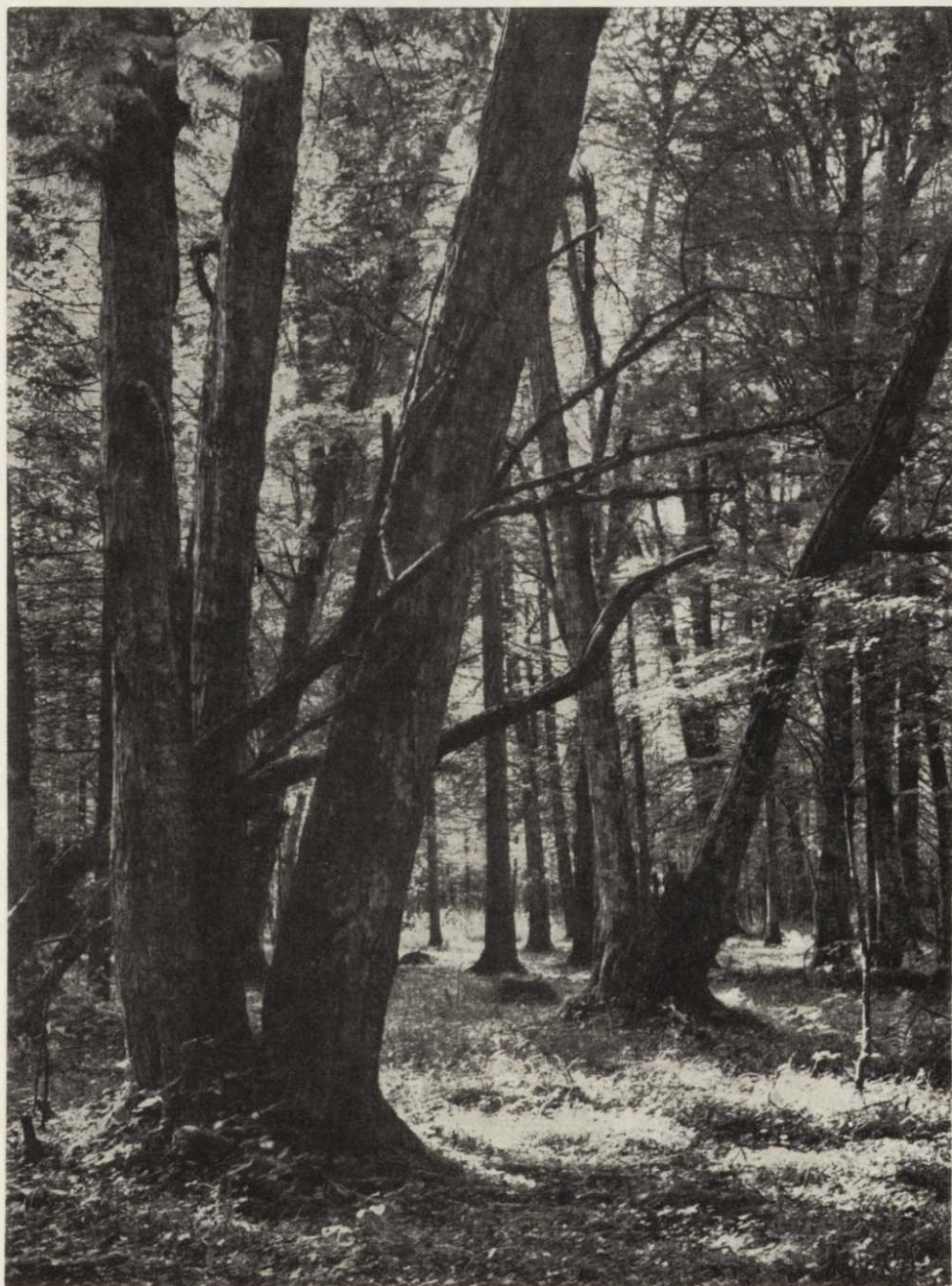


Photo 6. Hornbeam dominated fragment typical of some parts of plots CW and CE.

Photo by J. Hereźniak



Photo 7. Structure of a coniferous-deciduous mixed stand typical of plot GB.

<http://rcin.org.pl>
Photo by J. Herczaniak



Photo 8. Structure of a spruce-pine dominated stand typical of plots NW and NE.

<http://rcin.org.pl>
Photo by J. Heczniak

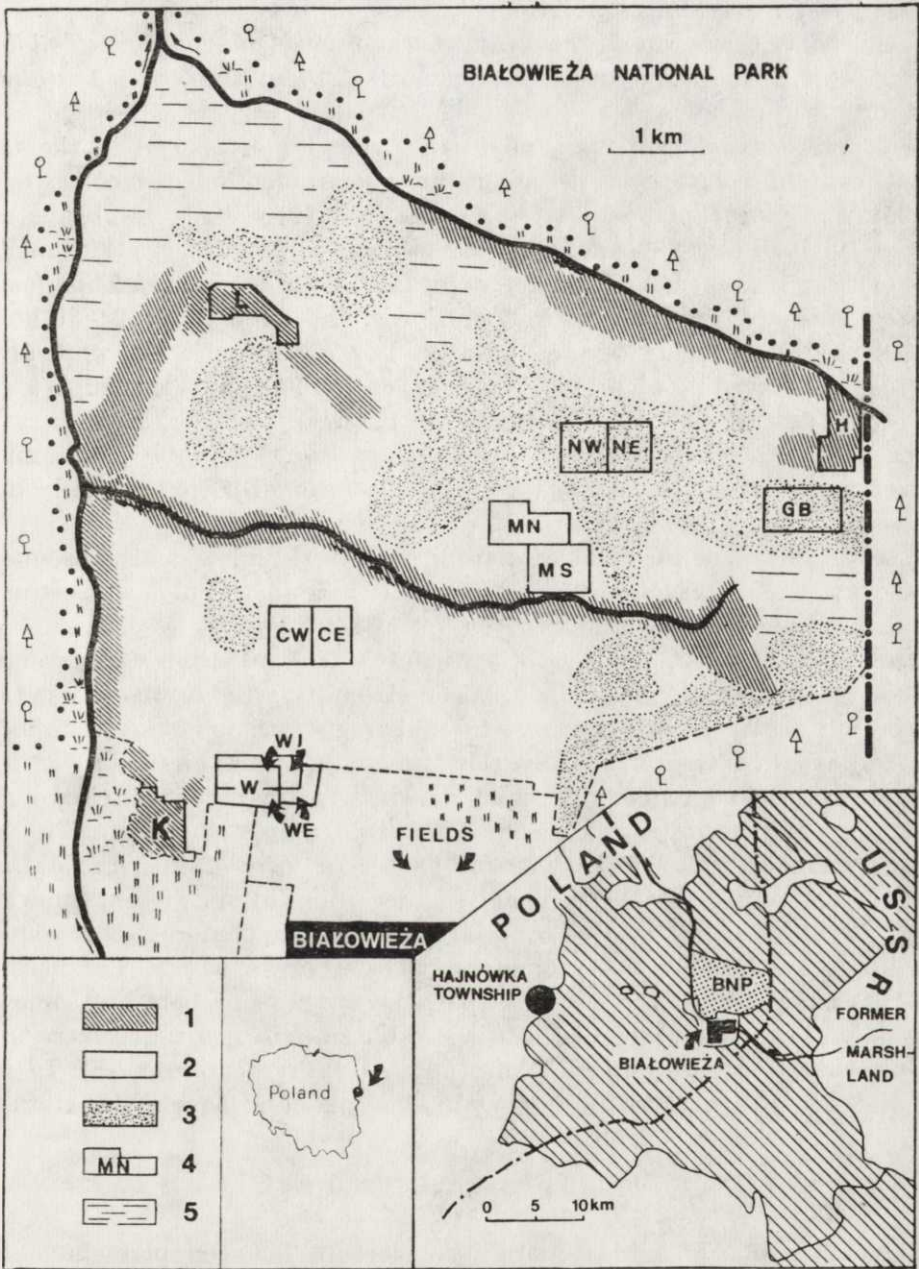


Fig. 1. Distribution of census plots in BNP and the positioning of BNP within the Forest.
 1 - alder and ash-alder swampy forest, 2 - oak-hornbeam forest, 3 - coniferous and mixed coniferous forest,
 4 - census plots, 5 - other forest habitats, mostly swampy dwarf forest.

many years of experience with local avifauna suggest that our density values for *Parus major* are also nearly correct.

In this paper the territories of bigamists (up to 40 % of *Phylloscopus sibilatrix* males in some habitats and years — WESOŁOWSKI 1980) were treated as equivalent to those of monogamists.

In order to avoid confusion, all further calculations shown in the tables do not contain corrections reducing the above mentioned inconsistencies.

While studying a plot at least ten (sometimes 12) visits were always made between 10 April and 25 June. One (sometimes two) visit was performed late in the evening for censusing dusk active birds, like *Turdus merula*, *T. philomelos*, *Erithacus rubecula*, *Scelopax rusticola* and owls. In such a case a 24–30 ha plot was censused after being divided between two observers. Plots were always censused by proceeding along marked lines, each 100 m apart, though leaving the line for careful side-penetrations when necessary, and each time starting the census from a different corner. For the purpose of high inter-plot comparability of results all plots were censused on a rotational basis uniformly by all persons conducting the field work.

Observations were recorded also from outside the plots and subsequently the proportion of a marginal territory situated within the plot was estimated judging from the number and distribution of records.

After the field work, all observations before their evaluation were assembled on species maps in the scale 1 : 1000. When elaborating the results it was taken into account that a higher number of double-registrations of the same individuals had resulted from relatively slow proceeding through the plot. While drawing the “paper territories” around the clusters of records we relied mainly on contemporary records which helped to avoid apparent tendency to some overestimation of number (TOMIAŁOJĆ 1980b). In view of this, the data for 1975 and partly 1976 have been reanalysed according to our present knowledge and to improved rules of the combined mapping technique. This explains some differences between our preliminary (TOMIAŁOJĆ *et al.* 1977) and present results. Compared with the earlier paper, the species numbers are somewhat higher because now we included also those bird territories which were found to occur only partly within the plots (marked with the sign “+”). In most cases, they constitute scarce but important elements of bird assemblages studied

Methods for results analysis

All comparisons of bird community structure between plots have been done with the application of the index of density similarity calculated according to SÖRENSEN's formula:

$$DS = \frac{2c}{a+b} \times 100,$$

where "a" denotes total bird density in sample A, "b" — total density in sample B, and "c" — density common to both samples. The last value is obtained by selecting the lower of two density values for each species (from two compared samples), and summing up.

The calculation has been based on mutually independent values (densities) instead of on relative ones (dominance = percentage), the latter often slurring over the real differences in abundance of several community components. For our further considerations similar density of a species in two habitats is more important than its similar percentage because we have found the "individualistic" community concept of WHITTAKER (1975) to be more consistent with our data than the "supraorganismal" concept of CLEMENTS (1936).

When dealing with a species diversity, the use of the species richness (S), as "the simplest and most basic measure" (WHITTAKER 1975), and the percentage of dominants (= species constituting over 5% of community) for expressing the evenness was given preference. This approach results from a serious criticism to which the popular diversity index of SHANNON-WIENER was subjected; it was repeatedly shown that it combines the species richness and evenness, though being dependent mostly on the richness (TRAMER 1969, PEET 1975, HURLBERT 1971, COUSINS 1977, JAMES and RATHBUN 1981). As we have studied rather large bird assemblages in extensive and of similar size plots (usually 100–200 pairs over 24–33 ha), the use of the rarefaction method (JAMES and RATHBUN 1981) before comparing the species numbers (richness) was not necessary. *E.g.* a tentative doubling of the plot size increased the species list only by 1–3 species.

For a more detailed analysis the bird community has been split into several ecological groups ("assemblage guilds"). The division was based on three categories of characters: 1) kind and place of food collected, 2) kind of nest-site, 3) migratory habits. Appendix 1 shows how the particular species values were attributed to some foraging, nesting or migrating categories.

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 cannot be analysed in greater detail.

Nesting-guilds. These guilds have been distinguished according to criteria of TOMIAŁOJĆ (1970) and TOMIAŁOJĆ and PROFUS (1977). They attempt to isolate 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 low 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, with the exception of WE plot in 1977.

As in the previous case, some species were partly included in more than one nesting guild. The estimation stating which part of a species population belonged to a given guild was based on our nest-card data of over 3000 nests.

The migratory habits. Here three groups have been distinguished:
 — tropical migrants = species wintering south of Sahara;
 — short-distance migrants = species wintering mainly in SW Europe and in the Mediterranean Basin;
 — residents: forest residents, species wintering outside the forest but within the same geographic and climatic region, and nomadic species.

The least precise is the distinction between some short-distance migrants and residents, as only very scarce ringing recoveries for Białowieża birds are available (DOLBIK 1975).

Year-to-year comparisons. As the basis for between-year comparisons the year 1977 has been chosen because only during this particular season all plots were censused simultaneously. The number of breeding pairs in a plot in a particular year was compared with that registered in 1977 assumed to be a 100%. Because of different numbers of plots censused each year the total number of pairs compared with 1977 was different in each pair of years compared. The results are presented in the form of indices.

MATERIAL AND RESULTS

Habitats and birds studied

Alder-swamp forest *Carici elongatae-Alnetum* — plot L. The most swampy plot (25 ha); such a plant association develops on acid organic soil inundated with stagnant water. Its subboreal variant occurring in BNP differs from the central European ones by the presence of spruces (110–130 per ha) contributing mainly to the lower canopy. The beginning of the spring growing season is the most retarded here of all BNP habitats (FALIŃSKA 1975). The elongated plot embraces the lower section of a slow-stream valley, surrounded by oak-hornbeam stands on mineral grounds. Its lowest part shows signs of an alder-swamp while the upper one gradually changes into an ash-alder association, which is reflected in the increasing amount of ash *Fraxinus excelsior* from 30 to 120 trees per ha, and the presence of *Padus avium* bushes. The upper

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

"+" - breeding, less than 0.5 territory, "-" - nonbreeding, bold type - dominants (constituting $\geq 5\%$ of community) in a particular year. In the species for which numbers range is given the values that constitute the mid-range were used for all further calculations

Species	Number of pairs		Mean density (p/10 ha)	dominance (%)
	1976	1977		
<i>Fringilla coelebs</i>	33	28	12.2	16.8
<i>Erithacus rubecula</i>	22	14	7.2	9.9
<i>Phylloscopus collybita</i>	14	13	5.4	7.4
<i>Sylvia atricapilla</i>	12-13	8.5	4.2	5.8
<i>Phylloscopus sibilatrix</i>	12	7	3.8	5.2
<i>Prunella modularis</i>	13	6	3.8	5.2
<i>Ficedula albicollis</i>	10.5	7.5	3.6	5.0
<i>Troglodytes troglodytes</i>	8	8.5	3.3	4.5
<i>Certhia familiaris</i>	8-9	7	3.1	4.3
<i>Turdus merula</i>	6	6.5	2.5	3.4
<i>Parus major</i>	7	5	2.4	3.3
<i>Regulus regulus</i>	6.5	5.5	2.4	3.3
<i>Sitta europaea</i>	6.5	5	2.3	3.2
<i>Parus caeruleus</i>	6.5	4.5	2.2	3.0
<i>Turdus philomelos</i>	6	4	2.0	2.8
<i>Ficedula hypoleuca</i>	5	3	1.6	2.2
<i>Muscicapa striata</i>	4	3	1.4	1.9
<i>Parus palustris</i>	3	4	1.4	1.9
<i>Sylvia borin</i>	3	2	1.0	1.4
<i>C. coccothraustes</i>	2	2-4	1.0	1.4
<i>Carduelis spinus</i>	2	2-3	0.9	1.2
<i>Dendrocopos medius</i>	1.5	2	0.7	1.0
<i>Dendrocopos major</i>	1	2	0.6	0.8
<i>Dendrocopos minor</i>	1	1.5	0.5	0.7
<i>Garrulus glandarius</i>	1	1.5	0.5	0.7
<i>Oriolus oriolus</i>	1	1	0.4	0.6
<i>Tringa ochropus</i>	1	1	0.4	0.6
<i>Columba palumbus</i>	1	0.5	0.3	0.4
<i>Picoides tridactylus</i>	1	0.5	0.3	0.4
<i>Cuculus canorus</i>	+	1.5	0.3	0.4
<i>Hippolais icterina</i>	1	-	0.2	0.3
<i>Anthus trivialis</i>	1	-	0.2	0.3
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	-	1	0.2	0.3
<i>Turdus iliacus</i>	-	1	0.2	0.3
<i>Dendrocopos leucotos</i>	0.5	+	0.1	0.1
<i>Aegithalos caudatus</i>	-	0.5	0.1	0.1
<i>Dryocopus martius</i>	+	+		
<i>Scolopax rusticola</i>	-	+		
Total	202	161.5	72.7	100.0

canopy is composed of alder *Alnus glutinosa*, ash and spruce (height 26–28 m, age 100–110 years, coverage 60 %). The whole-canopy layer is very open due to small and transparent crowns, a lot of dead standing stems (stumps) and many gaps where trees have fallen. The light penetrates to the ground in most places, helping the young-tree layer to develop. The young trees are, however, restricted to the drier “islands of ground” among which deep water places are interspersed. Some large bushes of *Frangula alnus*, *Salix*, *Corylus avellana* and *Padus avium* contribute to this layer. The well developed herb layer (1–1.5 m high, coverage up to 60 %), is composed of ferns *Dryopteris filix mas*, *Carex*, *Iris pseudacorus*, some *Caltha palustris*, *Phragmites communis*, *Cardamine amara*, *Filipendula ulmaria* *etc.* The number of fallen logs and uprooted trees is the highest here.

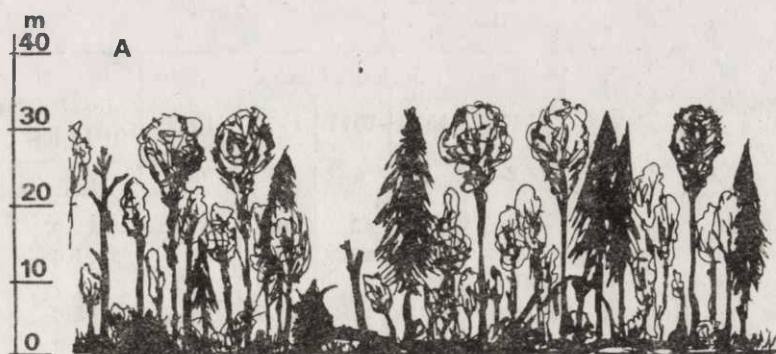
For breeding bird assemblage see Table 1.

Ash-alder riverside forest *Circaeo-Alnetum* — plots K and H. The second type of swampy forest (Fig. 2) develops on organic soils, usually only temporarily inundated, along streams with moving ground water. Most fertile of all the habitats studied, constituting c. 10 % of the Białowieża forests. An early start of the growing season is characteristic (FALIŃSKA 1975). Both plots studied suffer somewhat from a lowering of the water-level due to past channeling of the Narewka and Hwoźna rivulets adjoining the BNP area. Nowadays they seem to be somewhat less swampy than they must have been in pristine times. Both adjoin open areas: plot H has only 350 m long boundary with narrow swamp overgrown by *Phragmitetalia* and *Caricetalia* and created by beaver-damming, while plot K forms a “peninsula” of the forest penetrating the meadows of Białowieża clearing and having the edge over 1000 m long. The mean tree density (the trees of more than 13 cm in diameter) is c. 382 ex. per ha. In both plots the number of fallen trees, logs and “vykhrots” is locally very large, though, generally lower than in plot L.

Plot K (Table 2) — a mosaic-like terrain, including c. 6 ha of oak-hornbeam-covered “islands”, some with aspen *Populus tremula*, and c. 4 ha of alder-birch regeneration (50–80 years old) after past fellings. Old ash-alder stands intermixed with spruce dominate and form the upper canopy (height 23–26 m, age 120–140, sometimes 185 years, coverage 50 %) full of gaps. In the lower canopy spruces and alder dominate. Young-layer trees and tall bushes are represented by tree saplings and *Corylus avellana*, *Padus avium* and *Frangula alnus* (coverage c. 20 %). The herb layer luxuriant (up to 1.7 m high, coverage 80 %), composed of *Urtica dioica*, *Cardamine amara*, *Cirsium oleraceum*, *Cherophyllum hirsutum*, ferns, currants, sedges *etc.*

Plot H (Table 3). A rather forest-interior plot, because of the low percentage of forest-edge birds. It represents a transitional stage between ash-alder and oak-hornbeam bird assemblages, as its central part is relatively dry, with a considerable number of continental maple *Acer platanoides* and some large

ASH - ALDER F.



OAK - HORNBEAM F.



CONIFEROUS F.

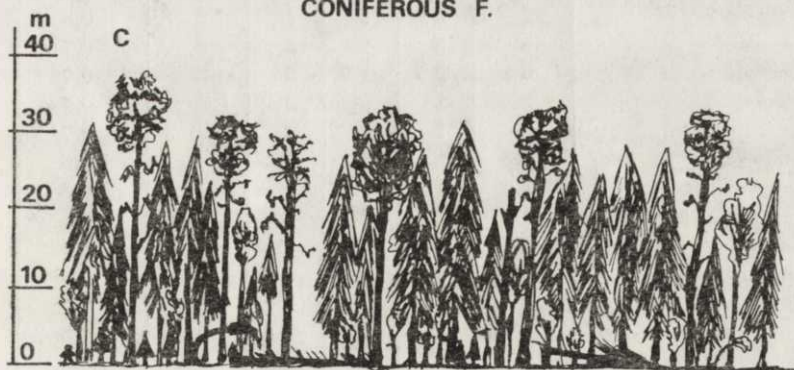


Fig. 2. The structure of BPN mature tree-stands.

