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Bird community dynamics in a primaeval forest - is interspecific competition important?

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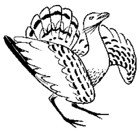

Views on the role of interspecific competition in shaping the structure and dynamics of bird communities vary widely, from negligible impacts on one hand, to being the leading ecological and evolutionary force, producing highly structured communities on the other. What role has this factor played in forming pristine European forest bird communities? Data collected in the primaeval temperate forest, the Białowieża National Park (E Poland) over a period of 25 years are used to answer this question. The bird community of the Białowieża Forest was composed of numerous species, usually breeding at low densities. Food resources and nest sites were usually superabundant, but production of young remained low, due to heavy nest predation. The population sizes of individual species/guilds changed either independently of each other or in parallel. These results indicate that interspecific competition has apparently been of minor importance in the primaeval conditions. This remains in sharp contrast to its frequently dominant role observed in secondary woods that contain nest boxes. The implications of these findings for our understanding of biological processes are discussed.

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1. Introduction

Deciduous and deciduous-coniferous forests of the temperate zone have undergone extermination, fragmentation or deep transformation well before the origin of ornithological research. Our knowledge of forest bird biology in pristine conditions is therefore full of gaps or misinterpretations. Consequently, research conducted in remnants of the ancient lowland temperate forests is of utmost importance and provides the reference points or baseline against which comparisons can be made with data collected in habitats transformed by human activity. This principle lay behind the decision to launch in 1975 a programme of ornithological studies in the Białowieża Forest, in which the last fragments of European primaeval temperate lowland forest are to be found. It was hoped that the old-growth primaeval forest stands preserved in the strictly protected part of the Białowieża National Park (BNP) would constitute 'a window into the past' through which one would gain insights into the ecology of pristine temperate plant and animal communities. The aims of the studies were to describe patterns found in primaeval forest breeding bird communities and to understand the ecological and behavioural processes generating the patterns.

To achieve these broadly defined goals, data on breeding bird densities were gathered in permanent study plots distributed in all types of old-growth stands in the

BNP. Censuses, using a modified 'combined mapping' technique (Tomiałojć 1980a; a method of producing near-absolute estimates), were repeated every year from 1975, producing a 25+ year data series. In addition to data on birds, information was gathered also on the variation in those environmental variables that might be relevant, such as weather, leaf-eating caterpillars, tree seed crops, holes and small mammals. The results of the first 20 years of census work have been summarised in a series of papers (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990, 1994 and 1996; Wesołowski & Tomiałojć 1997). In addition to this long-term community-wide approach, population studies of 12 individual species were carried out for shorter periods (see list of References); their results allowed one to gain better insights into processes that could have generated the observed patterns.

In the mid-1970s when the project began, the unitarian 'competitive' view of bird communities (as equilibrial, stable, strongly interacting units), as marshalled by MacArthur (1972) and his followers, prevailed. The opposing 'individualistic' model (communities non-equilibrial, comprised of loosely-knitted sets of species, changing numbers independently of one another, individuals responding to a varying array of factors) was rather uncommon (reviewed in Wiens 1989). Current views of animal community structure are much more pluralistic (McIntosh 1995), recognising that different processes can interact in shaping the structure and dynamics of communities. The pure 'equilibrial' and 'individualistic' models are now treated as special cases, lying at opposite ends of the continuum.

Results from bird studies in European woodlands transformed by human activity demonstrate that interspecific competition, both exploitation and interference types, can be common there. Interspecific competition is especially important in shaping numerical relationships among hole-nesting birds (reviewed in Newton 1998). Does this picture hold also true under the conditions prevailing in the BNP? How important has been proximately acting interspecific competition in forming breeding bird communities in pristine European forest? I shall come to these questions after introducing the Białowieża Forest and its breeding avifauna.

2. Białowieża Forest

The Forest is situated on the border between Poland and Belarus. Of its total area of 1250 km^2, some 580 km^2 belong to Poland. The geographic co-ordinates of Białowieża village (52°41'N, 23°41'E) correspond to the latitudes of Berlin and London. The climate is subcontinental, producing long snowy winters, the snow cover lasting usually for about three months, although almost snowless winters occasionally do occur. Biogeographically the Forest falls within the mixed forest (deciduous-coniferous) zone that contains a significant amount of native Norway spruce *Picea abies* in almost all types of tree-stands. For more detailed description, see Faliński (1968, 1986), Tomiałojć (1991), Tomiałojć *et al*. (1984), Tomiałojć & Wesołowski (1990, 1994) and Jędrzejewska & Jędrzejewski (1998).

The Białowieża Forest constitutes a remnant of the vast European lowland forests that once extended across the continent. Probably being the least changed remnant, it contains the largest amount of pristine features of any forest complex existing in temperate Europe, its relatively good state of preservation stemming from a long chain of fortunate historical events. Though people have inhabited the Białowieża Forest region since Neolithic times, colonisation of the forest complex proper became more intensive from only the 10th century onwards (Faliński 1968). Large-scale timber extraction in the Forest did not begin until the 1914-18 World War. Nevertheless, even by 1921, a 47.5 km^2 patch of the most diversified and best-preserved stands had been excluded from forestry use and declared a strictly protected nature reserve (currently within the BNP; see Tomiałojć & Wesołowski (1994) for details).