A - ash-alder riverside forest, B - oak-hornbeam forest, C - coniferous forest.

Table 2. The breeding bird assemblage of the ash-alder forest (plot K, 33 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
1	2	3	4	5	6	7	8
<i>Fringilla coelebs</i>	41	38	42	40.5	52	12.9	12.9
<i>Sturnus vulgaris</i>	49	49	47	21	25	11.6	11.6
<i>Erithacus rubecula</i>	21	28	23	26.5	28	7.7	7.7
<i>Phylloscopus sibilatrix</i>	10.5	26.5	11.5	25.5	19	5.6	5.6
<i>Sylvia atricapilla</i>	18	18.5	16	13	15	4.9	4.9
<i>Phylloscopus collybita</i>	15.5	12	18.5	15	16.5	4.7	4.7
<i>Ficedula albicollis</i>	7	11	12	14.5	16	3.7	3.7
<i>Troglodytes troglodytes</i>	13.5	8.5	12	9.5	14.5	3.5	3.5
<i>Turdus philomelos</i>	11.5	8.5	9	11	14	3.3	3.3
<i>Parus major</i>	9	11	9	8	9.5	2.8	2.8
<i>Prunella modularis</i>	9.5	8.5	8	6-7	8-9	2.5	2.5
<i>Muscicapa striata</i>	5	8.5	9	10	8.5	2.5	2.5
<i>Luscinia luscinia</i>	5	7.5	12.5	6.5	8	2.4	2.4
<i>Sylvia borin</i>	9	7	7	8	7-8	2.3	2.3
<i>C. coccythraustes</i>	7	10	8.5	6	7	2.3	2.3
<i>Turdus merula</i>	6.5	6.5	6.5	10	7	2.2	2.2
<i>Certhia familiaris</i>	5.5	7	9	8	6.5-7.5	2.2	2.2
<i>Parus caeruleus</i>	10	6.5	8	5	6	2.2	2.2
<i>Regulus regulus</i>	11	8	6.5	4	4	2.0	2.0
<i>Sitta europaea</i>	5.5	6	7	6.5-7	6	1.9	1.9
<i>Anthus trivialis</i>	7	5	6	5-6	5.5	1.8	1.8
<i>Hippolais icterina</i>	4.5	4	5	8	6.5	1.7	1.7
<i>Parus palustris</i>	3.5-4.5	6	6	4.5	2.5	1.4	1.4
<i>Turdus iliacus</i>	0.5	4	4	3-4	5	1.0	1.0
<i>Carpodacus erythrinus</i>	2	3.5	3-3.5	2	6	1.0	1.0
<i>Locustella fluviatilis</i>	2	3	2	4	2	0.8	0.8
<i>Carduelis carduelis</i>	3	3	2	2	2	0.7	0.7
<i>Columba palumbus</i>	3	2.5	1.5	2	2	0.7	0.7
<i>Oriolus oriolus</i>	2	3	2	2	1.5-2	0.7	0.7
<i>Regulus ignicapillus</i>	—	1	4	3	2.5-3	0.7	0.7
<i>Carduelis chloris</i>	0.5	2	2	2	4	0.6	0.6
<i>Dendrocopos medius</i>	3.5	1.5	1.5-2	1	1.5	0.6	0.6
<i>Dendrocopos major</i>	1.5	2	2	1	2.5	0.5	0.5
<i>Streptopelia turtur</i>	1	2	0.5	1	1.5	0.4	0.4
<i>Dendrocopos minor</i>	2.5	1	1	0.5	0.5	0.3	0.3
<i>Apus apus</i>	3	—	—	1	1-2	0.3	0.3
<i>Cuculus canorus</i>	1-2	1	1	1	1	0.3	0.3
<i>Ficedula hypoleuca</i>	2	2	1	—	—	0.3	0.3
<i>Carduelis spinus</i>	—	2	2	—	1	0.3	0.3
<i>Garrulus glandarius</i>	1	1.5	1	+	1	0.3	0.3
<i>Picoides tridactylus</i>	1	1	1	+	1	0.2	0.2
<i>Dendrocopos leucotos</i>	0.5	1	1	0.5	1	0.2	0.2

1	2	3	4	5	6	7	8
<i>Ficedula parva</i>	1	—	1	1	1	0.2	0.2
<i>Columba oenas</i>	—	1	1	1	1	0.2	0.2
<i>Parus ater</i>	1	2	—	—	—	0.2	0.2
<i>Jynx torquilla</i>	—	1	—	1	1	0.2	0.2
<i>Aegithalos caudatus</i>	—	1	1	—	1	0.2	0.2
<i>Aquila pomarina</i>	1	1	0.5	+	+	0.2	0.2
<i>Acrocephalus palustris</i>	—	1	+	1	—	0.1	0.1
<i>Corvus corone</i>	—	—	1	1	—	0.1	0.1
<i>Emberiza citrinella</i>	+	1	0.5	—	—	0.1	0.1
<i>Pyrrhula pyrrhula</i>	1	+	—	—	—	0.1	0.1
<i>Parus cristatus</i>	1	—	—	—	—	0.1	0.1
<i>Dryocopus martius</i>	—	1	+	—	—	0.1	0.1
<i>Strix aluco</i>	0.5	—	—	—	0.5	0.1	0.1
<i>Anas platyrhynchos</i>	—	—	—	1	—	0.1	0.1
<i>Milvus migrans</i>	—	0.5	—	—	—		
<i>Sylvia communis</i>	0.5	—	+	+	—		
<i>Buteo buteo</i>	+	—	—	—	—		
<i>Tetrastes bonasia</i>	+	—	—	—	—		
<i>Scolopax rusticola</i>	—	—	—	+	+		
<i>Motacilla alba</i>	—	—	+	—	+		
<i>Phylloscopus trochiloides*</i>	—	—	—	+	—		
Total	322	348	337	305.7	336	99.9	100.0

* Accepted by Faunistic Commission — KF 0358.

oaks. The upper canopy (height 25–30 m, age 100 and more years, cov. 55 %) is composed of ash, alder and spruce, while the lower canopy of spruce, maple, ash and hornbeam. Young-tree and bush-layer is less developed than in plot K, with hazel and ash saplings dominant. Herb layer (cov. 30–70 %) composed of ferns, *Impatiens noli-tangere*, *Urtica dioica*, sedges, generally less luxuriant than in plot K, in some places resembles that of oak-hornbeam stands.

Oak-hornbeam forest *Tilio-Carpinetum* — plots W, WE, WI, CW, CE, MN and MS. This is the dominant (c.47 % of acreage) plant association in the Białowieża Forest. It forms here extensive and rather monotonously looking stands subdivided into drier and more wet types. These, however, do not differ in their birds. This type of habitat has the earliest start of the growing season, of all BNP stands (FALIŃSKA 1975). The oak-hornbeam, or more properly “oak-linden-hornbeam”, forest covers fertile brown mineral soils on dry land and constitutes the most important historical, former, central-European plant association, replaced by fields. Its local sub-boreal form is distinguishable by a considerable number of small-leaved lime and good admixture of spruces. Strongly diversified multi-storey, multi-species and different-aged tree-stands are very specific

Table 3. The breeding bird assemblage of the ash-alder forest (plot H, 25 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
1	2	3	4	5	6	7	8
<i>Fringilla coelebs</i>	32	38	31	34.5	47	14.6	19.3
<i>Erethacus rubecula</i>	11	21	15.5-16.5	17.5	17.5-18	6.7	8.8
<i>Phylloscopus sibilatrix</i>	6.5	18	11.5	23.5	22	6.5	8.6
<i>Troglodytes troglodytes</i>	10.5	11	11	10	11.5	4.3	5.7
<i>Sylvia atricapilla</i>	10	10	6	5	7.5-8	3.1	4.1
<i>Ficedula albicollis</i>	9	11	7	4	6.5	3.0	4.0
<i>Ficedula hypoleuca</i>	5	7-8	10	6	9	3.0	4.0
<i>Turdus merula</i>	6.5	9	5.5	6.5	5.5-6	2.7	3.5
<i>Phylloscopus collybita</i>	7	8	5.5	6-7	5.5-6	2.6	3.5
<i>Parus major</i>	7	7-8	7	6	5	2.6	3.4
<i>Certhia familiaris</i>	7	6-7	7	5-6	5-6	2.5	3.3
<i>Parus caeruleus</i>	7-8	6-7	5	5	5.5	2.4	3.1
<i>Regulus regulus</i>	7.5	9	4.5	5	3	2.3	3.1
<i>Sitta europaea</i>	5	7	6.5	6.5	4	2.3	3.1
<i>Prunella modularis</i>	4.5	6-7	4.5	4.5	5.5	2.0	2.7
<i>Muscicapa striata</i>	3	6.5	5	6	5	2.0	2.7
<i>C. coccythraustes</i>	4	4	5-6	3.5	6-7	1.9	2.5
<i>Turdus philomelos</i>	3	6	2.5	3.5-4.5	6	1.7	2.3
<i>Parus palustris</i>	3.5	5	4	4.5	2.5	1.6	2.1
<i>Sturnus vulgaris</i>	8	2	2	1	1	1.1	1.5
<i>Apus apus</i>	3-4	3	0.5	+	2-3	0.8	1.1
<i>Dendrocopos medius</i>	2.5	2	2	2	1-2	0.8	1.1
<i>Dendrocopos major</i>	1	1.5	2	2	3	0.8	1.0
<i>Columba palumbus</i>	2	2	1	2	0.5	0.6	0.8
<i>Oriolus oriolus</i>	2.5	2	0.5	1	+	0.5	0.6
<i>Carduelis spinus</i>	-	-	1.5	2-3	1	0.4	0.5
<i>Garrulus glandarius</i>	1	1	1.5	-	1	0.4	0.5
<i>Dendrocopos minor</i>	1	1	1	1	+	0.3	0.4
<i>Cuculus canorus</i>	1	1	1	0.5	-	0.3	0.4
<i>Sylvia borin</i>	-	-	1	1.5	1	0.3	0.4
<i>Aquila pomarina</i>	1	1	1	-	+	0.2	0.3
<i>Dendrocopos leucotos</i>	+	1	0.5	0.5	1	0.2	0.3
<i>Ficedula parva</i>	0.5	1	1	-	+	0.2	0.3
<i>Aegithalos caudatus</i>	+	-	1	-	1	0.2	0.2
<i>Phylloscopus trochilus</i>	-	-	1	-	1	0.2	0.2
<i>Locustella fluxiatilis</i>	1	0.5	-	-	-	0.1	0.2
<i>Anthus trivialis</i>	0.5	-	-	1	+	0.1	0.2
<i>Picoides tridactylus</i>	-	-	1	0.5	+	0.1	0.2
<i>Parus ater</i>	1	+	-	-	-	0.1	0.1
<i>Dryocopus martius</i>	-	+	1	+	-	0.1	0.1
<i>Motacilla alba</i>	-	-	1	-	-	0.1	0.1
<i>Luscinia luscinia</i>	0.5	-	-	-	-	0.1	0.1

1	2	3	4	5	6	7	8
<i>Strix aluco</i>	—	0.5	—	—	—		0.1
<i>Tringa ochropus</i>	—	0.5	—	—	+		0.1
<i>Scolopax rusticola</i>	—	0.5	—	—	—		0.1
<i>Streptopelia turtur</i>	—	—	—	0.5	—		0.1
<i>Pyrrhula pyrrhula</i>	+	+	—	—	—		
<i>Picus canus</i>	—	—	—	—	+		
Total	176.5	218.5	176.5	180	196	75.8	100.0

to it (Fig. 2). When developed under optimum conditions, it can be subdivided into 6 layers:

- 0–0.5 m — herb layer (*Aegopodium*, *Anemone*, *Stellaria holostea*, *Allium ursinum*, *Oxalis*, *Impatiens noli-tangere* etc.),
- 0.5–5 m — shrub layer (moderately developed: *Corylus avellana*, *Evonymus europaeus*, several tree saplings),
- 5–10(15) m — Young-tree layer (mainly *Tilia*, *Acer*, *Carpinus*, large *Corylus avellana*),
- 10–20(25) m — under-canopy or lower canopy, mainly of *Carpinus*, *Tilia*, *Picea*,
- 20–30 m — main canopy (old *Tilia*, *Quercus robur*, *Picea*, *Acer*),
- 30–45 m — upper canopy (as emergents: spirelike *Picea*, some *Quercus*, *Fraxinus*, *Tilia*).

The mean density of trees is the lowest of all habitats (aver. 275 ex. per ha), but their crowns are larger than in other BNP stands, though still relatively small. The total volume of the tree-crown layers is very large, while the shrub-layer rather underdeveloped. The amount of dead timber, standing or fallen, is almost twice smaller than in swampy forests, the difference being especially sharp in the case of “vykhrets”.

Plot W (Table 4). The plot has been chosen at the forest edge so as to surround a 500 m long section of the main road entering the BNP. On some summer

Table 4. The breeding bird assemblage of the oak-hornbeam forest (plot W, 25.5 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
1	2	3	4	5	6	7	8
<i>Fringilla coelebs</i>	35	40	34.5	37	37.5	14.4	19.0
<i>Phylloscopus sibilatrix</i>	15	22	14.5	20.5	18	7.1	9.3
<i>Ficedula albicollis</i>	23	13	20	13	15.5	6.6	8.7
<i>Erithacus rubecula</i>	16	19	16.5	16	13.5	6.4	8.4
<i>C. coccothraustes</i>	12	15	11	10.5	18–19	5.3	6.9
<i>Turdus philomelos</i>	11	11	10	11	8.5	4.0	5.3
<i>Sturnus vulgaris</i>	19	11	9	4	6	3.8	5.1
<i>Sylvia atricapilla</i>	11	8–9	6.5	4	5–6	2.8	3.7

1	2	3	4	5	6	7	8
<i>Parus major</i>	7-8	6	4	5.5	7.5	2.4	3.2
<i>Parus caeruleus</i>	8	5	4.5	4.5	6	2.2	2.9
<i>Turdus merula</i>	5	5	4.5	3.5	5	1.8	2.4
<i>Regulus regulus</i>	5	3.5	4	3.5-	3.5-	1.6	2.1
				4.5	4.5		
<i>Troglodytes troglodytes</i>	3.5	3	4.5	4.5	5	1.6	2.1
<i>Certhia familiaris</i>	4	4.5	3	3	3.5	1.4	1.9
<i>Sitta europaea</i>	4	3.5	4	2.5	1.5	1.2	1.6
<i>Phylloscopus collybita</i>	2	3.5	3	3.5	2	1.1	1.4
<i>Ficedula parva</i>	2	2	3.5	2.5	3-3.5	1.1	1.4
<i>Dendrocopos medius</i>	4	3.5	3	1.5	1	1.0	1.4
<i>Parus palustris</i>	2	3	2.5	4	0.5	0.9	1.2
<i>Anthus trivialis</i>	4.5	2	1	1.5	2.5	0.9	1.2
<i>Columba palumbus</i>	2	2	3	1.5	2	0.8	1.1
<i>Prunella modularis</i>	2	2.5	—	1.5	3	0.7	0.9
<i>Oriolus oriolus</i>	3	3	3	1	1	0.7	0.9
<i>Hippolais icterina</i>	1.5	4	2	—	1	0.7	0.9
<i>Muscicapa striata</i>	2.5	3	1.5	—	1	0.6	0.8
<i>Carduelis chloris</i>	1-1.5	2	0.5	1.5	1.5	0.6	0.7
<i>Emberiza citrinella</i>	1	2	1.5	1	—	0.4	0.6
<i>Jynx torquilla</i>	1	1.5	1	1	1	0.4	0.6
<i>Garrulus glandarius</i>	1	1	1	1	1	0.4	0.5
<i>Cuculus canorus</i>	1	1	1	0.5	0.5	0.3	0.4
<i>Dendrocopos major</i>	1	+	1.5	0.5	1	0.3	0.4
<i>Strix aluco</i>	1-1.5	1	1	—	+	0.3	0.4
<i>Streptopelia turtur</i>	1-2	1	—	1	+	0.3	0.4
<i>Regulus ignicapillus</i>	1.5	—	—	—	1	0.2	0.3
<i>Aegithalos caudatus</i>	—	—	1	—	1-2	0.2	0.3
<i>Ficedula hypoleuca</i>	—	1	1	—	—	0.2	0.2
<i>Carduelis carduelis</i>	—	1	—	—	1	0.2	0.2
<i>Dendrocopos minor</i>	0.5	0.5	—	0.5	0.5	0.2	0.2
<i>Parus cristatus</i>	0.5-1	+	—	1	—	0.1	0.2
<i>Parus ater</i>	1	0.5	—	—	—	0.1	0.2
<i>Dendrocopos leucotos</i>	—	0.5	—	+	0.8	0.1	0.2
<i>Turdus iliacus</i>	—	—	—	—	1	0.1	0.1
<i>Sylvia borin</i>	—	—	0.5	—	0.5	0.1	0.1
<i>Carduelis spinus</i>	—	—	1	—	—	0.1	0.1
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	—	—	—	1	—	0.1	0.1
<i>Upupa epops</i>	0.5	—	—	—	—	—	0.1
<i>Luscinia luscinia</i>	0.5	—	—	—	—	—	0.1
<i>Dryocopus martius</i>	+	0.5	—	—	—	—	0.1
<i>Buteo buteo</i>	—	0.5	+	—	—	—	0.1
<i>Phylloscopus trochilus</i>	—	—	—	0.5	—	—	0.1
<i>Corvus corax</i>	+	+	+	—	—	—	—
<i>Pyrrhula pyrrhula</i>	—	—	+	—	—	—	—
<i>Carpodacus erythrinus</i>	—	—	+	—	—	—	—
<i>Picoides tridactylus</i>	—	—	—	+	+	—	—
<i>Columba oenas</i>	—	—	—	—	+	—	—
Total	219.2	212.5	182	170	184	75.9	100.0

Sundays as many as 1000 people are led along this road back and forth, which makes some birds rather tame. The tree-stand is very old (170–250 years), tall (aver. 30–36 m) and strongly diversified. In comparison to other oak-hornbeam plots this one contains a higher than average number of spruces (30–100 per ha). The upper canopy composed of spruces, oaks and some limes (cov. 20–40%), main canopy of several tree species (cov. 40–70%) and lower canopy mainly of limes, hornbeams and spruces (cov. 30–40%). Bush-layer scarce, ground-layer of two types: higher (*Urtica*, ferns, *Impatiens noli-tangere*) in small gaps, and lower (*Aegopodium*, *Anemone*, *Stellaria holostea*, locally *Oxalis*) in the shad. A few wet places are overgrown by aspen, ash and spruce. The amount of dead timber rather considerable.

Plots WE and WI (Tables 5 and 6). For the purpose of studying a longer stretch of the forest edge the original plot W was extended in 1977 into the eastern direction and afterwards divided into a c. 200 m wide forest-edge elongated belt (WE) and 300 m wide forest-interior belt (WI). The eastern areas, additionally included, are somewhat less finely diversified horizontally than plot W, and as a rule, they contain a smaller admixture of spruce. There are no significant differences between the forest-edge and forest-interior subplots in their vegetation structure. The 1550 m long forest/field edge is artificially abrupt, with a larger amount of bushes (c. 2 ha) concentrated in front of the plot in its westernmost part only, and this was not included into our plot.

Plots CW and CE (Tables 7 and 8). In comparison with plot W these ones, adjoining each other, are more uniform in their phytosociological and structural character, with a little younger (160–170 years) and lower (30–33 m) tree stand. The upper canopy contains fewer large spruces, while main canopy and lower canopy contain more spruces (80–160 per ha) of rather a moderate size. Bush-layer still poorer, some considerable parts of the ground covered by dense and wet patches of *Allium ursinum*.

Plots MN and MS (Tables 9 and 10). Here the forest is very uniform in larger patches. It differs from other oak-hornbeam stands by the lowest admix-

Table 5. The breeding bird assemblage of the oak-hornbeam forest (plot WE, 26.1 ha)

For explanations see Table 1

Species	Number of pairs			Mean	
	1977	1978	1979	density (p/10ha)	dominance (%)
1	2	3	4	5	6
<i>Fringilla coelebs</i>	33.5	36.5	43.5	14.5	19.8
<i>Phylloscopus sibilatrix</i>	13.5	16	18.5	6.1	8.4
<i>Erithacus rubecula</i>	16.5	14	15–15.5	5.8	8.0
<i>Ficedula albicollis</i>	17	12.5	15.5	5.7	7.8

1	2	3	4	5	6
<i>C. coccothraustes</i>	11	11	19.5- -20.5	5.4	7.3
<i>Sturnus vulgaris</i>	13.5	7.5	13	4.3	5.9
<i>Turdus philomelos</i>	9.5	9	9	3.5	4.8
<i>Sylvia atricapilla</i>	7.5	5	6	2.4	3.2
<i>Parus major</i>	5	4.5-5.5	6.5	2.1	2.9
<i>Turdus merula</i>	5.5	3.5	6.5	2.0	2.7
<i>Parus caeruleus</i>	5-6	4.5	5	1.9	2.6
<i>Troglodytes troglodytes</i>	4.5	3	4.5	1.5	2.1
<i>Certhia familiaris</i>	3	4.5	3.5-4	1.4	2.0
<i>Anthus trivialis</i>	3	3	3.5	1.2	1.7
<i>Sitta europaea</i>	4.5	3	1.5	1.1	1.6
<i>Regulus regulus</i>	4-4.5	2.5-3.5	1.5	1.1	1.5
<i>Ficedula parva</i>	2.5-3	2.5	3	1.1	1.4
<i>Emberiza citrinella</i>	3	2.5	1.5	0.9	1.2
<i>Parus palustris</i>	2.5	4	0.5	0.9	1.2
<i>Carduelis chloris</i>	1.5	2	3	0.8	1.1
<i>Muscicapa striata</i>	3	-	3	0.8	1.0
<i>Hippolais icterina</i>	3	1	2	0.8	1.0
<i>Columba palumbus</i>	2	2.5	1.5	0.8	1.0
<i>Phylloscopus collybita</i>	1	3	2	0.8	1.0
<i>Jynx torquilla</i>	2	1	2	0.6	0.9
<i>Oriolus oriolus</i>	1.5	1	2-3	0.6	0.9
<i>Garrulus glandarius</i>	1	1.5	2	0.6	0.8
<i>Dendrocopos medius</i>	2.5-3	0.5-1	0.5	0.5	0.7
<i>Streptopelia turtur</i>	1	2	0.5	0.4	0.6
<i>Turdus iliacus</i>	1	-	2	0.4	0.5
<i>Aegithalos caudatus</i>	1	1	1	0.4	0.5
<i>Carduelis spinus</i>	2	-	0.5	0.3	0.4
<i>Dendrocopos major</i>	1.5	0.5	0.5	0.3	0.4
<i>Sylvia borin</i>	1	-	1.5	0.3	0.4
<i>Carduelis carduelis</i>	1	-	1	0.3	0.3
<i>Buteo buteo</i>	0.5	1	+	0.2	0.3
<i>Regulus ignicapillus</i>	-	-	1.5	0.2	0.3
<i>Strix aluco</i>	1	+	+	0.1	0.2
<i>Dendrocopos minor</i>	0.5	0.5	-	0.1	0.2
<i>Dendrocopos leucotos</i>	+	-	1	0.1	0.2
<i>Cuculus canorus</i>	-	0.5	0.5	0.1	0.2
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	-	1	-	0.1	0.2
<i>Prunella modularis</i>	-	-	1	0.1	0.2
<i>Parus cristatus</i>	-	-	1	0.1	0.2
<i>Ficedula hypoleuca</i>	0.5	+	+	0.1	0.1
<i>Corvus corax</i>	0.5	-	-	0.1	0.1
<i>Phylloscopus trochilus</i>	-	0.5	-	0.1	0.1
<i>Picoides tridactylus</i>	-	-	0.5	0.1	0.1
<i>Carpodacus erythrinus</i>	+	-	-	-	-
<i>Columba oenas</i>	-	-	+	-	-
Total	194.7	169.7	209.5	73.4	100.0

Table 6. The breeding bird assemblage of the oak-hornbeam forest (plot WI, 24 ha)

For explanations see Table 1

Species	Number of pairs			Mean	
	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	30.5	34.5	36.5	14.1	22.3
<i>Ficedula albicollis</i>	20	14.5	15	6.9	10.9
<i>Phylloscopus sibilatrix</i>	12.5	18.5	16.5	6.6	10.4
<i>Erithacus rubecula</i>	13.5	16	15	6.2	9.8
<i>C. coccothraustes</i>	12	7	12	4.3	6.8
<i>Turdus philomelos</i>	8	9	8	3.5	5.5
<i>Parus major</i>	5.5	4.5	6.5	2.3	3.6
<i>Troglodytes troglodytes</i>	6	5	4	2.1	3.3
<i>Turdus merula</i>	3.5-4	3	5	1.6	2.6
<i>Sylvia atricapilla</i>	3.5	2.5	5.5	1.6	2.5
<i>Regulus regulus</i>	3	3.5	3.5-4.5	1.5	2.3
<i>Certhia familiaris</i>	4.5	2.5	3	1.4	2.2
<i>Parus caeruleus</i>	4	3	3	1.4	2.2
<i>Ficedula parva</i>	2.5-3	2.5	4	1.3	2.0
<i>Phylloscopus collybita</i>	3	3	2.5	1.2	1.9
<i>Sitta europaea</i>	3	2.5	1	0.9	1.4
<i>Parus palustris</i>	2.5	3	0.5-1	0.9	1.4
<i>Columba palumbus</i>	2.5	2	1.5	0.8	1.3
<i>Prunella modularis</i>	0.5	2.5	3	0.8	1.3
<i>Dendrocopos medius</i>	2	1.5	2	0.8	1.2
<i>Sturnus vulgaris</i>	3.5	1.5	—	0.7	1.1
<i>Dendrocopos major</i>	1.5	—	1.5-2	0.5	0.7
<i>Ficedula hypoleuca</i>	1.5-2.5	+	—	0.3	0.5
<i>Cuculus canorus</i>	1	0.5	0.5	0.3	0.4
<i>Garrulus glandarius</i>	1	0.5	+	0.2	0.3
<i>Dendrocopos minor</i>	0.5	—	1	0.2	0.3
<i>Loxia curvirostra</i>	1	—	—	0.1	0.2
<i>Parus cristatus</i>	—	1	—	0.1	0.2
<i>Muscicapa striata</i>	—	—	1	0.1	0.2
<i>Buteo buteo</i>	0.5	—	+	0.1	0.2
<i>Oriolus oriolus</i>	0.5	—	—	0.1	0.1
<i>Picoides tridactylus</i>	—	+	0.5	0.1	0.1
<i>Regulus ignicapillus</i>	—	—	0.5	0.1	0.1
<i>Anthus trivialis</i>	—	—	0.5	0.1	0.1
<i>Streptopelia turtur</i>	—	—	0.5	0.1	0.1
<i>Carduelis spinus</i>	—	—	0.5	0.1	0.1
<i>Corvus corax</i>	0.5	+	—	0.1	0.1
<i>Pyrrhula pyrrhula</i>	+	—	—	—	—
<i>Dendrocopos leucotos</i>	—	+	—	—	—
<i>Carduelis chloris</i>	—	—	+	—	—
Total	155	144	155.5	63.2	100.0

Table 7. The breeding bird assemblage of the oak-hornbeam forest (plot CW, 24 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10ha)	dominance (%)
<i>Fringilla coelebs</i>	34	37	38.5	35.5	43	15.7	25.2
<i>Phylloscopus sibilatrix</i>	16	21	12.5	21	13	7.0	11.2
<i>Erithacus rubecula</i>	12-13	20	15.5	14.5	13	6.3	10.1
<i>Ficedula albicollis</i>	12	13.5	16.5	6.5	7	4.6	7.4
<i>Turdus philomelos</i>	14	13-14	5.5	8.5	8	4.1	6.6
<i>C. coccothraustes</i>	10	8	7.5	6	9	3.4	5.4
<i>Parus major</i>	5	4	6	3.5-4.5	3.5	1.9	3.0
<i>Regulus regulus</i>	6.5	4.5-5.5	5.5	2	1.5	1.7	2.7
<i>Turdus merula</i>	5	5	2	4	4.5	1.7	2.7
<i>Sylvia atricapilla</i>	4	4	3.5	3.5-4.5	4.5	1.7	2.7
<i>Troglodytes troglodytes</i>	4.5	4	3.5	3.5	3	1.5	2.5
<i>Sitta europaea</i>	3.5	5	3.5	4	2.5	1.5	2.5
<i>Certhia familiaris</i>	3	3.5	3	5	2.5	1.4	2.3
<i>Parus caeruleus</i>	6	3	2.5	3	2	1.4	2.2
<i>Phylloscopus collybita</i>	2	3	2.5	2	3.5	1.1	1.7
<i>Prunella modularis</i>	2	3	1.5	3	2.5	1.0	1.6
<i>Dendrocopos medius</i>	2.5	2-3	2	2	1.5	0.9	1.4
<i>Parus palustris</i>	1	3	3	1.5	0.5	0.8	1.2
<i>Ficedula parva</i>	1	1.5	2	1	1.5	0.6	0.9
<i>Ficedula hypoleuca</i>	1	4	—	2	—	0.6	0.9
<i>Cuculus canorus</i>	1	1	2	1.5	1	0.5	0.9
<i>Dendrocopos major</i>	1.5	0.5	1-1.5	1	2	0.5	0.8
<i>Garrulus glandarius</i>	1	1	1-1.5	—	1.5	0.4	0.6
<i>Columba palumbus</i>	1	1	1.5	1	+	0.4	0.6
<i>Parus ater</i>	2	1.5	—	0.5	—	0.3	0.5
<i>Oriolus oriolus</i>	1	1	—	1.5	—	0.3	0.5
<i>Dendrocopos minor</i>	0.5	1	—	1	—	0.2	0.3
<i>Parus cristatus</i>	1.5	—	—	—	0.5	0.2	0.3
<i>Anthus trivialis</i>	0.5	1	—	—	—	0.1	0.2
<i>Apus apus</i>	1	—	—	—	—	0.1	0.1
<i>Muscicapa striata</i>	—	+	—	1	—	0.1	0.1
<i>Strix aluco</i>	—	0.5	0.5	—	—	0.1	0.1
<i>Loxia curvirostra</i>	—	—	1	—	—	0.1	0.1
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	—	—	—	—	1	0.1	0.1
<i>Dendrocopos leucotos</i>	0.2	0.2	+	+	—	—	0.1
<i>Tetrastes bonasia</i>	0.5	+	—	—	—	—	0.1
<i>Aegithalos caudatus</i>	—	—	+	0.5	+	—	0.1
<i>Pyrrhula pyrrhula</i>	+	—	—	—	—	—	—
<i>Picoides tridactylus</i>	+	+	—	—	—	—	—
<i>Dryocopus martius</i>	—	+	—	—	—	—	—
<i>Corvus corax</i>	+	—	—	—	—	—	—
<i>Regulus ignicapillus</i>	—	—	—	+	+	—	—
<i>Carduelis spinus</i>	—	—	+	—	—	—	—
Total	157.2	172.2	144	141	132.5	62.2	100.0

Table 8. The breeding bird assemblage of the oak-hornbeam forest (plot CE, 24 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	31.5	34	38.5	30.5	50	15.4	24.0
<i>Phylloscopus sibilatrix</i>	11.5	24	13	21	16.5	7.2	11.2
<i>Erethacus rubecula</i>	15	20	15.5	14	16	6.7	10.5
<i>Ficedula albicollis</i>	12	16.5	17.5	7	13	5.5	8.6
<i>Turdus philomelos</i>	13.5	9	5	8	8.5	3.7	5.7
<i>C. coccothraustes</i>	10	9	5	9	9.5	3.5	5.5
<i>Parus major</i>	5	7	5.5	2	4-5	2.0	3.1
<i>Turdus merula</i>	4.5	6	4	4	3.5	1.8	2.9
<i>Troglodytes troglodytes</i>	4.5	3.5	5	4.5	4	1.8	2.8
<i>Regulus regulus</i>	4	6	4.5	3-4	3	1.7	2.7
<i>Certhia familiaris</i>	3.5-4.5	4.5	5	4	3.5	1.7	2.7
<i>Sylvia atricapilla</i>	4-5	3.5	3	3-4	5	1.6	2.5
<i>Parus caeruleus</i>	4	2	4	4	4	1.5	2.3
<i>Sitta europaea</i>	3	5	4	4.5	1.5	1.5	2.3
<i>Parus palustris</i>	1	4	2	3.5	0.5	0.9	1.4
<i>Phylloscopus collybita</i>	2	2.5	2	2	2.5	0.9	1.4
<i>Dendrocopos medius</i>	2	2	3	2	1.5	0.9	1.4
<i>Ficedula parva</i>	1.5	1	2	1	2	0.6	1.0
<i>Columba palumbus</i>	1.5	1.5	2-3	1	1	0.6	1.0
<i>Prunella modularis</i>	—	2.5	1	2	1	0.5	0.8
<i>Apus apus</i>	1	2	1	1	1	0.5	0.8
<i>Dendrocopos major</i>	1.5	0.5	1	+	1.5	0.4	0.6
<i>Cuculus canorus</i>	1	1	1	1	0.5	0.4	0.6
<i>Ficedula hypoleuca</i>	1	1-2	1	1	—	0.4	0.6
<i>Parus cristatus</i>	2	—	1	—	1	0.3	0.5
<i>Garrulus glandarius</i>	1	1	1	—	0.5	0.3	0.5
<i>Parus ater</i>	1-2	1	—	0.5	—	0.3	0.4
<i>Dendrocopos minor</i>	0.5	—	1	1-2	—	0.3	0.4
<i>Oriolus oriolus</i>	1	0.5	0.5	—	—	0.2	0.3
<i>Carduelis chloris</i>	—	0.5	1	—	—	0.1	0.2
<i>Sturnus vulgaris</i>	1	—	—	—	—	0.1	0.1
<i>Dendrocopos leucotos</i>	0.2	0.2	0.5	—	+	0.1	0.1
<i>Phylloscopus trochilus</i>	1	—	—	—	—	0.1	0.1
<i>Aegithalos caudatus</i>	—	1	+	+	+	0.1	0.1
<i>Regulus ignicapillus</i>	—	+	—	—	1	0.1	0.1
<i>Strix aluco</i>	0.5	0.5	+	—	+	0.1	0.1
<i>Muscicapa striata</i>	—	—	+	1	+	0.1	0.1
<i>Carduelis spinus</i>	—	—	1	—	—	0.1	0.1
<i>Anthus trivialis</i>	0.5	—	—	—	—	—	0.1
<i>Dryocopus martius</i>	—	0.5	—	—	—	—	0.1
<i>Corvus corax</i>	+	—	—	—	—	—	—
<i>Sylvia borin</i>	—	—	+	—	—	—	—
<i>Streptopelia turtur</i>	—	—	+	—	—	—	—
Total	148.7	173.7	152	137	156.5	64.0	100.0

Table 9. The breeding bird assemblage of the oak-hornbeam forest (plot MN, 24 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	30	33	23	31	45	13.5	21.9
<i>Phylloscopus sibilatrix</i>	8.5	21	15	20.5	20	7.1	11.5
<i>Erithacus rubecula</i>	13-14	17	11	13	22	6.4	10.4
<i>Ficedula albicollis</i>	10.5	14	12	7	10	4.5	7.2
<i>C. coccothraustes</i>	8	10	10	9	7-8	3.7	6.0
<i>Parus major</i>	7	5-6	8	4.5	3.5	2.4	3.9
<i>Turdus merula</i>	7.5	5.5	4	4.5	6	2.3	3.7
<i>Turdus philomelos</i>	5-6	5-6	5-6	4	6	2.2	3.6
<i>Parus caeruleus</i>	7	4	5	5	5-5.5	2.2	3.6
<i>Sylvia atricapilla</i>	5	5	4	5	4.5	2.0	3.2
<i>Certhia familiaris</i>	3.5	5-6	5.5	3.5	3.5	1.8	2.9
<i>Troglodytes troglodytes</i>	4.5	4.5	3.5	4	4	1.7	2.8
<i>Sitta europaea</i>	3	4	5	3	2	1.4	2.3
<i>Phylloscopus collybita</i>	3	3	4	2	2	1.2	1.9
<i>Dendrocopos medius</i>	2.5	2.5	3.5-4	2	2.5	1.1	1.8
<i>Regulus regulus</i>	4	3.5	3	1	1	1.0	1.7
<i>Parus palustris</i>	2.5	4-5	1.5	3	0.5	1.0	1.6
<i>Dendrocopos major</i>	1.5	2	2.5	1.5	2.5	0.8	1.4
<i>Columba palumbus</i>	1	2.5	2	3	1	0.8	1.3
<i>Anthus trivialis</i>	4	1.5	1	—	1.5-2	0.7	1.1
<i>Ficedula hypoleuca</i>	1	2	2	2.5	0.5	0.7	1.1
<i>Ficedula parva</i>	1.5	1	2	1.5	2	0.7	1.1
<i>Garrulus glandarius</i>	1.5	1	1.5	+	1	0.4	0.7
<i>Muscicapa striata</i>	—	2.5	1	1	—	0.4	0.6
<i>Prunella modularis</i>	+	2	—	1-2	1	0.4	0.6
<i>Cuculus canorus</i>	1	1	1.5	+	0.5	0.3	0.5
<i>Oriolus oriolus</i>	1.5	1	+	+	0.5	0.3	0.4
<i>Strix aluco</i>	1	0.5	1	+	—	0.2	0.3
<i>Dendrocopos minor</i>	0.5	1	1	—	—	0.2	0.3
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	—	—	1	—	0.5	0.1	0.2
<i>Sturnus vulgaris</i>	1	—	—	—	—	0.1	0.1
<i>Aegithalos caudatus</i>	—	—	—	1	—	0.1	0.1
<i>Dryocopus martius</i>	—	0.5	+	—	—	—	0.1
<i>Phoenicurus phoenicurus</i>	0.5	—	—	—	—	—	0.1
<i>Corvus corax</i>	0.5	—	—	—	—	—	0.1
<i>Tetrastes bonasia</i>	+	—	—	—	—	—	—
<i>Dendrocopos leucotos</i>	—	—	+	+	—	—	—
<i>Parus ater</i>	+	+	—	—	—	—	—
<i>Regulus ignicapillus</i>	—	+	—	—	—	—	—
Total	142	166.5	140.2	134	156.5	61.6	100.0

Table 10. The breeding bird assemblage of the oak-hornbeam forest (plot MS, 30 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	40	47	32	37	49	13.7	22.3
<i>Phylloscopus sibilatrix</i>	19	26.5	22	28	22	7.8	12.8
<i>Erithacus rubecula</i>	21	20	22.5	22	18.5	6.9	11.3
<i>Ficedula albicollis</i>	15-16	20	20	16.5	16	5.9	9.6
<i>C. coccythraustes</i>	10	10	15	9	11	3.7	6.0
<i>Turdus philomelos</i>	9-10	9.5	6	4.5	6	2.4	3.9
<i>Parus caeruleus</i>	8.5- -9.5	4.5	7	6	5.5	2.1	3.5
<i>Parus major</i>	9	7.5	5-6	5	4.5	2.1	3.4
<i>Turdus merula</i>	6-7	8	6	4	4-4.5	1.9	3.1
<i>Certhia familiaris</i>	5	6	5.5	4	3.5	1.6	2.6
<i>Troglodytes troglodytes</i>	4	3.5	4.5	4.5	4.5	1.4	2.3
<i>Sitta europaea</i>	4.5	4	4.5	4	3.5	1.4	2.2
<i>Sylvia atricapilla</i>	4	6	2.5	4	3.5	1.3	2.2
<i>Parus palustris</i>	4	4	3.5	5	1.5	1.2	2.0
<i>Anthus trivialis</i>	4	4	3.5	1	3-4	1.1	1.7
<i>Ficedula hypoleuca</i>	4	4	3	1.5	1.5	0.9	1.5
<i>Dendrocopos medius</i>	3-4	2.5	3	2-3	2	0.9	1.5
<i>Regulus regulus</i>	4.5	1.5	3	2	2	0.9	1.4
<i>Ficedula parva</i>	3	2	3	2.5	2	0.8	1.4
<i>Columba palumbus</i>	1	2.5	2.5	2	-	0.5	0.9
<i>Dendrocopos major</i>	1.5	0.5	2.5	1	1	0.4	0.7
<i>Oriolus oriolus</i>	-	2.5	1-1.5	1	1	0.4	0.6
<i>Garrulus glandarius</i>	1	2	1-1.5	-	1	0.4	0.6
<i>Phylloscopus collybita</i>	1	1	1.5	-	-	0.2	0.4
<i>Buteo buteo</i>	1	1	-	-	1	0.2	0.3
<i>Dendrocopos leucotos</i>	0.5	1	0.5	+	1	0.2	0.3
<i>Muscicapa striata</i>	-	+	-	1	2	0.2	0.3
<i>Cuculus canorus</i>	1	0.5	1-1.5	+	-	0.2	0.3
<i>Sturnus vulgaris</i>	1	1	-	-	-	0.1	0.2
<i>Carduelis spinus</i>	-	-	1	-	-	0.1	0.1
<i>Prunella modularis</i>	-	1	-	-	-	0.1	0.1
<i>Aegithalos caudatus</i>	-	-	-	-	1	0.1	0.1
<i>Strix aluco</i>	-	+	0.5	-	-	-	0.1
<i>Dryocopus martius</i>	-	+	0.5	-	-	-	0.1
<i>Sylvia borin</i>	-	-	0.5	-	-	-	0.1
<i>Ficedula albicollis</i> × <i>F. hypoleuca</i>	-	-	-	-	0.5	-	0.1
<i>Accipiter nisus</i>	-	-	+	-	-	-	-
<i>Tetrastes bonasia</i>	+	-	-	-	-	-	-
<i>Dendrocopos minor</i>	-	-	+	+	-	-	-
<i>Corvus corax</i>	+	-	-	-	-	-	-
<i>Picoides tridactylus</i>	-	-	+	-	-	-	-
Total	188	203.5	185.2	168	172.7	61.2	100.0

ture of spruces (10–20 per ha), many of them being small-sized, as well as by rather a considerable amount of *Acer platanoides* trees. The scarcity of bush-layer presumably results from strong grazing pressure of *Cervus elaphus* and wild boars; the stand is somewhat “park-like” being only normally (densely) afforested. The upper canopy (30–33 m high, 160–230 years old, coverage 30%) of oaks, spruces and maples, younger layers dominated by hornbeam and lime. Plot MN has little higher diversity of tree-stand, with higher amount of hornbeam and spruce, more younger trees, and more fallen logs. It adjoins an extensive wind-broken forest area primarily overgrown by oak-pine-spruce forest, but now dominated by c. 20-year old lime stands.

Mixed coniferous-deciduous forest *Pino-Quercetum* — plot GB (Table 11). This is a meso-eutrophic plant community intermediate between the oak-hornbeam and the true coniferes dominated stands; it constitutes 20–25% of the Białowieża forests. Its canopy is composed of two layers: the upper of spruce and pine with an admixture of birch, oak and aspen (29–30 m, 120–130 years, coverage 60–80%) and the lower — spruce, oak, and birch (coverage 20–40%). Young-tree layer composed of hornbeam, spruce and larger hazel bushes. Bush-layer absent or very scarce (spruce). Poor herb-layer (*Oxalis acetosella*, *Vaccinium myrtillus*), more luxuriant in small openings (*Calamagrostis arundinacea*, *Pteridium aquilinum*), having 50–60% of coverage. The mean density of trees very high (aver. 480 per ha). The amount of dead timber (mainly broken stumps or logs) moderate, while “vykhrots” very few.

Pine-bilberry coniferous forest *Peucedano-Pinetum* — plots NW and NE (Tables 12 and 13). This association (8–12% of the Białowieża forests, Fig. 2) develops in upper parts of sandy elevations and trophically represents one of the poorest habitats in BNP. Trees are of moderate size here but they grow very densely (aver. 560 per ha). The main canopy formed of pines and birches (26–30 m, 110–180 years, coverage 40–70%), while the lower one of spruces with few pines, birches and oaks. Young-tree layer (hornbeam, spruce, lime) covers only c. 20% of the area. Bush-layer poorly developed (5–10%), mainly in gaps. Herb-layer composed of low vegetation (mosses, *Oxalis*, scattered *Vaccinium myrtillus*) covering c. 40%. In plot NW spruce dominates numerically over pine (*Vaccinio myrtilli-Piceetum*), while in adjoining NE plot the percentage of pines is much higher (*Vaccinio myrtilli-Pinetum*), though in recent decades diminishing due to their dying out. Plot NE contains more marginal intrusions (c. 5 ha) of the *Pino-Quercetum* stands, *i.e.* those which dominate in the surroundings of these plots. The amount of fallen and standing dead timber higher than in previous habitat, though consisting mainly of dry pines avoided by most hole-nesters. See also the description of these plots by PIOTROWSKA and WOŁK (1983).

Table 11. The breeding bird assemblage of the mixed coniferous-deciduous forest (plot GB, 32 ha)

For explanations see Table 1

Species	Number of pairs			Mean	
	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	32	24.5	29.5	9.0	26.1
<i>Phylloscopus sibilatrix</i>	18.5	21	19	6.1	17.8
<i>Erithacus rubecula</i>	17	14.5	14.5	4.8	14.0
<i>Regulus regulus</i>	8	5-6	5.5	2.0	5.8
<i>Turdus philomelos</i>	3.5	4.5	7	1.6	4.6
<i>Certhia familiaris</i>	4.5	4	4-4.5	1.3	3.9
<i>Parus cristatus</i>	4	4	4.5	1.3	3.8
<i>Troglodytes troglodytes</i>	2.5	2.5	3.5	0.9	2.6
<i>Parus ater</i>	3	4	1	0.8	2.4
<i>Phylloscopus collybita</i>	2.5	1.5	3.5	0.8	2.3
<i>Carduelis spinus</i>	3	3-3.5	1	0.8	2.2
<i>Ficedula hypoleuca</i>	3.5	1	2	0.7	2.0
<i>Columba palumbus</i>	3.5	1.5	1	0.6	1.8
<i>Turdus merula</i>	2	1.5	2	0.6	1.7
<i>Oriolus oriolus</i>	1	2	1	0.4	1.2
<i>Sylvia atricapilla</i>	1.5	—	1	0.3	0.8
<i>Ficedula parva</i>	0.5	1.5	0.5	0.3	0.8
<i>Garrulus glandarius</i>	1	1.5	+	0.3	0.8
<i>Parus caeruleus</i>	1.5	0.5	—	0.2	0.6
<i>Dendrocopos major</i>	+	0.5	1.5	0.2	0.6
<i>C. coccothraustes</i>	—	1	1	0.2	0.6
<i>Pyrrhula pyrrhula</i>	—	—	2	0.2	0.6
<i>Anthus trivialis</i>	1	1	+	0.2	0.6
<i>Ficedula albicollis</i>	1	—	0.5	0.2	0.5
<i>Phylloscopus trochilus</i>	1	—	—	0.1	0.3
<i>Loxia curvirostra</i>	1	—	—	0.1	0.3
<i>Tetrastes bonasia</i>	+	—	1	0.1	0.3
<i>Parus major</i>	+	1	—	0.1	0.3
<i>Cuculus canorus</i>	—	1	+	0.1	0.3
<i>Columba oenas</i>	—	1	+	0.1	0.3
<i>Muscicapa striata</i>	—	—	1	0.1	0.3
<i>Prunella modularis</i>	—	0.5	+	0.1	0.2
<i>Buteo buteo</i>	—	+	—		
<i>Scelopax rusticola</i>	—	+	—		
<i>Picoides tridactylus</i>	—	+	—		
<i>Dryocopus martius</i>	—	+	—		
<i>Parus palustris</i>	+	—	—		
<i>Sitta europaea</i>	+	—	—		
Total	117	104.7	107.7	34.3	100.0

Table 12. The breeding bird assemblage of the pine-bilberry coniferous forest (plot NW, 25 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coelebs</i>	27	27.5	19	23.5	22.5	9.6	27.7
<i>Phylloscopus sibilatrix</i>	11.5	16	8.5	12.5	11.5	4.8	13.9
<i>Erithacus rubecula</i>	8.5	14	12	10	15	4.8	13.8
<i>Regulus regulus</i>	8	9	4.5	5	4	2.4	7.1
<i>Turdus philomelos</i>	5	4.5	6.5	4.5	6	2.1	6.1
<i>Parus ater</i>	6.5	6.5	2.5	3	2	1.6	4.7
<i>Certhia familiaris</i>	4	4.5	2.5	3	4	1.5	4.4
<i>Parus cristatus</i>	3	3	1.5	4	2.5-3.5	1.2	3.4
<i>Phylloscopus collybita</i>	1.5	2	2	2	3.5	0.9	2.5
<i>Oriolus oriolus</i>	+	2	2	2.5	2	0.7	2.0
<i>Prunella modularis</i>	1.5	1	1	1	4	0.7	2.0
<i>Turdus merula</i>	2	2.5	1	1	1	0.6	1.7
<i>Ficedula parva</i>	-	2	-	1.5	2	0.4	1.3
<i>Carduelis spinus</i>	1	-	1	2-3	1	0.4	1.3
<i>Troglodytes troglodytes</i>	1	1	0.5	1	1.5	0.4	1.2
<i>Columba palumbus</i>	1	2	0.5	1	0.5	0.4	1.2
<i>Sylvia atricapilla</i>	1	1	-	-	1.5	0.3	0.8
<i>Garrulus glandarius</i>	0.5	1.5	0.5	1	+	0.3	0.8
<i>Anthus trivialis</i>	1	1	0.5	-	0.5	0.2	0.7
<i>Parus major</i>	1	-	0.5	1	-	0.2	0.6
<i>Dendrocopos major</i>	0.5	+	0.5	0.5	1	0.2	0.6
<i>Cuculus canorus</i>	-	1	1	0.5	+	0.2	0.6
<i>Pyrrhula pyrrhula</i>	-	1	-	-	1	0.2	0.5
<i>C. coccothraustes</i>	1	-	+	1	+	0.2	0.5
<i>Columba oenas</i>	-	0.5	-	1	+	0.1	0.3
<i>Ficedula hypoleuca</i>	1	-	-	-	-	0.1	0.2
<i>Parus palustris</i>	-	1	-	-	-	0.1	0.2
<i>Phylloscopus trochilus</i>	-	-	0.5	-	0.5	0.1	0.2
<i>Accipiter nisus</i>	0.5	-	-	-	-		0.1
<i>Sitta europaea</i>	-	+	-	-	-		
<i>Muscicapa striata</i>	-	-	-	-	+		
<i>Dryocopus martius</i>	-	-	+	-	-		
<i>Tetrastes bonasia</i>	-	-	+	-	-		
<i>Picoides tridactylus</i>	-	+	-	-	-		
<i>Nucifraga caryocatactes</i>	-	-	+	-	-		
Total	88	104.5	68.5	83	88	34.6	100.0

Table 13. The breeding bird assemblage of the pine-bilberry coniferous forest (plot NE, 25 ha)

For explanations see Table 1

Species	Number of pairs					Mean	
	1975	1976	1977	1978	1979	density (p/10 ha)	dominance (%)
<i>Fringilla coclebs</i>	23	30.5	27	21.5	23.5	10.0	26.2
<i>Phylloscopus sibilatrix</i>	10	24	11	18.5	12.5	6.1	15.9
<i>Erethacus rubecula</i>	12	12-13	13.5	17.5	12.5	5.4	14.2
<i>Regulus regulus</i>	9	8	3.5	4	3	2.2	5.7
<i>Turdus philomelos</i>	4	5	5	4.5	3.5-4.5	1.8	4.7
<i>Parus ater</i>	5	3.5	3.5	4	2	1.4	3.8
<i>Certhia familiaris</i>	3	3.5-4.5	3	4	4	1.4	3.8
<i>Parus cristatus</i>	3	4	3	4	2.5-3	1.3	3.5
<i>Phylloscopus collybita</i>	2.5	3.5	2	1	3.5	1.0	2.6
<i>Turdus merula</i>	2	2.5	1.5	2	1.5-2	0.8	2.0
<i>Oriolus oriolus</i>	2	2	2	1.5	1.5	0.7	1.9
<i>Prunella modularis</i>	0.5	3	2	—	3	0.7	1.8
<i>Ficedula parva</i>	—	2	—	2.5	3	0.6	1.6
<i>Carduelis spinus</i>	—	3	3	1	+	0.6	1.5
<i>Pyrrhula pyrrhula</i>	1	1	+	—	2.5-3	0.4	1.0
<i>Columba palumbus</i>	—	1.5	1	1.5	0.5	0.4	0.9
<i>Ficedula hypoleuca</i>	2	1	1	—	—	0.3	0.8
<i>Anthus trivialis</i>	1	1	1	1	—	0.3	0.8
<i>Parus montanus</i>	1	2	1	—	—	0.3	0.8
<i>Garrulus glandarius</i>	0.5	1	1	1	—	0.3	0.7
<i>Dendrocopos major</i>	0.5	+	1	—	2	0.3	0.7
<i>Cuculus canorus</i>	1	1	+	0.5	1	0.3	0.7
<i>Columba oenas</i>	1	2	—	—	0.5	0.3	0.7
<i>Tetrastes bonasia</i>	+	1	1	1	—	0.2	0.6
<i>Sylvia atricapilla</i>	—	+	—	0.5	1.5	0.2	0.4
<i>C. coccothraustes</i>	1	—	—	+	1	0.2	0.4
<i>Troglodytes troglodytes</i>	—	—	0.5	—	1	0.2	0.3
<i>Accipiter nisus</i>	0.5	1	—	—	—	0.1	0.3
<i>Sitta europaea</i>	—	1	+	—	—	0.1	0.2
<i>Parus major</i>	—	1	—	—	—	0.1	0.2
<i>Muscicapa striata</i>	—	1	—	—	—	0.1	0.2
<i>Dryocopus martius</i>	1	+	+	—	+	0.1	0.2
<i>Parus caeruleus</i>	1	—	+	—	—	0.1	0.2
<i>Loxia curvirostra</i>	—	—	1	—	—	0.1	0.2
<i>Phoenicurus phoenicurus</i>	1	—	—	—	—	0.1	0.2
<i>Strix aluco</i>	—	0.5	—	—	—	—	0.1
<i>Scolopax rusticola</i>	—	—	—	+	—	—	—
<i>Picoides tridactylus</i>	—	—	—	—	+	—	—
Total	88.5	123.5	88.5	91.5	87.2	38.3	100.0

RESULTS

Structure of bird community. The structure of a breeding bird assemblage from a particular plot when compared on a year-to-year basis showed high, usually exceeding 80%, similarity in bird density composition (DS). Only exceptionally were the year-to-year fluctuations in structure more pronounced, *e.g.* in plot NW between 1976 and 1977 similarity of densities was only 74%. Therefore, we assume that when DS between two samples is 80% or more they represent essentially the same bird community.

A comparison of bird samples from different BNP plots shows that between-plot similarities are very high (Table 14). Even if we take the case of the lowest value (DS = 45.7%) the inconsistency between two plots GB and K appears to have resulted mainly from their different overall densities. Almost 90% of birds from the poorer plot (GB) were identical with birds breeding in the rich plot (K), though they constituted only 30% of total bird density in the latter one. Thus, the coniferous forest bird assemblage from BNP is nothing else than the impoverished mixed-deciduous bird community plus a few additional features (some new scarce species, higher densities of coniferous specialists).

The bird assemblage from our coniferous stands appeared to be the most distinct one (Fig. 3). However, in spite of clear phytosociological differences between plot GB and other coniferous stands (see description of habitats), they all harbour identical bird community.

Oak-hornbeam stands constitute another compact group of bird habitats,

Table 14. Density similarities (DS) of bird assemblages from different forest types

The DS's have been calculated for multiyear averages. Forest type: 1 - ash-alder; 2 - alder; 3 - oak-hornbeam
4 - mixed coniferous-deciduous; 5 - pine-bilberry coniferous

K	1		2		3					4		5		Forest type Plot
	H	L	W	WE	WI	CW	CE	MN	MS	GB	NW	NE		
X	75.3	76.1	72.5	71.1	66.2	65.9	66.6	68.2	65.2	45.7	46.6	49.5	K	
	X	83.4	75.8	72.8	76.1	78.0	78.7	80.6	77.7	55.9	51.4	58.4	H	
		X	65.5	66.3	69.9	71.5	71.0	75.5	71.2	58.5	57.0	54.4	L	
			X	92.3	88.6	85.3	86.1	86.1	84.2	55.5	54.7	58.1	W	
				X	84.6	80.7	82.2	82.1	81.1	55.7	54.3	56.6	WE	
					X	89.9	91.5	88.6	87.6	61.5	60.7	63.4	WI	
						X	94.9	90.1	87.4	62.9	62.6	65.9	CW	
							X	90.0	89.6	62.7	61.5	63.9	CE	
								X	92.3	62.6	60.5	63.5	MN	
									X	61.4	58.7	60.9	MS	
										X	89.4	93.4	GB	
											X	91.4	NW	
												X	NE	

their within-group DS values exceeding 87.3%, with a slight deviation in the case of forest-edge plot (its DS to other plots being only 80.7–84.6%).

The bird assemblage from alder-swamp forest (plot L) appeared to be essentially identical with those found in ash-alder riverside stands, both plant associations constituting one bird habitat — a mature swampy forest. Some deviation due to edge-effect is evident in the case of plot K (Fig. 3); eventual omitting of *Sturnus vulgaris* would significantly increase its overall similarity to other swampy stands.

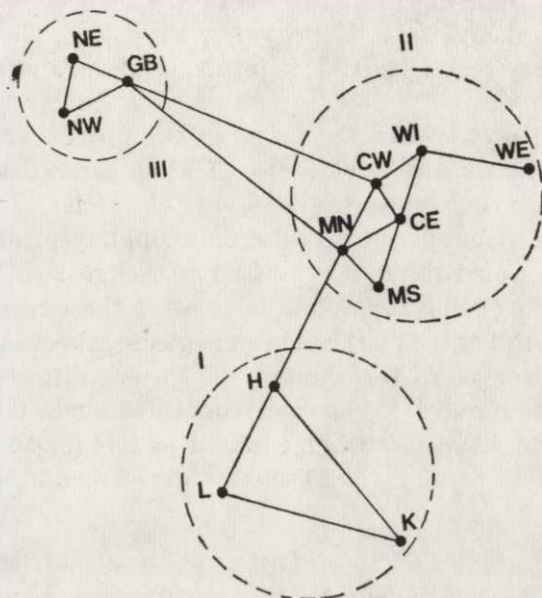


Fig. 3. Similarity in the composition of bird assemblages studied in BNP

I — riverside swampy forests group, II — oak-hornbeam group, III — mixed coniferous group. The points denote the plots studied, the distance between them reflects the difference between composition of their avifauna.

The difference between swampy forests and those of the oak-hornbeam type is less sharp than between oak-hornbeam and coniferous ones. This is especially evident for plot H which has some phytosociological characteristics intermediate between ash-alder and oak-hornbeam habitats. Here also some bias is present, because all swampy forests contain small islands of dry (oak-hornbeam covered) land, as well as contain some intrusions of dry ground on their margins; all this increases the similarity of their avifauna.

Concluding, it appears that all BNP plots are inhabited by the same bird community. It shows only small local deviations, such as its impoverished form occurring in coniferous stands or the enriched by ecotonal species

a forest-edge variant (see similar conclusion of TOMIAŁOJĆ 1974 for Silesian forests).

Species richness. The total pool of true forest birds (excluding all species inhabiting either anthropogenic habitats, such as settlements, mid-forest fields, meadows and artificial water reservoirs, or formerly extensive marshes of Byelorussian side), contains in the Białowieża Forest 99 breeding species plus three extinct ones (*Falco peregrinus*, *Aquila clanga*, *Strix nebulosa*). In the 47.5 km² of afforested area of BNP there are 88 breeding species, and 75 of them were found breeding within our census plots in five years of studies. Species occurring outside the plots are either very scarce and with big home ranges (*Accipiter gentilis*, *Hieraaetus pennatus*, *Circaetus gallicus*), or specialists restricted to some very scarce in BNP habitats, as *Lullula arborea* or *Caprimulgus europaeus*.

The highest number of species was found in swampy deciduous forests — 66 species, then in oak-hornbeam — 60 (or c. 57 when corrected to the same size of area studied), and in coniferous stands — only 45 species.

The average number of species breeding in a single year on an average plot was 25–36, depending on habitat type. The forest-edge localizations increased this number by c. 30 % (Table 15). While calculating these results the difference in plot size (extremes: 24 and 33 ha) has been neglected, because it had appeared that for plots as big as ours the number of species differed insignificantly. *E.g.* the swampy plots H and L (25 ha each) contained separately 34–38 breeding species in 1976–77 and 42 species when counted jointly for 50 ha. On the other hand, in the same years as many as 51 species were breeding over 33 ha of the forest-edge plot K.

Total bird density. The total bird density varied between 27.4 (plot NW in 1977) and 105.5 pairs/10 ha (plot K — 1976). Average density for several plots and years (Table 15) was the lowest in the coniferous stands. In oak-hornbeam forest it was higher by 70 % while in swampy forests twice as high as in the coniferous ones.

The forest-edge localization of a plot led to 25 % increase in the total bird density in the oak-hornbeam forest (WE), and by 33 % in the ash-alder riverside one (plot K). There is a strong positive correlation ($r = 0.908$; $p < 0.001$) between the average number of species constituting a bird assemblage and the average total bird density. Thus, differences in total bird density between three types of habitats result mostly from differences in their species richness. However, this was only one factor influencing the total bird density, because the very low density in coniferous stands was caused both by lower number of species and by the very low abundance of those breeding there (Table 15).

Edge effect. In the preliminary publication (TOMIAŁOJĆ *et al.* 1977) it has been claimed that there are signs of a significantly higher total bird density

Table 15. Some structural parameters of bird assemblages in different forest types

	Forest type (plot)	Sample size*	Species number ($\bar{x} \pm SD$)	Total density (p/10 ha) ($\bar{x} \pm SD$)	Mean values of species density (p/10 ha) ($\bar{x} \pm SD$)	dominants percentage (%)
Forest edge	Swampy (K)	5	50.0 \pm 1.0 <i>P</i> < 0.001**	99.9 \pm 4.92 <i>P</i> < 0.001	2.0 \pm 0.09	39.8
	Oak-horn-beam (W 1975-76, WE 1977-79)	5	41.4 \pm 2.88 <i>P</i> < 0.01	77.9 \pm 8.30 n.s.	1.9 \pm 0.15	59.9
Forest interior	Swampy (H,L)	7	36.4 \pm 1.81 <i>P</i> < 0.001	74.9 \pm 7.70 <i>P</i> < 0.001	2.1 \pm 0.22	46.6
	Oak-horn-beam (WI, CW, CE, MN, MS)	23	30.7 \pm 2.90 <i>P</i> < 0.001	62.4 \pm 4.97 <i>P</i> < 0.001	2.0 \pm 0.16	61.9
	Coniferous (GB, NW, NE)	13	25.8 \pm 2.86	36.0 \pm 5.12	1.4 \pm 0.20	65.7

*A sum of census years in every plot.

**Probabilities shown refer to STUDENT's *t* test.

at the forest edge of BNP. Closer examination of all available data (Table 16) has shown, however, that the forest-edge increase in bird density (by 25-33 %) results almost exclusively from the presence of additional "forest-edge species". Among them there are species restricted to the forest margins (*Emberiza citrinella*, *Locustella fluviatilis*, *Luscinia luscinia*, *Carpodacus erythrinus* etc.), as well as those only strongly favouring such locations. *E.g.*, single pairs of *Sturnus vulgaris*, *Carduelis chloris*, *Streptopelia turtur* can sometimes be found deep in the forest, though most of them occur at the forest margins or in anthropogenic habitats. With somewhat greater ease the forest-edge species penetrate forest interior through more open swampy alder or riverside ash-alder stands. *E.g.* *Hippolais icterina*, *Sylvia borin* and *Turdus iliacus* sporadically breed in plot L. *Anthus trivialis*, in spite of its preference to the edges, can occur in oak-hornbeam mature stands throughout the whole BNP, sometimes in quite considerable numbers (plots CW, MN, MS), being dependent on small gaps of fallen big trees. Similarly behaves *Phylloscopus collybita*, though this species seems to originate from the open-canopy swampy stands, and only secondarily became numerous in fragmented managed forests and in pine plantations (own data, unpubl.).

The total density of remaining forest-interior birds alone shows a very

Table 16. Total bird density (p/10 ha) in the oak-hornbeam forests in relation to the distance to the forest edge (mean values for 1977-79)

Plot	WE	WI	CW	CE	MN	MS
Distance to the forest edge (km)	0-0.2	0.2-0.5	1-1.6	1-1.6	2-2.5	2.5-3
Total density ($\bar{x} \pm SD$)	73.4 \pm 7.72	63.2 \pm 2.69	58.0 \pm 2.48	61.9 \pm 4.24	58.4 \pm 2.94	59.8 \pm 4.85
Density of forest interior species ($\bar{x} \pm SD$)	64.0 \pm 4.42	62.4 \pm 2.58	58.0 \pm 2.48	61.7 \pm 4.17	57.5 \pm 2.59	59.4 \pm 4.52

slight increase at the forest edge (Table 16). There are some indications that even this result is rather incidental, because of the special structural properties of plot W, which demonstrates a somewhat higher phytosociological patchiness and most luxuriant tree stand, independently of the forest-edge position (FALIŃSKI 1968). *E.g.* in spite of its penetrating up to 500 m deep into the forest it does not show a lower density of forest-interior birds (64.9 \pm 1.9 p/10 ha) than in plot WE restricted to the forest-edge zone (64.0 \pm 4.42) in equivalent years.

It cannot be ruled out either that the forest-edge effect will be still less conspicuous in the case of a forest wall exposed to the north, instead as in our case, to the south. It can be predicted that the warmer early-spring microclimate on sun-exposed southern edges may have some influence, which is less probable along cooler northern fringes of the forest.

The results from BNP confirm some earlier claims (TOMIAŁOJĆ 1974, TOMIAŁOJĆ and PROFUS 1977) that on the edges of large natural forests the forest-edge effect is evident mainly due to additional occurrence of "ecotonal species". It is even far from certain whether such species as *Buteo buteo*, *Pernis apivorus*, *Columba palumbus*, *Turdus merula*, *T. philomelos* or *Erithacus rubecula*, used to prefer the forest-edge in pristine times, unless it was valid only for their populations from the forest-steppe ecotonal biome. Even today, their densities in some forest-interior plots of BNP exceed the values from the forest-edge samples. These birds are still typical forest-interior inhabitants here. Hence, they can hardly be considered the "primarily ecotonal species", or "preadapted to park-like habitats". Presumably their deeper adaptations or adjustments to man-made open landscape, so apparent in some regions of Europe, have only been secondarily developed under the pressure of overpopulation in island-like remnants of the forests surrounded by centuries-old, extensive, and fertile farmland (see also TOMIAŁOJĆ and PROFUS 1977).

It is concluded that there is no conspicuous increase in density of forest-interior birds at the forest-edge of large natural forests in Poland.

Percentage composition. Dominant species (constituting $\geq 5\%$ of bird assemblage) contributed to 37.1% (plot K-1978) or 75.6% (NW-1975) of the whole breeding assemblage. The average proportion (Table 15) was negatively correlated to the average total bird density ($r = (-) 0.80$; $p < 0.01$). Hence, the natural habitats most abundant in bird species and the most populated with birds (with the highest density) show also the most even distribution of the species-specific abundances (Fig. 4).

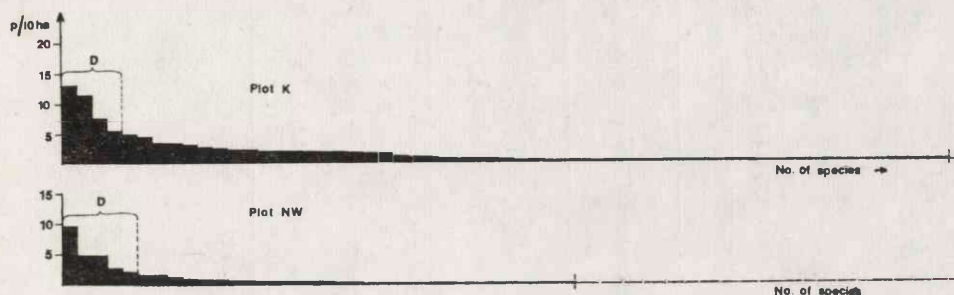


Fig. 4. Comparison of the structure of two extreme bird assemblages studied in BPN (average values).

D - dominants.

The group of dominants was composed of 10 species, five others joining it only sporadically (1–4 cases). Two species (*Fringilla coelebs*, *Erithacus rubecula*) were dominant in all plots and in all years. *Phylloscopus sibilatrix* always belonged to dominants in dry-land forests while in swampy ones only during the years of its high abundance. *Turdus philomelos* belonged to dominants in dry-land forests, while in swampy stands even when corrected by 10 or even 20% for its low detectability (see methods) it still remained well below 5% limit. Other species belonged to dominants only in some habitats: in swampy forests it was *Troglodytes troglodytes* and *Sylvia atricapilla*, in oak-hornbeam — *Ficedula albicollis* and *Coccothraustes coccothraustes*, in the coniferous — *Regulus regulus*, while in forest-edge plots — *Sturnus vulgaris*.

Foraging guilds and feeding habits. This analysis starts from a common assumption that bird distribution and abundance is strongly dependent on the distribution of available food resources. The total bird densities have been split according to major places and types of bird foraging (Table 17), neglecting the fact that such divisions are not flexible enough to follow satisfactorily year-to-year variation in bird behaviour (see below.) The results indicate that:

(a) About 90% of birds in the forest feed on small invertebrates. 40–60% of them consist of crown foragers, which is in accordance with the considerable total volume of this stratum and with the numerical dominance of invertebrates (mainly insects) in bird diets.

Table 17. Foraging guilds in relation to the forest type and location*

Upper rows – mean density (p/10ha ± SD); bottom rows – percentage

Forest type		Insectivorous, collect food from:			Raptorial	Vegetarian	Total, foraging in the forest	Foraging outside the forest
		ground	bark	crowns or in flight				
Forest edge	Swampy	31.7 ± 1.22	5.6 ± 0.49	42.7 ± 1.85	0.3 ± 0.23	6.9 ± 0.63	87.1 ± 3.28	12.8 ± 3.26
		31.7	5.6	42.7	0.3	6.9	87.1	12.8
	Oak-horn-beam	18.2 ± 2.22	4.0 ± 0.93	39.3 ± 4.51	0.6 ± 0.12	9.0 ± 1.10	71.4 ± 7.54	4.7 ± 2.13
		23.9	5.3	51.6	0.8	11.8	93.8	6.2
Forest interior	Swampy	21.2 ± 3.41	6.8 ± 0.74	38.5 ± 4.50	0.3 ± 0.19	6.7 ± 0.83	73.5 ± 7.69	1.4 ± 1.38
		28.3	9.0	51.4	0.4	8.9	98.1	1.9
	Oak-horn-beam	15.5 ± 1.94	4.3 ± 0.93	34.3 ± 2.78	0.3 ± 0.21	7.6 ± 0.71	62.0 ± 4.91	0.3 ± 0.36
		24.9	6.9	55.1	0.5	12.2	99.5	0.5
	Coniferous	7.8 ± 2.03	1.7 ± 0.33	21.7 ± 4.86	0.3 ± 0.23	4.6 ± 1.8	35.8 ± 5.02	0.1 ± 0.14
		21.7	4.7	60.4	0.8	12.8	99.7	0.3

*Distribution of study plots among different forest types and sample sizes as in Table 15.

(b) In broad frames the abundance of particular foraging guilds shows a clear parallelism with a gradient of increasing trophic value from coniferous through oak-hornbeam to swampy forests; all foraging guilds, except, perhaps, raptors, are least abundantly represented in coniferous stands, the most abundantly in swampy forests, and chiefly at the forest edge. *E.g.* vegetarians and insectivores foraging in tree-crowns are on average 1.5–1.8 times more numerous in deciduous than in coniferous stands, while the ground-foragers are in oak-hornbeam 2.1 times, and even 3.3 in swampy stands, more numerous than in coniferous stands.

(c) Some minor deviations from this general picture have also been noticed. The total canopy volume of the high oak-hornbeam forest is almost twice as large as that in more open and lower treestands of swampy forests composed of small-crown trees, and is c. 100–120 versus 70–80 thousand m³/ha (these values have been achieved by multiplying the average thickness of a canopy layer by its coverage, and subsequent summarising of the values for all canopy layers). Moreover, the caterpillar outbreaks, so heavy sometimes in our oak-hornbeam stands, were hardly noticed in swampy forests. Therefore it is rather unexpected that the average density of crown-foraging birds was higher in swampy stands ($\bar{x} = 38.5 \pm 4.50$ p/10 ha for forest-interior plots) than in the equivalent oak-hornbeam ones ($\bar{x} = 34.3 \pm 2.78$; the difference significant: STUDENT'S $t = 2.34$, $p < 0.05$). It suggests a lack of closer correlation between food resources and the density of this group.

(d) The abundance of bark-gleaning or probing birds also shows between-habitat distribution patterns somewhat deviating. There were 2.5 times more birds in oak-hornbeam and 3.8 times more in swampy forests than in coniferous ones, in spite of the highest number of trees per hectare found in coniferous stands. The 1.5 times higher abundance of this group in swampy than in oak-hornbeam stands also suggests a dependence rather on the amount of decaying timber than on the total bark surface.

The Białowieża Forests have preserved some primaevial patterns of bird foraging activity. Since the interior of BNP lies more than 3 km away from the Białowieża clearing (which contains a limited acreage of fields — c. 4.5 km²) and more than 10 km from extensive farmland surrounding the Forest, many birds are devoid of the possibility of economic feeding flights to the fields. Such distant flights seem a rather secondary habit of several forest birds. *E.g.* the whole forest population of *Buteo buteo*, *Pernis apivorus* or *Columba palumbus*, almost evenly distributed throughout the Forest, forages in the breeding season almost exclusively within the forest areas, including small clearings. This has been confirmed by direct observations of several individuals foraging under close canopy, as well as was inferred from a negligible number (single or few individuals only) feeding in the Białowieża clearing. Some other species considered by European authors as typical of the forest-edge zone, also do not rely here on food from open areas. *E.g.* *Turdus philomelos*, *Erithacus rubecula* or *Frin-*

gilla coelebs only in single cases, mainly during early-spring cold-spells, were observed foraging in front of the forest-wall, while for *Turdus merula* there were no such cases at all.

On the contrary, a high flexibility of foraging behaviour was recorded when there were outbreaks of caterpillars in BNP forests. In such periods even *Emberiza citrinella*, *Corvus cornix* and *Sturnus vulgaris*, usually exploiting food resources of open areas were observed to forage regularly several hundred metres inside the forest. Flocks of the latter species used to travel from the village park to the forest, a direction opposite to the normal one. Among forest animals even so clumsy species as *Dendrocopos major*, *D. medius*, *D. leucotos*, *Garrulus glandarius* or *Sciurus vulgaris* were observed at that time regularly collecting caterpillars from the leaves on very thin twigs. During outbreaks the majority of bird species used to exploit this food source, an observation in agreement with other authors (PFEIFER and KEIL 1958, LACK 1966, EDINGTON and EDINGTON 1972, HILDEN 1977 and others).

Nesting guilds. Another important factor shaping the bird distribution during the breeding season is the nest-site requirements. If so, one can expect to find the densities of particular nesting guilds to follow the differences in availability of nest-sites or nest-substrates.

An analysis of data on nesting guilds (Table 18) reveals the following facts and suppositions:

(a) All three guilds are the least represented in coniferous stands and the most abundant in swampy forests. Thus, a positive correlation between structural complexity of habitats and the bird densities parallels the correlation between

Table 18. Nesting guilds in relation to the forest type and location*

Upper rows - mean density (p/10ha±SD); bottom rows - percentage

	Forest type	Open or domed nesters		Hole-nesters	
		low - up to 1.5 m above the ground	high - above 1.5 m	Total	Without <i>Sturnus vulgaris</i>
Forest edge	Swampy	35.4±2.29 35.4	32.5±2.08 32.5	37.7±4.86 37.7	20.1±1.01
	Oak-hornbeam	18.6±2.14 23.9	33.9±5.05 43.5	25.1±4.33 32.2	20.1±3.04
Forest interior	Swampy	24.6±4.09 32.8	26.8±3.21 35.8	23.3±3.17 31.1	22.5±2.76
	Oak-hornbeam	16.6±2.21 26.6	27.0±3.06 43.2	18.4±3.03 29.5	18.2±2.95
	Coniferous	11.0±2.45 30.5	17.2±2.48 47.7	7.5±2.21 20.8	7.5±2.21

*Distribution of study plots among different forest types and sample sizes as in Table 15.

the trophic value and bird numbers. We have no data to separate these two factors here.

(b) The density of low-nesting birds is 1.5 times lower in coniferous stands with their mostly litter-covered soil than in oak-hornbeam stands, 2.2 times lower than in forest-interior swampy plots and 3.2 times than in swampy stand at the forest-edge with luxuriant herb-layer and plenty of uprooted trees. In swampy forests standing water forms a lot of small islands hardly accessible to some ground predators, this can be an important additional factor in increasing security of such nest-sites.

(c) Hole-nesters are 2.4 times more numerous in oak-hornbeam and 3 times in swampy stands (sometimes up to 5 times, when at the forest-edge and calculated with *Sturnus vulgaris*) than in coniferous ones. Low density of this group in coniferous, chiefly spruce, forests is a well known fact (HAAPANEN 1965, KNEITZ 1961). We should comment briefly on the situation in swampy stands and in oak-hornbeam ones, the latter being found to contain as many as 500–780 holes/10 ha (KNEITZ 1961, SZYMURA unpubl.). It seems reasonable to suggest that swampy forests, though lower in height, but being composed of soft-timber trees, easily decaying and containing more woodpeckers (on average 2.1 instead of 1.6 p/10 ha), should shelter the highest number of hole-nesters. In fact the difference is hardly conspicuous.

(d) The overall densities of arboreal open-nesting birds vary in BNP stands in relatively narrow limits between 17 and 34 p/10 ha (see also TOMIAŁOJĆ and PROFUS 1977). Only in coniferous stands is it 1.5–2 times lower (Table 18). At first glance this result seems rather unexpected, as the total canopy volume in coniferous forest (c. 100 000m³/ha) is of comparable size to that in oak-hornbeam stands. At closer inspection, however, we see that it is not a disagreement between data. In coniferous stands most mature spruces are very transparent when observed from below; it is hardly possible to overlook in careful search a bulky nest of *Turdus philomelos* or *Fringilla coelebs* attached to their smooth and straight stems. The same must apply to the finding efficiency of visually oriented corvids and *Martes martes* or *Sciurus vulgaris* hunting by day. Hence, only birds able to hide their nests in flag-shaped side branches of spruces (*Regulus regulus*, *Carduelis spinus*, *Fringilla coelebs*, perhaps *Loxia curvirostra*) can thrive better in this habitat. It should be added also that the dense upper parts of spruce crowns are either too exposed to wind, or eliminated by heavy snow (hundreds of them were broken during the snowy winter 1978/79).

In contrast, the canopy in deciduous stands is much more diversified structurally. Spruces standing singly develop here denser crowns, or denser lower (flat) branches. The more complicated branching of deciduous stems, presence of offshoots on trunks, abundance of semi-holes, is important here as well.

The identical density of arboreal birds in both deciduous types of the forest (Table 18) is rather unexpected, as the total canopy volume of the oak-hornbeam forest is almost twice that in swampy forest. Looking for explanation we cannot rule out the interpretation offered by BROSSET (1974) for a tropical forest. The fact that swampy stands in BNP have an open canopy causes many trees to stand apart, which makes it impossible for arboreal mammals to wander directly through their crowns, forces them to climb repeatedly up and down, and produces an "island-like" canopy apparently with serious consequences for predator-prey relations. This possibility should be checked when larger material in Białowieża nest-record scheme will be collected.

Migratory habits. There are no clear between-habitat differences in the percentage of a particular bird-group distinguished according to the migratory habits (Table 19). In all stands short-distance migrants dominate numerically. This similarity stems partly from the uniformity in age of our climax stands. Only a slight tendency to a little higher percentage of tropical migrants and a lower one of short-distance migrants can be noticed in the oak-hornbeam forests.

Table 19. Percentage of birds with different migratory habits in bird assemblages of various forest types

Forest type	Tropical migrants		Short-distance migrants		Residents or local movements	
	mean	range	mean	range	mean	range
Swampy	21.8	18.0-24.3	54.7	51.8-56.5	23.3	19.6-25.4
Oak-hornbeam	24.7	22.5-28.4	50.6	46.7-53.9	24.7	23.4-26.8
Coniferous	21.7	19.4-23.6	55.1	54.0-56.4	23.2	21.3-24.0

Year-to-year fluctuations in community structure. The five-year period of studies allows us to evaluate the stability of some bird community parameters. Here the negative of stability, the coefficients of variation in several parameters, have been calculated (Table 20). The variation of total density seems to be the highest in coniferous stands (on average 15.6%) and the lowest (twice as low) in swampy stands (7.2%). This difference cannot be tested directly because sample size is too small. It must be significant, however, because it is significant even between oak-hornbeam and coniferous stands more resembling each other (MANN-WHITNEY test $U = 0$, $p < 0.05$).

A similar result has been obtained by the coefficient of variation in the species number which shows that variation in coniferous bird assemblages is three times that in swampy forest ones. In this case, however, a sharper and significant difference was between swampy and oak-hornbeam stands ($U = 0$, $p < 0.05$) than between oak-hornbeam and coniferous ones.

Table 20. Stability of bird assemblage structure in BNP plots during 1975-79.

Habitat	Plot	Coefficients of variation (in %) of		Average species turnover* (\bar{T})
		total density	number of species	
Swampy forests	K	4.9	2.0	0.105
	H	9.6	4.7	0.125
Oak-hornbeam forest	W	10.9	6.0	0.166
	CW	10.4	11.6	0.156
	CE	8.7	9.9	0.143
	MN	9.0	7.9	0.099
	MS	7.6	11.1	0.129
Mixed coniferous forests	NW	14.9	6.8	0.209
	NE	16.2	14.4	0.225

*Calculated according to the formula given by JÄRVINEN (1979). The average species turnover is an arithmetic mean of $\bar{T} = (I + E)/(S_1 + S_2)$, where I and E are the numbers of species that immigrated and disappeared between season 1 and 2, respectively and S_1 and S_2 are total numbers of species breeding within the plot in year 1 and 2. Only successive years are compared.

The correlation between variation in species number and variation in total bird density was found to be insignificant ($r = 0.382$).

The average species turnover (\bar{T}) has revealed similar differences to the variation in species number. It shows greater year-to-year changes in coniferous stands (average 0.217), lower in oak-hornbeam (significant difference), and the lowest in swampy stands (0.115).

We may conclude that all three indices show the lowest stability of bird assemblages in poor coniferous forests and the highest one in swampy forests, especially in those at the forest edge, which are the most abundant in birds.

Year-to-year fluctuations in bird numbers. The total bird density fluctuated consistently among all census plots (Fig. 5) confirming the validity of the averaged results and satisfactory accuracy of the census method applied. The average total bird density fluctuated in BNP rather moderately around the values of 1977, which were assumed to be 100% level. Only 1976 values were significantly (by 19%) higher.

When splitting the bird assemblage into groups with different migratory habits (Fig. 6), the results reveal that tropical migrants have shown a strong increase (by 28%) in 1976, short-distance migrants two peaks in numbers (1976 and 1979), while residents demonstrated more or less pronounced decrease during the years 1976-78.

The impact of the severe winter 1978/79 on the numbers of residents and short-distance migrants was, however, rather slight. Total density of each of these groups decreased already after the much milder though snowy winter of 1977/78 and remained at the same level (residents) or even recovered somewhat (short-distance migrants) after the 1978/79 winter. An analysis on the

species level (Table 21) also shows that only few species (*Parus palustris*, *Sitta europaea*, *Columba palumbus*) have shown a marked decrease after the severe winter of 1978/79.

All nesting guilds showed the highest population level in 1976 (Fig. 7). Then the arboreal (high-nesting) birds were decreasing in numbers till 1978 and reached their second peak in 1979. Ground and low-nesters fluctuated less

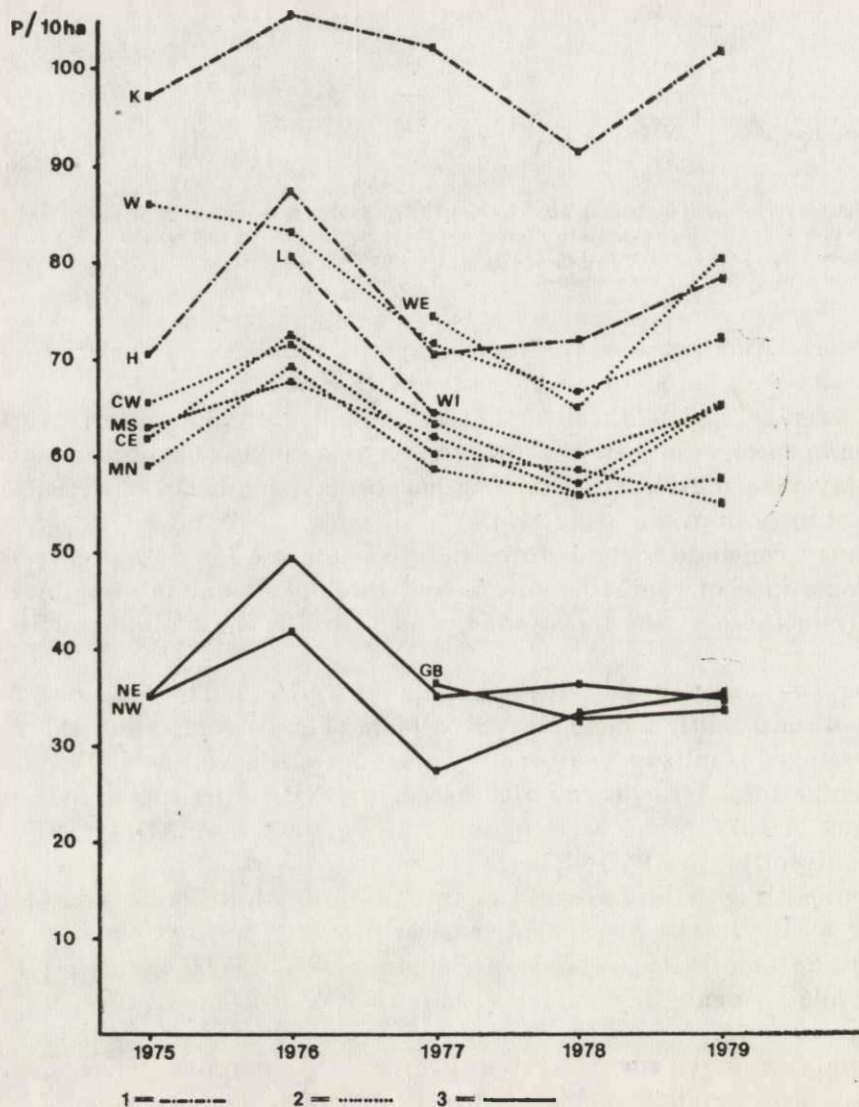


Fig. 5. Year-to-year changes of total bird density in particular plots.

1 - swampy forests, 2 - oak-hornbeam forests, 3 - coniferous forests.

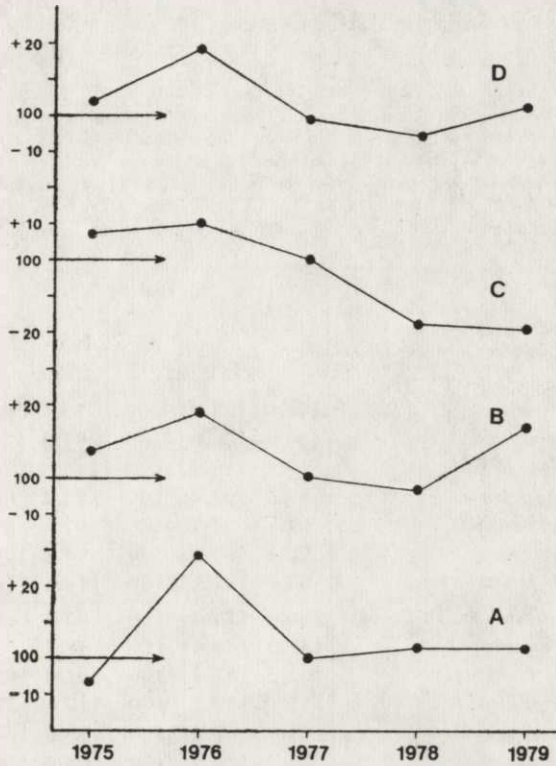


Fig. 6. Year-to-year changes in abundance of three migrational guilds.

A - tropical migrants, B - short-distance migrants, C - residents, D - total avifauna. The calculations are based on the assumption that 1977 values were equal to 100%.

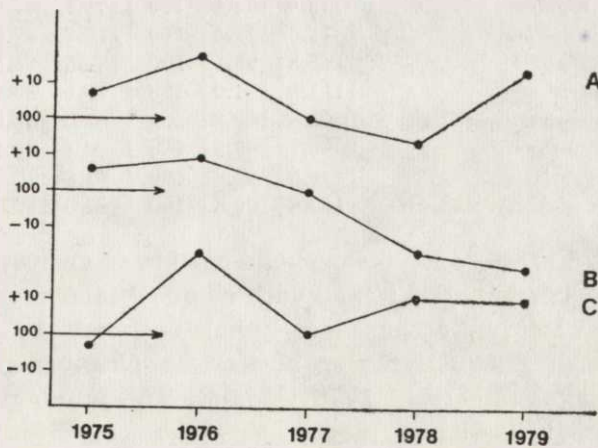


Fig. 7 Year-to-year changes in abundance of particular nesting guilds.

A - canopy open-nesters, B - hole-nesters, C - ground and low nesters. For other explanations see Fig. 6.

Table 21. Percentage indices of population numbers of more numerous bird species breeding in BNP

The year 1977 was chosen as the basis for comparisons because only in that spring all plots were censused simultaneously. The indices have been calculated by comparing the number of pairs breeding within all plots censused in a compared year with the number of pairs breeding within the same plots in 1977. Due to the varying number of plots censused in different years the number of pairs constituting 100% was different for different comparisons. For example there were 13 pairs of *Anthus trivialis* breeding in 1977 in plots censused in both 1975 and 1977, but the number of *Anthus trivialis* pairs breeding in 1977 in plots censused in both 1977 and 1979 was 16. The range of the number of pairs taken as 100% in different comparisons is shown below

Migratory habits	Species	Year					Number of pairs constituting 100%
		1975	1976	1977	1978	1979	
Tropical migrants	<i>Anthus trivialis</i>	176.9	126.9	100	78.1	95.3	13-16
	<i>Sylvia atricapilla</i>	138.6	138.0	100	87.9	124.3	41.5-53.5
	<i>Phylloscopus sibilatrix</i>	90.8	166.8	100	145.5	127.5	119.5-172.5
	<i>Ficedula hypoleuca</i>	89.5	103.4	100	71.4	63.4	19-28
	<i>Ficedula albicollis</i>	84.8	97.3	100	67.6	81.8	105-132
	<i>Ficedula parva</i>	72.4	86.2	100	94.3	109.1	14.5-22
	<i>Muscicapa striata</i>	67.7	137.8	100	118.4	118.4	15.5-19
Short-distance migrants	<i>Columba palumbus</i>	80.6	115.6	100	95.7	43.5	15.5-23
	<i>Sturnus vulgaris</i>	132.2	108.6	100	48.5	59.1	58-66
	<i>Troglodytes troglodytes</i>	102.2	87.9	100	101.6	102.4	45-63.5
	<i>Prunella modularis</i>	111.1	179.2	100	117.0	151.1	18-24
	<i>Phylloscopus collybita</i>	87.8	97.2	100	90.0	105.4	41-54
	<i>Erithacus rubecula</i>	89.7	121.3	100	106.8	110.4	145.5-195
	<i>Turdus merula</i>	130.0	134.9	100	110.6	113.2	35-47.2
	<i>Turdus philomelos</i>	140.0	133.1	100	107.6	125.7	55-72
<i>Fringilla coelebs</i>	102.8	114.2	100	99.9	127.8	285.5-391.5	
Residents	<i>Dendrocopos major</i>	73.7	49.2	100	57.1	116.9	14.2-19.2
	<i>Dendrocopos medius</i>	110.8	97.6	100	62.4	59.4	18.5-25.2
	<i>Regulus regulus</i>	152.6	134.8	100	75.1	64.6	39-57.2
	<i>Parus palustris</i>	75.6	126.4	100	110.7	42.0	22.5-28
	<i>Parus caeruleus</i>	145.8	93.8	100	84.5	88.5	36-50
	<i>Parus major</i>	111.0	111.9	100	76.9	80.2	45.5-50.5
	<i>Sitta europaea</i>	82.6	106.3	100	85.0	58.9	34.5-45
	<i>Certhia familiaris</i>	89.7	107.9	100	90.1	85.1	43.5-60.5
	<i>Carduelis spinus</i>	9.5	53.8	100	61.8	26.3	10.5-19
	<i>Coccothraustes coccothraustes</i>	100.8	103.8	100	81.6	112.3	62.5-81.5

distinctly, while hole-nesters have shown a continuous decrease between 1976 and 1979. The last result parallels well with similar patterns of changes found in resident species which, in fact, are mostly hole-nesters.

Numbers of both ground foraging and crown gleaning guilds fluctuated parallelly, with peak numbers in 1976 (Fig. 8). The numbers of vegetarians were the highest in 1979, whereas those of bark gleaners or probers in 1976-79.

What seems important, is that the abundance of crown gleaning and sallying group did not follow closely the changes in availability of its main food resource — the leaf-eating caterpillars (Fig. 8).

Species-specific indices of population change (Table 21) are difficult to compare with each other because the amount of variation depends on the sample size. For the species listed in Table 21 the differences between minimum and maximum values of the index exceeding 90% are, in fact, significantly more common among species with sample size less than 20 pairs (chi-square = 13.12, $p < 0.001$). Keeping this reservation in mind we can see that some species remained at rather stable population level, e.g. *Coccothraustes cocco-*

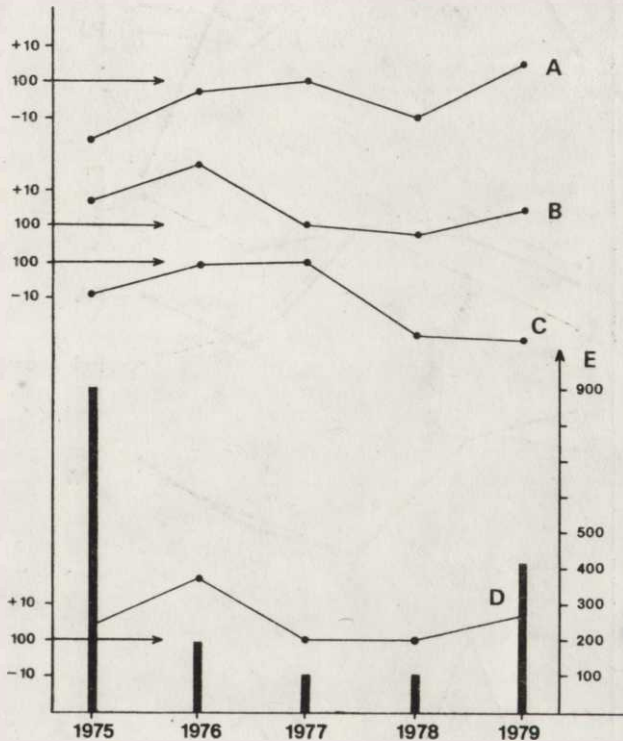


Fig. 8. Year-to-year changes in abundance of particular foraging guilds.

A - vegetarians, B - ground insectivores, C - bark insectivores, D - canopy insectivores. In all cases the 1977 data equal to 100%. E - changes in caterpillar abundance in lower canopy (bars).

thraustes, *Troglodytes troglodytes* or *Phylloscopus collybita*. Most species showed small (below 25%) fluctuations in number, though in the case of *Phylloscopus sibilatrix*, *Prunella modularis* and *Dendrocopos major* they approached 80–100% of the lower value. It is remarkable that these three species represent three different types of migratory, foraging and nesting habits.

Some species have shown a more or less pronounced permanent decrease during a part of the period under study. These were: *Sturnus vulgaris*, *Regulus regulus*, *Parus ater* or *Anthus trivialis*, again, each representing different kind of

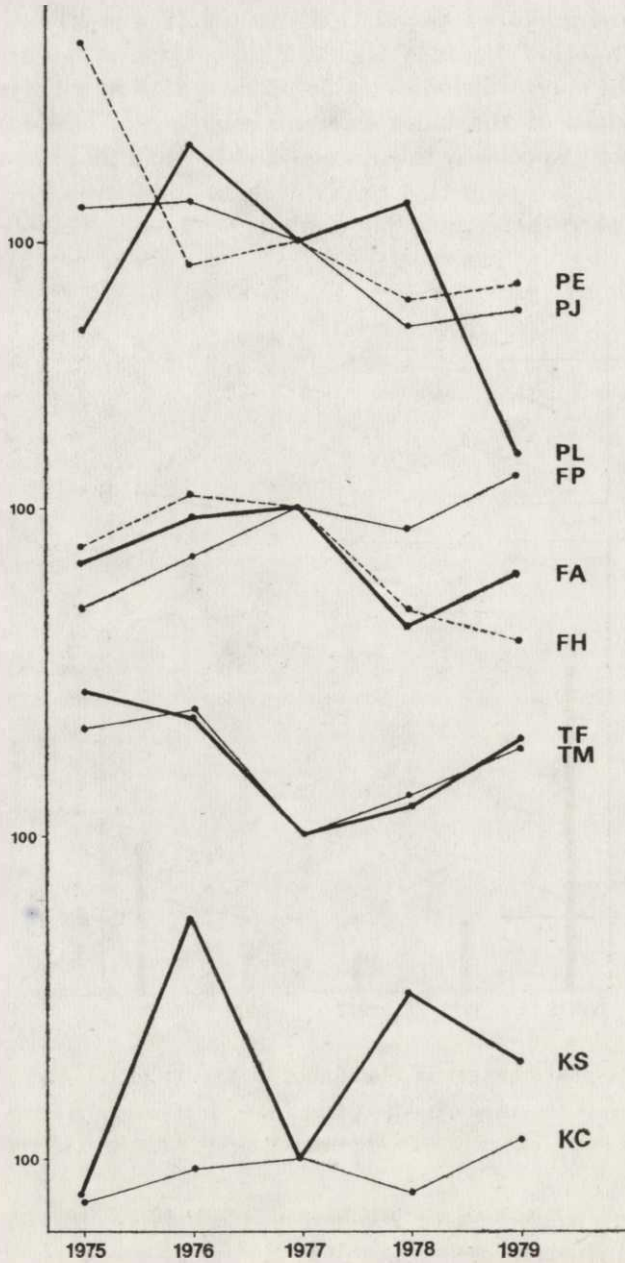


Fig. 9. Year-to-year changes in abundance of some congeneric bird species.

FA, FH, FP - *Ficedula albicollis*, *F. hypoleuca*, *F. parva*; KO, KS - *Phylloscopus collybita*, *Ph. sibilatrix*; PE, PJ, PL - *Parus caeruleus*, *P. major*, *P. palustris*; TF, TM - *Turdus philomelos*, *T. merula*.

nesting, feeding and migratory habits. On the other hand, no species has shown a continuous increase in numbers.

A comparison of population fluctuations in closely related, congeneric, species (Fig. 9) reveals that in most cases changes in numbers are parallel (e.g. *Turdus*, *Parus*, *Ficedula*) or one species of a pair strongly fluctuates while the population of the other remains stable (*Phylloscopus* spp.). This strongly suggests that they do not restrict numbers of their congeneric relatives by competition but are rather similarly affected by some other limiting factors.

DISCUSSION

Interhabitat differences in BNP

The plots studied represent three bird habitats and their forest-edge variants (Fig. 3). All these units differ somewhat between each other in features like species richness, abundance in various guilds and total density of birds. These differences have displayed sufficient stability throughout the study to look for a general explanation.

Recently, it has been commonly believed that habitat selection by birds and the distribution of their numbers reflect mainly differences in the availability of food resources (LACK 1954, CODY 1974 and others). Our results (see foraging guilds analysis) are consistent with this explanation for trophically poor coniferous stands are inhabited by fewer species and fewer individuals than the more fertile stands. Moreover, the comprehensive data collected for *Phylloscopus sibilatrix* show that the breeding success is also the lowest in coniferous, moderate in oak-hornbeam and the highest in riverside swampy forest (WESOŁOWSKI 1980).

In contrast to the majority of recent authors analysing only the food resources/bird numbers relation we believe, however, that nesting requirements of birds are an equally, or even more, important factor shaping their distribution and abundance. Unfortunately, both these factors frequently operate not independently but often in parallel, both being dependent on the structural complexity of habitats. Hence, bird census data alone, which usually suggest a positive correlation between structural complexity of a habitat and the total bird density and diversity, cannot be taken for granted as indicating the food limitation of bird populations, a reasoning plaguing recent ornithological literature. At least under conditions of BNP the observed interhabitat differences in bird distribution and abundance are equally well consistent with a possibility of predatory pressure shaping bird assemblages.

The two factors, food resources and predation, can operate together in a very complicated way. Such an example was registered during 1979 outbreak in caterpillar numbers, when an overt switching of nest-predators such as

Garrulus glandarius, *Sciurus vulgaris* and *Dendrocopos major* (also acting as nest-predator — LÖHRL 1977, HILDÉN 1977) to almost exclusive foraging on caterpillars was observed in BNP. The percentage of robbed nests of *Fringilla coelebs* was found to be almost twice as low as in other years (TOMIAŁOJĆ unpubl.). An identical situation has been noticed in Finland, where during the outbreak of caterpillars (1975) the broods of hole-nesters and thrushes suffered clearly lower losses; HILDÉN (1977) suggests this was partly owing to a weaker pressure of predators (*Dendrocopos major* and *Garrulus glandarius*) switching to insect prey.

Hence, the better breeding success of passerines during the outbreak years and poor in other years does not necessarily result mainly from differences in food resources, though some (by c. 6%, HILDÉN 1977) difference in clutch size indicates this. The main difference seems to be a change in predator functional response which obscures a simple correlation usually sought for between predator numbers and the losses in prey species.

Comparisons with other forests

National Park stands versus managed Białowieża forests. The detailed data on the breeding bird assemblages found in some stretches of the managed Białowieża forests have been presented in separate papers (PIOTROWSKA and WOŁK 1983, LEWARTOWSKI and WOŁK 1983). Here, it is necessary, however, to quote some general results for the purpose of a proper evaluation which features are characteristic of the undisturbed stands.

First of all it should be made clear that there is no pesticide or herbicide treatment in the Białowieża Forest, and that several mature stands since only very recently have been managed according to a clear-felling practice. Hence, the present mature managed stands of the Białowieża Forest are still more similar to those undisturbed from BNP than several other managed forests of Poland. Local Białowieża oak-hornbeam stands are nowadays managed according to a long-cycle (c. 120 years) rotational clear-felling performed over circular patches of c. 50 m in diameter, so called "nests", subsequently planted with seedlings. Among such patchy old-and-young stands of oak-hornbeam and secondarily grown birches an area of 52.46 ha was censused in 1977 and 1978 by L. T. In all, 46 breeding species were found (41 in 1977 and 36 in 1978). This can be compared with the equivalent 38 species (35 and 37) in 48 ha of the forest-interior plot C, and with 49 species (46 and 40) in 50.1 ha of the forest-edge plot W. Thus, a moderate fragmentation of uniform mature forest in the course of management of the type described leads to a slight increase in the species richness, though a less pronounced than that found in the case of the forest-edge position. This increase was due to the addition of *Hippolais icterina*, *Carduelis chloris*, *Locustella fluviatilis*, *Carpodacus erythrinus*, *Motacilla alba*, *Lanius collurio*.

Total bird density (calculated for the whole area of 52.46 ha, young plantations and clearings included), was 49.3 p/10 ha on average (55 and 43.6 respectively), which indicates some decrease in comparison with undisturbed BNP stands. Because the clearings and young plantations are very thinly populated with birds, the actual density calculated per remaining c. 40 ha of mature managed stand is only slightly lower than in BNP (compare Table 16).

Coniferous stands of the Białowieża Forest are managed according to a different procedure. Here, a clear-felling is performed over much larger fragments (2–6 ha) of the forest (whole-block fellings), creating a large-grained mosaic of open areas, young plantations and mature stands. In 1975–76 a large plot (571 ha) of such a mosaic was studied with the aid of a quick version of the mapping method (7 visits per season). All bird species but four most numerous ones (*Fringilla coelebs*, *Erithacus rubecula*, *Phylloscopus sibilatrix* and *Turdus philomelos*) were counted. The species list has appeared to be quite long, including many species never recorded in closed primaeval coniferous stands of BNP, e.g. *Turdus viscivorus*, *Lanius collurio*, *Jynx torquilla*, *Motacilla alba*, *Sylvia nisoria*, *S. communis*, *S. curruca* etc.

Bird density calculated for the whole mosaic of managed coniferous-dominated stands was in 1976 only 12.3 p/10 ha, while the comparable value (without four most numerous species) for BNP plots was 18.8. Obviously, this difference is less sharp when one compares only blocks of mature managed stands with the undisturbed BNP ones. E.g. PIOTROWSKA and WOLK (1983) found the total density of birds in mature managed coniferous stands embraced by our large plot, to be 34.3 p/10 ha on average (24.8–53.9), thus, slightly lower than in the undisturbed BNP ones (40.5 on average).

Concluding it can be stated that forest management practised in the past in the Białowieża region caused a moderate decrease in the total bird density, a result similar to that by HAAPANEN (1965), and in contrast to NILSSON's (1979) finding. The inconsistency of NILSSON's and our results is entirely due to astonishingly high bird density found in his undisturbed mixed forest (148.8 p/10 ha), which is probably a secondary phenomenon (S. NILSSON, pers. comm.) resulting from anthropogenic influences from the neighbouring areas.

Moderate fragmentation of old forests, either deciduous or coniferous, brings a clear increase in species richness, but does not cause an increase in bird density within remaining fragments of mature stands. The abundance of some bird species strongly dependent on old decaying timber (*Dendrocopos leucotos*, *Picoides tridactylus*) markedly decreases. All these changes seem to be the immediate bird adjustment reactions to the changes in forest structure, without involvement of true adaptation processes, which can be launched only when forest remnants are surrounded by anthropogenic habitats.

Comparisons with other European forests. In spite of the dynamic development of bird census studies, the amount of directly comparable data

remains still very low. Many results of earlier studies are incomparable with our data because of their different methods of field work (*e.g.* KARPIŃSKI 1954, GOLODUSHKO and DANILUK 1961, NOVIKOV 1959 or WASILEWSKI 1961), studying small woods strongly influenced by the surrounding man-made landscape (*e.g.* TURČEK 1951, PIKULA 1969, TOMIAŁOJĆ 1974), or finally because of their much younger age of stands. For example, it is hardly possible to find in Europe another ash-alder riverside climax forest not only surviving to these days but also not neighbouring on open farmland. Therefore in the following discussion we are dealing mainly with the situation in oak-dominated deciduous forests of Europe.

Before proceeding further, however, a few remarks on coniferous habitats are necessary. The bird densities recorded in BNP (PIOTROWSKA and WOLK 1983, present data) correspond well to the data from most productive coniferous stands in southern Finland (HAAPANEN 1965). They also fall into the range of typical densities — 25 to 40 p/10 ha — reported from the spruce-dominated samples scattered over central Europe (OELKE 1980). Some data collected in mixed pine-spruce-broadleaved managed stands of western Poland suggest a somewhat higher bird densities (TOMIAŁOJĆ 1974, MRUGASIEWICZ 1974) than those in equivalent BNP climax stands. These were mainly “island-like” blocks of older forest among younger stands. Much higher densities — even exceeding 200 p/10 ha — have been recorded only in some island-like spruce stands planted in the lowlands of Federal Republic of Germany, southern Sweden and southern Norway (OELKE 1980), as well as in Great Britain and Ireland (BATTEN 1976). On the other hand, more extensive and semi-natural coniferous stands of southern England, like the pine-larch-spruce-birch stand of New Forest, have appeared to be thinly populated with birds — 21.8 p/10 ha, according to GLUE (1973). Thus, the overall bird density seems to be more dependent on the size and the kind of surroundings of the wood than on its geographical location.

(a) Oak-hornbeam forests of Central Europe. Oak-hornbeam forests once covered vast areas of the European lowland. Since they grow in fertile soils they have been turned into fields and only few remnants thrived to these days (FALIŃSKI 1968, KORNAŚ 1972, THOMASUS 1978). Now it is even difficult to find adequately large plots comparable with BNP bird censusing (see discussion by TOMIAŁOJĆ and PROFUS 1977). To our best knowledge the only comparable data on bird community in mature stands of this kind have been collected in Niepołomice Forest near Cracow (GŁOWACIŃSKI 1975, 1978), in Colbitzer Lindenwald in GDR (ULLRICH 1970), in Burgundy (FERRY and FROCHOT 1968, 1970 and *in litt.*), and finally, though with some reservations, in the Odra river valley forests of Silesia (TOMIAŁOJĆ 1974, TOMIAŁOJĆ and PROFUS 1977). The last-mentioned forests in fact do not represent a typical oak-hornbeam category, being originally riverside *Fraxino-Ulmetum* stands gradually transformed into

oak-hornbeam ones under the influence of management and 19th century drainage of the Odra valley (KUCZYŃSKA *et al.* 1965). Perhaps it is still more important that they seem to remain under the influence of the neighbouring big city (Wrocław) and the surrounding anthropogenic open habitats.

The species composition of bird assemblages in all these plots is remarkably similar. In spite of the over 1500 km distance separating the Białowieża and Burgundy sites, all species found in Burgundy plots nest also in the Białowieża Forest, with the only exception of the sibling-species of *Certhia* or *Luscinia* replacing each other. The longer list of species breeding only in the Białowieża Forest contains additional species connected with spruce, and some eastern species.

Unlike the species-composition, the quantitative composition of bird assemblages has appeared to be very different, as the total densities recorded in all but the French study well exceed our figures from Białowieża (Tables 4–10), ranging from 91 p/10 ha (Niepołomice) to 142 (Colbitzer Lindenwald). Other central-European data, though less easily comparable, *e.g.* those quoted in earlier paper (TOMIAŁOJC and PROFUS 1977), decidedly suggest densities higher than the BNP ones. To some extent these differences result from different positioning of the plots in respect to the forest edge. However, even when subtracting the combined densities of all forest-edge species from the total densities, still this will not reduce them to the level found in the Białowieża Forest: Odra forests — remaining density still 89 p/10 ha, Niepołomice — 77 and Colbitzer Lindenwald — 92.5 p/10 ha. A closer examination reveals that there is no inconsistency among sites in their density of non-hole-nesters, which is similar among sites. The main difference is in the combined density of hole-nesters which is much lower in BNP plots (18 p/10 ha on average) than in other forests compared (from 37 p/10 ha in Burgundy to 88 p/10 ha in Colbitzer Lindenwald). Contributing to this difference are not only forest-edge species like *Sturnus vulgaris*, but also much higher densities of the tits *Paridae* and *Sitta europaea* than those in the Białowieża Forest.

(b) Equivalent woods of British Isles. In contrast to most of the post-glacial period when the predominant vegetation of the British Isles was a continuous forest (RACKHAM 1976), some two thousand years ago still covering c. 60 % of the area (SIMMS 1971), the present British landscape contains only c. 8 % of forested areas. This partly explains the difficulty with selecting British or Irish data which would be comparable to the Białowieża ones. With some reservations (small size, habitat islands, differences in plant and structural composition) we have chosen four plots as representing bird communities of oakwoods or mixed woods from the British lowland (Table 22). In order to test whether our choice was correct, two other sources of information have been exploited. One of them are the data collected during 1970–74 within the frames of Common Bird Census monitoring programme (BATTEN 1972, 1973, BATTEN and MERCHANT 1976) including 60 woodland plots each year. The second

Table 22. Densities (pairs/10 ha) of some bird species and total densities in the oak-hornbeam stands of BNP and some English oak woods.

Species	Four plots in BNP, jointly 112 ha 1975-79 ¹		New Forest, 17.5 ha 1971 ²	Wytham Wood, 6.7 ha 1972-74 ³ mean	Somerset Wood, 7.7 ha 1972-74 ⁴ mean	Northward Hill, 25 ha 1972 ⁵
	mean	maxi- mum				
<i>Columba palumbus</i>	0.6	0.8	1.1	no data	c. 58.4	22-36
<i>Troglodytes troglodytes</i>	1.6	2.5	5.7	23.2	38.0	23.5
<i>Prunella modu- laris</i>	0.5	1.3	0.6	7.1	6.5	21.4
<i>Sylvia atricapilla</i>	1.6	4.3	0.6	8.0	13.0	4.9-7.8
<i>Erithacus rubecula</i>	6.6	9.0	3.4	13.1	33.7	17.2
<i>Turdus philomelos</i>	3.3	5.6	2.0	5.3	13.0	4.9-7.8
<i>Turdus merula</i>	1.9	3.1	1.7	19.1	32.0	15.0
<i>Parus caeruleus</i>	1.8	3.1	5.7	16.1	24.2	17.2
<i>Parus major</i>	2.1	3.0	2.3	8.0	11.2	12.9
<i>Fringilla coelebs</i>	14.5	20.8	8.6	10.4	13.0	4.9-7.8
All species	62.2	72.5	75.5	mean 194.6 ⁶ max. 252.2	c.400	c. 340-350

¹Pooled data from plots CW, CE, MN and MS.²After GLUE (1973)³Unpublished data from a Common Bird Census study plot.⁴Recalculated data from PARSONS (1976).⁵Recalculated data from Fig.1 and Table 1 in FLEGG and BENNETT (1974).⁶Density without *Columba palumbus*.

source are the data on relative abundance of birds in c. 300 British woods collected and discussed by SIMMS (1971). With some small discrepancies all these sources agree as to the relative abundance of various species in British woods, with the data in our Table 22 representing the extremely densely, and one (New Forest) extremely scarcely populated one. The species composition of British bird communities of oak woods is very similar to that from the Białowieża Forest. Among the numerically important Białowieża species only *Ficedula albicollis* does not breed in Britain, and conversely, *Phylloscopus trochilus* constituting an important part of the British avifauna only exceptionally breeds in mature Białowieża stands. Other species which do not breed in Britain

(*Dendrocopos medius*, *D. leucotos*, *Picoides tridactylus*, *Ficedula parva*, *Carpodacus erythrinus*, *Turdus iliacus*, *Ciconia nigra*) are not numerous in BNP either. The other difference is a much higher proportion of non-woodland species (*Pica pica*, *Corvus monedula*, *Athene noctua*, *Acanthis cannabina* etc.) in the English avifauna of woods, an obvious result of their fine fragmentation, and a relatively open character.

Due to the admixture of spruce, the oak-hornbeam Białowieża stands contain several "spruce-liking" birds, *i.e.* those species which under central European conditions are restricted to the presence of coniferes. These are: *Parus ater*, *Regulus regulus*, *R. ignicapillus*, *Pyrrhula pyrrhula*. Such species do not occur in the purely deciduous stands of other central European oak-hornbeam forests (see previous paragraph), but breed frequently and sometimes abundantly in British woods even in those devoid of spruce. This is presumably made possible by the presence of other evergreens (*Hedera helix*, *Ilex aquifolium*, *Rhododendron ponticum*) in British woods.

Despite similar species composition of trees and birds, the numerical composition of the bird communities compared is dramatically different. Except for the ubiquitous *Fringilla coelebs* the British and Irish densities are as a rule significantly higher than the Białowieża ones, in several cases by one order of magnitude or more (Table 22) (see also DYRCZ 1969, TOMIAŁOJĆ 1980a, WESOŁOWSKI 1983). Some other species not mentioned in the Table, *e.g.* *Regulus regulus*, *Turdus viscivorus*, *Parus ater*, *Parus montanus*, *Pyrrhula pyrrhula*, *Strix aluco* show astonishingly high densities in British woods as well.

Attempting to find some general patterns one can notice that the high densities in British tit populations (*Parus major*, *P. caeruleus*) agree well with the same tendency observed in other continental deciduous forests except Białowieża. On the contrary, British data differ most pronouncedly from the majority of the continental ones owing to a very high density of low-nesting and ground-foraging birds (*Troglodytes troglodytes*, *Prunella modularis*, *Erithacus rubecula*, *Turdus merula*, partly *T. philomelos*).

Total bird density in small British woods frequently approaches a very high level of 150–200, sometimes even 410 p/10 ha. In central European forests the total densities are 2–4 times lower as a rule, with very high densities being restricted only to some old urban parks or to very small mid-field woods isolated by open farmland (for review see GROMADZKI 1970 and TOMIAŁOJĆ and PROFUS 1977).

The remarkable exception represented by the New Forest plot (GLUE 1973) with its low bird density found not only for low-nesting birds restricted by a heavy grazing pressure but also for *Columba palumbus*, *Sturnus vulgaris*, *Parus* etc., suggests that even in the British Isles the primaeval extensive forests must have been equally thinly populated with birds, as the Białowieża stands. It can be concluded that low or moderate bird densities found in mature and fertile deciduous forests constitute a primaeval feature usually lost by the

majority of fragmented, and of a reduced size, woods of western and central Europe. The exceptional position of some extensive and natural western forests like the New Forest or Forêt de Citeaux in Burgundy (FERRY and FROCHOT 1968, 1970) seems to confirm this generalization.

Why so low densities in Białowieża Forest?

As it follows from previous paragraphs, the overall bird densities in the Białowieża Forest are significantly lower than in most woods of western and central Europe. Theoretically two different situations can contribute to this uniqueness:

- (a) Densities are low because habitats are undersaturated with birds;
- (b) Habitats are saturated with birds and low densities result from a low carrying capacity of the habitat.

Białowieża birds offer examples for both these possibilities.

Habitats undersaturated. The best way of demonstrating the existence of this situation is the analysis of year-to-year changes in number and distribution of territories. If the same habitat patch is occupied by a species in one year (proof of suitability of the site) and, in spite of the absence of a significant change in its structure remains unoccupied in other years, and, at the same time, the unoccupied gaps do not result from territorial exclusion by another species, it shows that in some years undersaturation occurs. As no signs of overt interspecific territorialism have been observed among the Białowieża birds, their territories extensively overlapping on our maps, this factor can be excluded as the cause of the observed gaps.

It should be also emphasized that during the whole period of our studies some species could not be numerous enough to occupy all available space. It is impossible to test this suggestion with the present five-year data, but this possibility should not be overlooked.

Clear-cut examples of undersaturation are offered by several species breeding within our plots erratically, present only in some years (see bottom parts of the tables with census results). The same phenomenon can be observed in species which strongly declined during the study period. *E.g.* in peak years *Sturnus vulgaris* bred not only along the forest-edge but also deep in the forest (plots MN and MS), while in the low-number years no breeding occurred there. Another species, *Anthus trivialis*, bred in four pairs in plot MN in 1975 and did not in 1978. In both these cases no detectable change in habitat structure was found which could account for this pattern. Even in the second most numerous species in BNP, *Phylloscopus sibilatrix*, undersaturation was observed, as it bred in the ash-alder parts of plot K in 1976 and in 1978, but was absent in 1977. In the case of species showing undersaturation one is tempted to assume that due

either to low production, high mortality outside the breeding season or/and outside the breeding grounds, or any combination of these factors the number of birds surviving till the spring is not sufficient to fill all the available space. In migratory birds the situation can be more complicated, and one can observe saturation in one year and undersaturation in another, even without any change in numbers of birds surviving till breeding. This can result from the so-called "prolonged spring migration" (SVÄRDSON 1949), *i. e.* tendency of some migrants to fly and settle further north in warm springs and settle earlier in cold ones. This is the most probable cause of the undersaturation recorded in some years for *Phylloscopus sibilatrix* (WESOŁOWSKI 1980).

Habitats saturated. When glancing at the species-maps showing territory distribution over the area of our plots, a patchy picture can frequently be seen. This does not imply that the particular habitat is undersaturated by the species, as the same picture emerges also due to the patchiness of the habitat itself. *E.g.* *Troglodytes troglodytes* in coniferous stands of BNP leaves large areas unoccupied, however, each suitable (larger) wind-fallen tree area becomes occupied almost immediately (WESOŁOWSKI 1983).

In more numerous species the territories cover more or less uniformly the whole area of our census plots; areas of no man's land are not discernible when delineating the "paper territories" on the species maps. This is evident not only for *Fringilla coelebs*, *Erithacus rubecula* or *Phylloscopus sibilatrix* in high-density years, but equally well in the case of much scarier species like *Turdus merula*, *T. philomelos*, *Sitta europaea*. By following the particular individuals or stimulating them by playing back their specific song it was found that in spite of so low densities as 2.5 p/10 ha in the case of *Parus major* and 1.2 p/10 ha for *Certhia familiaris* the whole area of plot W was saturated with their territories in 1979 (TOMIAŁOJĆ 1980b). This was confirmed still more strongly on colour-ringed *Troglodytes troglodytes*, a tiny bird which in BNP holds in its suboptimal (oak-hornbeam) habitat territories of 5.4 ha of average size, and as large as 8 ha in an exceptional case (WESOŁOWSKI 1981, 1983).

A further possibility in our gradual analysis is when a species saturates all suitable habitats, but does not produce a "surplus" of individuals able to reproduce but failing to establish territories. This theoretical possibility can be excluded in the case of some, few, BNP species. *E.g.* several incidental observations of territorial fights showed that expelled individuals of *Fringilla coelebs* or *Ficedula albicollis*, departed further than this would be in the case of agonistic encounters between territorial neighbours. The crucial experiments with removal of territorial males in two common BNP breeders, a tropical migrant (*Phylloscopus sibilatrix*) and a short-distance migrant (*Troglodytes troglodytes*) have convincingly shown the presence of numerous males ready to breed in territories occupied by other (removed) males (WESOŁOWSKI 1980, 1981).

It is of interest that also on the Baltic coast, while studying dynamics of bird migration, PAYEVSKY (1976) came to the conclusion that in *Erithacus rubecula*, *Turdus philomelos*, *Carduelis spinus*, *Fringilla coelebs* and *F. montifringilla* the number of juveniles migrating in spring through the Courland Spit well exceeds the number necessary to replace the adult mortality. These young birds should therefore, either die still before the breeding season or to create a "surplus" ready to breed.

It can be concluded here that in spite of low breeding densities several species saturate the BNP forests and even develop in some (all?) years a non-breeding "floating population". If so, it will be reasonable to ask why these birds cannot compress the territories of earlier settlers to the level comparable to that in western Europe? In other words, why the carrying capacity of BNP habitats is so low, or which factors set its level. We will pursue this problem below.

Food resources and interspecific competition in BNP. Limited food resources and competition for them have been frequently quoted as a primary selective force limiting the size of bird populations (LACK 1954, 1966) and shaping the structure of bird communities (MAC ARTHUR 1972, CODY 1974, CODY and DIAMOND 1975).

A considerable group of BNP bird species cannot be limited by shortage of food for the simple reason of being in some years or permanently undersaturated. A long list of species very scarce in our samples can be quoted here, *i.e.* the part of bird community totally ignored in several analyses, *e.g.* by CODY (1974).

On the other hand, it can be claimed that those species apparently saturating BNP habitats, at least the deciduous ones, are kept in low densities because of food shortage in some or most breeding seasons. Such a suggestion remains, however, in clear disagreement with several data at our disposal.

A considerable abundance of invertebrates in BNP stands can be inferred from comparisons with other European woods. Several data from the European continent indicate that oak-dominated forests constitute a habitat very rich in invertebrate fauna. *E.g.* during the outbreaks of *Lymantria dispar* in oak-hornbeam forests of southern Slovakia the biomass of caterpillars was estimated at c. 60 000 kg per km² while the biomass of birds only 14.1 kg (TURČEK 1951).

The impressions from Ludwik TOMIAŁOJĆ's own field work in English woods around Tring during May and June 1974 were also unequivocal in this respect. The luxuriant though much lower deciduous stands of that region seemed to be almost devoid of mosquitoes, butterflies or *Tabanidae*. There were remarkably few frogs and rodents seen. The checks of several dozen of leafy twigs and of the ground-litter suggested rather a moderate number of lower animals, except *Lumbricidae*, which seemed to be more numerous than in Poland. Other travels to southern France and Corsica have shown that their bushy-formation-like forests, harbouring almost as many birds as BNP stands (c. 60 p/10 ha), contained

in April and May only single specimens of invertebrates per c. 50 leafy twigs inspected, and hardly any bigger insect in the dry litter.

Against such a background the BNP stands seem to be a habitat quite rich in invertebrates (see description of the study area). It would be too conservative an assumption that its invertebrate biomass is not poorer than that from English woods, and that it is certainly not as many times poorer as the BNP bird densities are lower than the English ones. Thus, if English dense bird populations do not completely exploit their food resources during the breeding season (BERTS 1955, LACK 1966, 1971 and others), then this is still less probable for the several times less dense BNP populations. It can also be added that the clutch sizes of some Białowieża birds are clearly larger than those of British populations (WESOŁOWSKI 1980, 1983).

Other facts also contradict the possibility of shortage of food resources in BNP:

(a) The year-to-year fluctuations of the insectivores guild, or of the majority of insectivorous species, show evident lack of coincidence with the index of caterpillar abundance (Figs 8 and 9).

(b) In a few carefully studied bird species (*Phylloscopus sibilatrix*, *Ph. collybita*, *Troglodytes troglodytes*) no cases of nestling starvation were noticed, even in low-caterpillar years (WESOŁOWSKI 1980, 1983, unpubl.).

(c) Even the removal of several *Phylloscopus sibilatrix* males did not cause nestling starvation, as the lone females were able to feed them at a satisfactory rate (WESOŁOWSKI 1980). This is valid at least for the optimal habitat and the high abundance of caterpillars.

(d) It is usually assumed that polygyny develops at superabundance of food (VERNER and WILLSON 1966, von HAARTMAN 1969, WITTENBERGER 1976), hence, its regular occurrence in BNP deciduous stands (WESOŁOWSKI 1980, 1983) is of importance for this discussion.

The above listed arguments allow one to expect that also interspecific competition for food during the breeding season cannot act as a factor limiting breeding populations in BNP. Almost ideally parallelly, not compensatorily, fluctuating numbers of some closely related species (*Turdus merula* and *T. philomelos*, or *Ficedula albicollis* and *F. hypoleuca* — Fig. 9) confirm this opinion. The more so as in spite of our efforts no cases of undisputable interspecific territorial aggression, other than combats for nest sites or females, were noticed. The switching of *Dendrocopos*, *Garrulus glandarius* to feeding on caterpillars, not infrequent even in caterpillar low abundance years, also suggest some superabundance of this resource at that time.

It is therefore concluded that neither interspecific competition, nor shortage of food resources set the upper limit for the bird density in BNP. This conclusion is in accordance with the situation found by WIENS and ROTENBERRY (1979) and ROTENBERRY (1980) in North-American grasslands, by ROSENBERG *et al.* (1982) in riparian woods. Also ALATALO (1981) excludes the possibility of strong interspecific competition during the breeding season among woodland birds of northern Finland.

Predation pressure and nest sites. Quite consciously the nest sites are discussed jointly with predation, because following TOMIAŁOJĆ (1980a) we claim that the number of nest-sites is mainly the function of predation pressure, *i.e.* that predation determines what fraction of physically and microclimatically suitable nesting places will become acceptable as "safe nest sites". In this context predation pressure is viewed as a very important evolutionary force shaping bird requirements and even deciding about the carrying capacity of the habitats (understood here in terms of the number of safe or well-hidden nest places).

Keeping in mind what has been said above, the shortage of nest-sites in its classical sense, as a source of bird number limitation, should be evaluated. It is convenient to use the best known case of hole-nesters.

The idea that the carrying-capacity of a habitat is set by the availability of holes conflicts with the following data:

(a) At least old deciduous stands contain large amount of natural holes: up to 50 holes/10 ha (LUDESCHER 1973), 155 (EDINGTON and EDINGTON 1972) or 170 (KNEITZ 1961). There are no reasons to suppose that BNP climax stands so rich in dead timber are poorer in this respect, the more so as a special study in BNP has shown a density of c. 780 holes per 10 ha, including those obviously unsuitable (A. SZYMURA unpubl.). Yet the overall hole-nester densities in BNP reach only 22.5 p/10 ha, or 38 p/10 ha at the forest-edge if *Sturnus vulgaris* is included.

(b) Numerous holes in BNP are exploited only in some years and remain unoccupied in others (A. SZYMURA unpubl.), while in urban parks most holes are occupied almost each year (TOMIAŁOJĆ unpubl.).

(c) *Sturnus vulgaris* occurs almost exclusively along the forest edge, while the densities of woodpeckers excavating holes are similar at the forest edge and in the forest interior. In spite of this, forest-interior densities of hole-nesters other than *Sturnus vulgaris* are not higher but lower than those at the forest-edge.

(d) Rather frequent cases of hole-nesting were found for unspecialized breeders: *Erithacus rubecula*, or more rarely for *Turdus merula* and *Troglodytes troglodytes*.

The experiments with providing nest-boxes in BNP (WALANKIEWICZ, WOLK unpubl.) did not cause a significant increase in numbers of any species in coniferous and ash-alder stands. The only species showing a positive response were *Sturnus vulgaris* at the forest edge, and *Ficedula albicollis* and *F. hypoleuca* in the oak-hornbeam forest. However, in the case of *Ficedula* flycatchers it would be premature to state that they were earlier limited by the shortage of holes, because it has been shown by van BALEN *et al.* (1982) that even when natural holes are superabundant *Ficedula hypoleuca* in Holland strongly prefers nest-boxes and breeds almost exclusively in them.

Almost total absence of response of Białowieża Forest tits, even *Parus major*, to the erecting of nest-boxes deserves special attention. It is well known

that most other European populations of tits, either British, western and central European, or eastern European ones (e.g. NOVIKOV 1959), frequently occupy artificial nest-sites and dramatically increase in numbers even in coniferous stands (e.g. LÖHRL 1977). Against such a background the behaviour of Białowieża populations is clearly mysterious. Judging from the results of studies on hole-nester competition for nest-boxes (BUSSE and GOTZMAN 1962) one could suspect that the low density of Białowieża tits results from their overcompeting by two aggressor-species *Ficedula albicollis* and *F. hypoleuca*. This is not so, however, as tits do not occupy, as a rule: a) many nest-boxes distributed in coniferous stands where flycatchers are almost absent, and b) nor those in deciduous forest-interior fragments which had been left unoccupied by flycatchers and other serious competitors absent, like *Passer montanus* and *Jynx torquilla*, or recently declining like *Sturnus vulgaris*.

Summing up, low hole-nester densities (Table 18) found in climax stands of BNP cannot result from limitation by the shortage of physically suitable nesting sites. This agrees well with the VLADYSHEVSKI's (1975) claim that holes were clearly superabundant in the undisturbed forest along the Angara river (Siberia).

The finding that the number of holes has not a limiting effect on the abundance of hole-nesters does not mean that all of them are equally suitable for nesting (dry, safe), to eliminate competition completely. In fact, only in this particular group of birds several aggressive encounters have been noticed in BNP: *Sturnus vulgaris* versus *Sitta europaea*, *Sitta europaea*/*Parus major*, *Parus major*/*Ficedula albicollis*, or *Ficedula albicollis*/*F. hypoleuca*. How frequently such competition occurs, and what are its consequences, it remains to be studied. One can suggest, however, that this factor could rather influence the relative abundance of the particular species within a hole-nesting guild (e.g. limit the number of some subordinate species), than to set the carrying-capacity of a habitat for the whole guild.

While we failed to find convincing evidence indicating a limiting effect of breeding season food resources on bird reproduction in BNP or on their abundance, as regards predation, we are able to confirm that this factor plays an important role in reducing the reproduction rates of Białowieża birds. This point will be discussed in detail in several specialized studies to be published separately. Here, it can be said only briefly that, e.g. the breeding success in *Phylloscopus sibilatrix* reaches only 13–45%, depending on the year, and in *Troglodytes troglodytes* it fluctuates around 40% (WESOŁOWSKI 1980, 1983). All *Columba palumbus* nests found till now (14) failed to produce young. The preliminary data for *Fringilla coelebs*, *Turdus merula* and *T. philomelos* suggest that in several years their breeding success was lower than 30% (Białowieża nest-record scheme). Similarly, the intensive searching for families during the second half of June gives an impression of a remarkably low percentage of successful pairs. E.g. in *Fringilla coelebs*, apart from years with a heavy

outbreak of caterpillars, young on wing were recorded usually only in 3–5 places out of c. 40 pairs known to occur in a plot. Young *Columba palumbus* on wing were noticed only twice during the five-year period of studies. Noisy *Parus* families were recorded in numbers close to 40% of those known for territorial pairs, *etc.*

These values are well below those given for the same species or for similar temperate species in several other studies conducted mostly in man-transformed or -influenced habitats of Europe (LACK 1966, RICKLEFS 1969, TOMIAŁOJĆ 1980a, WESOŁOWSKI 1983).

These data suggest that in a primaeval forest predation pressure is much stronger than in other areas studied till now. In view of this it can be expected that several antipredator adaptations will be rewarded especially strongly. Wide scattering of nests in a habitat was frequently considered as one of the most common and important anti-predator escapes (*e.g.* LACK 1968, HORN 1968, CODY 1971, TOMIAŁOJĆ 1980a) and was tested experimentally (TINBERGEN *et al.* 1967, ANDERSSON and WIKLUND 1978). In view of this the low density of breeding birds in BNP can also be explained in the simplest way as a primaeval adaptation to the presence of a species-rich and abundant group of predators using diverse techniques of attacking (see description of the study area), well exceeding those from the majority of other European woods and forests studied ornithologically.

Additional strong support for such an explanation comes from the studies carried out in habitats devoid of or poor in predators, *e.g.* from islands (LACK 1968, WELLER 1980), human settlements (TOMIAŁOJĆ 1980, 1980a), or from sites inaccessible to predators because of active defence (LACK 1968, SLAGSVOLD 1980, DYRCZ *et al.* 1981). In all such cases two features opposite to those found in BNP are evident: a much higher breeding density than in the equivalent places accessible to predators, and a clearly higher production of young.

Final remarks. The above analysis of several possibilities and of the role of several possible factors has led us to the conclusion that the overall bird density level in BNP forests can be explained in the most satisfying way as being the result of a combined action of two phenomena:

(a) Undersaturation of some species populations, *i.e.* too low numbers of individuals starting to breed in relation to the carrying capacity of a habitat. This can result from the limitation by several factors but always executed before the current breeding season (on winter grounds or migration, as well as because of too low production in the previous season).

(b) Low carrying capacity for those species which saturate the BNP habitats, with the predation pressure being the main factor evoking the widely scattered distribution of prey populations.

A more accurate evaluation of the proportions between these two phenomena (*i.e.* how many populations, and which ones precisely, belong to the particular

categories) is not possible at present and should be the subject of future field studies and experiments. One can only suggest, for example, that much higher densities found in other places of Europe reflect different proportions between the relative importance of these two phenomena. Much more species seem to saturate those other habitats, which remains in agreement with a much milder winter climate and absence of migration, and with a generally lower predation pressure in man-transformed landscapes of western Europe. A more comprehensive analysis of the differences existing between several regions of Europe, with emphasis laid on anthropogenic transformations, lies outside the frames of this paper and will be presented elsewhere.

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STRESZCZENIE

[Lęgowe zgrupowania ptaków w pierwotnych lasach Białowieskiego Parku Narodowego.]

W latach 1975–79 przeprowadzono coroczne cenzusy ptaków lęgowych na łącznej powierzchni 260–358 ha Białowieskiego Parku Narodowego (BPN), stosując kombinowaną odmianę metody kartograficznej. Badano tylko klimaksowe stadia trzech głównych siedlisk leśnych: olsu-łęgu, grądu i boru mieszanego. Rozmieszczenie powierzchni próbnych przedstawiono na ryc. 1, a wyniki cenzusów w tabelach 1–13. Stwierdzone łączne zagęszczenie ptaków lęgowych wahało się od 27,4 p/10 ha w borze do 105,5 p/10 ha w łęgu przylegającym do skraju lasu, przy najczęstszych wartościach w granicach 50–70 p/10 ha. Gęstość populacji zdecydowanej większości gatunków nie przekraczała 3 p/10 ha. Zdumiewająco niskie okazało się łączne zagęszczenie dziuplaków: 4,6 p/10 ha w borach, 22,3 p/10 ha w grądach i maksymalnie 36,2 p/10 ha w łęgu przy brzegu lasu (tab. 18). Szczególny wpływ na ten wynik miała bardzo niska liczebność sikor, kontrastująca z dość obfitym występowaniem muchołówek, *Ficedula* spp.

Analiza materiału wykazała, że we wszystkich trzech typach siedlisk występuje zasadniczo jedno zgrupowanie ptaków (tab. 14), tworzące jedynie dość słabo wyróżniające się odmiany: zubożoną w borach, a wzbogaconą jakościowo i ilościowo w łęgach na skraju lasu. Stabilna w przebiegu lat struktura zbiorowisk ptasich wykazywała większe wahania roczne w siedlisku najuboższym, a mniejszą zmienność składu w siedliskach bogatych w gatunki (tab. 20).

Położenie powierzchni na skraju lasu podwyższało liczbę gatunków o około 30 %, a łączne zagęszczenie o 25–33 % (tab. 16). W strefie styku lasu z terenem otwartym nie stwierdzono podwyższenia zagęszczenia właściwych gatunków leśnych.

Analizując zagęszczenie różnych grup ptaków (tab. 17 i 18), dostrzeżono istnienie paralelizmu między złożonością strukturalną siedliska a liczebnością ptaków, co może oznaczać zarówno istnienie zależności troficznych, jak i typu drapieżnik-ofiara.

U gatunków prawdziwie leśnych (wnętrza lasu) dostrzeżono obecność konserwatywnych cech w ich ekologii, które gatunki te utraciły w przypadkach zasiedlania bardziej rozczłonkowanych lasów lub krajobrazu antropogenne, np. gniazdowanie *Apus apus* w lasach, a *Turdus merula* w półdziuplach, czy też zbieranie pokarmu prawie wyłącznie w obrębie lasu zamiast wylatywania na tereny otwarte: *Buteo buteo*, *Pernis apivorus*, *Columba palumbus*, *Turdus merula* itp.

Podobnie jak w białowieskich borach, także w liściastych drzewostanach Puszczy Białowieskiej łączne zagęszczenie ptaków jest nieco wyższe w niezaburzonych drzewostanach BPN, niż w pobliskich lasach zagospodarowanych, choć różnica ta jest niewielka.

Na tle danych z Europy, drzewostany liściaste BPN odznaczają się nadzwyczaj niskim łącznym zagęszczeniem ptaków, zwłaszcza dziuplaków. Cecha ta wydaje się oznaczać stan pierwotny. Przykłady równie niskich zagęszczeń w rozleglejszych lasach Burgundii czy New Forest w Anglii sugerują, że dawniej niskie zagęszczenia dominowały również w Europie Zachodniej, a spotykane obecnie bardzo wysokie zagęszczenia są cechą wtórną.

Niskie zagęszczenia ptaków lęgowych stwierdzone w tak bujnym i wielowarstwowym siedlisku leśnym jak lasy BPN, autorzy wyjaśniają tymczasowo jako wynik współdziałania dwóch czynników. Pierwszym z nich jest zjawisko niewysycania siedliska przez liczną grupę gatunków, reprezentowanych przez bardzo niewielkie populacje. Drugim czynnikiem, działającym głównie u gatunków wysycających siedlisko (co sprawdzono w kilku przypadkach za pomocą eksperymentów usuwania terytorialnych samców), zdaje się być występowanie rozrzedzenia populacji, jako adaptacji wytworzonej w warunkach silnej presji drapieżnictwa. Hipoteza ta będzie sprawdzana w serii prac szczegółowych, wykonanych na kilku gatunkach modelowych.

APPENDIX

A classification of birds breeding in the Białowieża National Park, according to feeding, nesting and migratory habits.

Feeding habits: O – foraging outside the forest independently of the feeding method; P – predators on vertebrates; V – vegetable food, mainly buds or seeds; I – feeding on invertebrates. The last category is subdivided according to places of food collection among bark foragers – IB, birds foraging on the ground or in the herb layer – IG, and birds collecting food from leaves, small twigs and/or in the air – IL

Nesting habits: G – ground nesting, open or domed nests on the ground or in vegetation up to 1.5 m high; C – crown nesting, open nests in bushes or in trees above 1.5 m high; H – hole nesting, all holes independently of the height are included in this category.

Migratory habits: T – tropical migrants, species wintering south of Sahara; S – short-distance migrants, species wintering in SW Europe and North Africa; R – resident species only of local movements and irruptions; true forest residents (RF), the last species stay the whole year in their breeding habitats

Species	Feeding habits	Nesting habits	Migratory habits
1	2	3	4
<i>Ciconia nigra</i>	O (0,8), P (0,2)*	C	T
<i>Anas platyrhynchos</i>	O (0,5), IG (0,5)	G	S
<i>Pernis apivorus</i>	O (0,9), IG (0,1)	C	T
<i>Milvus migrans</i>	O	C	T
<i>Accipiter gentilis</i>	P	C	R
<i>Accipiter nisus</i>	P	C	R
<i>Buteo buteo</i>	O (0,1), P (0,9)	C	R
<i>Aquila pomarina</i>	O (0,9), P (0,1)	C	T
<i>Tetrastes bonasia</i>	V	G	RF
<i>Tringa ochropus</i>	IG	C	T
<i>Scolopax rusticola</i>	IG	G	S
<i>Columba palumbus</i>	O (0,1), V (0,9)	C	S
<i>Columba oenas</i>	O (0,6), V (0,4)	H	S
<i>Streptopelia turtur</i>	O	C	T
<i>Cuculus canorus</i>	IL	—**	T
<i>Glaucidium passerinum</i>	P	H	RF
<i>Strix aluco</i>	P	H	RF
<i>Apus apus</i>	O (0,9), IL (0,1)	H	T
<i>Upupa epops</i>	O	H	T
<i>Jynx torquilla</i>	O (0,5), IG (0,5)	H	T
<i>Picus canus</i>	O (0,9), IG (0,1)	H	R
<i>Dryocopus martius</i>	IB	H	FR
<i>Dendrocopos major</i>	V (0,4), IB (0,5), IL (0,1)	H	R
<i>Dendrocopos medius</i>	IB (0,9), IL (0,1)	H	RF
<i>Dendrocopos leucotos</i>	IB	H	RF
<i>Dendrocopos minor</i>	IB (0,9), IL (0,1)	H	RF
<i>Picoides tridactylus</i>	IB	H	RF
<i>Anthus trivialis</i>	IG	G	T
<i>Motacilla alba</i>	O (0,9), IG (0,1)	G	TR
<i>Oriolus oriolus</i>	IL	C	T
<i>Sturnus vulgaris</i>	O (0,8), IG (0,1), IL (0,1)	H	S
<i>Garrulus glandarius</i>	P (0,4), V (0,2), IG (0,1) IL (0,3)	C	R

1	2	3	4
<i>Nucifraga caryocatactes</i>	V	C	RF
<i>Corvus corone</i>	O (0,9), P (0,1)	C	R
<i>Corvus corax</i>	O (0,9), P (0,1)	C	R
<i>Troglodytes troglodytes</i>	IG	G***	S
<i>Prunella modularis</i>	IG (0,8), IL (0,2)	G***	S
<i>Locustella fluviatilis</i>	IG	G	T
<i>Acrocephalus palustris</i>	IG	G	T
<i>Hippolais icterina</i>	IL	G (0,25), C (0,75)	T
<i>Sylvia borin</i>	IG (0,8), IL (0,2)	G	T
<i>Sylvia atricapilla</i>	IG (0,5), IL (0,5)	G (0,71), C (0,29)	S
<i>Sylvia communis</i>	IG	G	T
<i>Phylloscopus trochilus</i>	IG (0,2), IL (0,8)	G	T
<i>Phylloscopus collybita</i>	IG (0,1), IL (0,9)	G	S
<i>Phylloscopus sibilatrix</i>	IL	G	T
<i>Phylloscopus trochiloides</i>	IG (0,2), IL (0,8)	G	T
<i>Regulus regulus</i>	IL	C	R
<i>Regulus ignicapillus</i>	IL	C	S
<i>Ficedula hypoleuca</i>	IL	H	T
<i>Ficedula albicollis</i>	IL	H	T
<i>Ficedula parva</i>	IL	C	T
<i>Muscicapa striata</i>	IL	G (0,25), C (0,75)	T
<i>Phoenicurus phoenicurus</i>	IG (0,5), IL (0,5)	H	T
<i>Erithacus rubecula</i>	IG	G (0,66), H (0,34)	S
<i>Luscinia luscinia</i>	IG	G	T
<i>Turdus merula</i>	IG (0,9), IL (0,1)	G (0,2), C (0,8)	S
<i>Turdus iliacus</i>	IG	G (0,5), C (0,5)	S
<i>Turdus philomelos</i>	IG (0,8), IL (0,2)	C	S
<i>Aegithalōs caudatus</i>	IL	C	RF
<i>Parus palustris</i>	IG (0,2), IL (0,8)	H	RF
<i>Parus montanus</i>	IL	H	RF
<i>Parus cristatus</i>	IL	H	RF
<i>Parus ater</i>	IL	H	RF
<i>Parus caeruleus</i>	IL	H	R
<i>Parus major</i>	IG (0,5), IL (0,5)	H	R
<i>Sitta europaea</i>	V (0,2), IB (0,8)	H	RF
<i>Certhia familiaris</i>	IB	H	RF
<i>Fringilla coelebs</i>	V (0,2), IG (0,1), IL (0,7)	C	S
<i>Carduelis chloris</i>	O (0,9), V (0,1)	C	R
<i>Carduelis spinus</i>	V	C	R
<i>Carduelis carduelis</i>	O	C	R
<i>Carpodacus erythrinus</i>	O	G	T
<i>Loxia curvirostra</i>	V	C	R
<i>Pyrrhula pyrrhula</i>	V (0,9), IL (0,1)	C	R
<i>Coccothraustes coccothraustes</i>	V (0,6), IL (0,4)	C	R
<i>Emberiza citrinella</i>	O (0,9), IG (0,1)	G	R

*As regards the species whose manner of feeding or nesting could not be included unambiguously into one category, an approximate frequency of their feeding or nesting in the particular categories was given.

**Brood parasite, not included into the classification.

***About 30 % of nests of *Troglodytes troglodytes* and *Prunella modularis* were situated above 1.5 m high, but as almost all such nests were placed in the root systems of fallen trees, they are classified as ground nesters.

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Abstrakt (w 3 egzemplarzach, z podanym na końcu adresem) należy napisać na osobnych kartkach papieru.

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Pozycje literatury cytuje się w tekście prac, podając nazwisko autora i rok wydania, np. Maciejewski (1969), (Maciejewski 1969), przy więcej niż dwóch autorach: Kowalski et al. (1972), (Kowalski et al. 1972). Cytując kilka prac jednego autora wydanych w tym samym roku, należy oznaczyć je literami a, b itd., stawianymi za rokiem wydania. Cytując kilku autorów, należy ich umieścić w kolejności lat publikacji. Cytuje się wyłącznie prace wydrukowane lub przyjęte do druku, wszystkie inne podaje się jako "materiały niepublikowane" i nie umieszcza się w spisie piśmiennictwa (w tekście należy podać tylko nazwisko ich autora).

Spis piśmiennictwa powinien zawierać tylko pozycje cytowane w pracy, ułożone w porządku alfabetycznym wg nazwisk pierwszych autorów (wzór — patrz wersja angielska Wskazówek). Skróty tytułów czasopism należy podawać wg pracy J. Roźnowskiej-Feliksiakowej "Wydawnictwa ciągłe w Bibliotece Instytutu Zoologii Polskiej Akademii Nauk" lub wg "World List of Scientific Periodicals", Butterworths, London. Skróty tytułów czasopism polskich podawać wg pracy Borowiec M., Wesolowski T. 1981. *Polska bibliografia ornitologiczna II. Lata 1961-1970*. Acta orn. 18: 5-140.

Wszystkie tabele i ryciny (rysunki, wykresy, mapy, fotografie — w skrócie ryc.) muszą być przygotowane osobno (nie w tekście). Tabele i ryciny powinny mieć osobną arabską numerację. Każda tabela powinna być napisana na osobnej stronie, zaopatrzona w numer, tytuł oraz wszelkie niezbędne objaśnienia. Ryciny mogą być wykonane tuszem (na kalce technicznej albo białym kartonie) lub ołówkiem na papierze milimetrowym. Wszelkie napisy na rycinach należy wykonywać ołówkiem.

Liczbę rycin, zwłaszcza fotografii, należy ograniczyć do niezbędnego minimum. Należy unikać dużych tabel nie mieszczących się na jednej stronie (wymiar strony druku 13,5 × 20 cm). Przygotowując ryciny, należy pamiętać, że w czasie kliszowania będą one zmniejszone dwu-, trzykrotnie. Objasnienia do tabel i rycin muszą być przejrzyste i w zasadzie umożliwiać ich zrozumienie bez odwoływania się do tekstu. Na samej rycinie umieszczać jak najmniej napisów, przenosząc je w podpis.

Autor zobowiązany jest do przepisania tekstu lub pokrycia kosztów przepisania po poprawkach redakcyjnych. Obowiązuje go także wykonanie jednej korekty bez prawa wprowadzania zmian w stosunku do tekstu zatwierdzonego do druku. Autor otrzymuje bezpłatnie 25 odbitek. Dodatkowe odbitki (25, 50 lub 75) można zamówić na koszt własny przy składaniu maszynopisu.

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