The old-growth stands preserved in the BNP are distinguished from those in other temperate forests by these features:

1. They are multi-storied, mixed-species and unevenly aged (the oldest trees dating from 1500-1600).
2. They contain trees reaching unusual heights (the tallest spruces reaching 57 m and several other species 42-45 m).
3. They contain a large amount of undisturbed dead timber and uprooted trees (the latter structures being very important as nesting substrates (review in Wesołowski & Tomiałojć 1995).

The study plots were situated in three main types of BNP forest habitats, upland deciduous woods of the oak-lime-hornbeam *Tilio-Carpinetum* type (44% of the BNP area) and swampy deciduous (22%) and coniferous stands (28%). Detailed descriptions of the habitats and plots studied in the BNP are given in Tomiałojć *et al.* (1984), Tomiałojć & Wesołowski (1990, 1994, 1996) and Wesołowski & Tomiałojć (1995).

3. Breeding bird community of the primaeval forest

So far, 111 forest and forest-edge species have been recorded breeding in the Białowieża Forest, 90 of them (81%) within its strictly protected part (47.5 km^2) (Tomiałojć & Wesołowski 1990, T. Wesołowski unpubl). Non-passerines, amongst which are eight raptor species, four owls, eight woodpeckers, Black Stork *Ciconia nigra*, Hazel Grouse *Bonasa bonasia* and Green Sandpiper *Tringa ochropus* form as much as 40% of the BNP avifauna. These values appear to be among the highest recorded for a single forest complex, especially when set against those pertaining to the equivalent western European forests (Tomiałojć & Wesołowski 1990).

Within the permanent census plots (total area 1.9 km^2) 84 breeding species have been recorded, 64 of them as annual breeders, and 20 additional and scarce species that have bred at least once since the mid-1970s. With minor exceptions, the species composition has not changed during the whole period (Tomiałojć *et al.* 1984, Tomiałojć 1995, T. Wesołowski unpubl). The number of species breeding within a single plot (sizes 25-33 ha) depended on habitat type and plot position. The highest number - total number of species was 72 (48-52 species/year) - was recorded in the riverine forest at the forest edge, followed by the oak-hornbeam plot at the edge - total number of species was 63 (40 species/year). In the first years of the study, deep in the forest interior, riverine habitat harboured more species (35) than did either oak-hornbeam (29-31) or coniferous habitats (26 species/year) (Tomiałojć *et al.* 1984). However, due to increasing species richness in coniferous habitat in the 1990s these differences ceased to exist, and since then all areas have held 33-36 breeding species annually (Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl).

As a rule, individual species bred in the BNP in low densities, only two species, Chaffinch *Fringilla coelebs* and Robin *Erithacus rubecula* exceeding a density of 5 pairs/10 ha regularly. Examples of species that achieved that level of abundance irregularly are Wood Warbler *Phylloscopus sibilatrix*, Collared Flycatcher *Ficedula albicollis*, Song Thrush *Turdus philomelos*, Hawfinch *Coccothraustes coccothraustes*, Blackcap *Sylvia atricapilla* and Starling *Sturnus vulgaris*, but not necessarily in all habitats. The remaining species occurred in much lower numbers, the mean density range being only 1.4-2.6 pairs/10 ha (Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl). Overall, the breeding densities of the above species in the BNP (see below) are much lower than those recorded in woods transformed by human activity, as they are also for several other species. Densities of Wren *Troglodytes troglodytes* and Dunnock *Prunella modularis* are *c*8 times lower, of Great Tits *Parus major* 10 times, Blackbirds *Turdus merula* 40 times and of Woodpigeon *Columba palumbus* as much as 400 times lower than the highest densities reported from secondary woods (Tomiałojć *et al.* 1977, 1984, Tomiałojć 1980b, Wesołowski 1983, Wesołowski *et al.* 1987).

The overall density of the bird community in the BNP was rather low, reaching only 100-110 pairs/10 ha in the most densely populated areas, 124 pairs/10 ha being the maximum value recorded in a single season (Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl). Densities declined from the forest edge to the interior and from deciduous to coniferous habitats. Densities in the latter, 35-50 pairs/10 ha, were always lowest (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl). In contrast to the late 1970s (Tomiałojć *et al.* 1984), bird community densities increased during the study period, the mean densities in all plots being higher by 13-38% by the late 1990s. These increases resulted from the simultaneous numerical growth of several species, such as Chaffinch, Collared Flycatcher, Blackbird and Marsh Tit *Parus palustris*. The tendency towards parallel changes in species that differ so much in their food requirements, nest sites, and migratory patterns suggests that a number of different causal factors had to be involved, as it would be difficult to conceive of a common denominator, a single factor which could account for all those increases. Neither reduced severity of winters, nor increased seed crops, rodent numbers, or caterpillar abundance (see below) showed long-term trends in the BNP, and so these could be ruled out as causes of the observed increases of bird numbers in the Forest (Wesołowski & Tomiałojć 1997, Wesołowski unpubl).

Irrespective of these temporal changes, in all habitat types, insectivores collecting invertebrates in tree crowns constitute *c*50% of the whole breeding community and ground insectivores (*c*30%) are the second most numerous group. In terms of nesting requirements, approximately half of bird species build open nests in tree crowns, one-third use holes, and the rest breed on the ground or just above it. Due to rather severe winters, short-distance (*c*50%) and tropical migrants (*c*25%) migrants form the bulk of the community (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl).

In summary, the BNP breeding bird community is composed of numerous species, but they usually breed in low to moderate densities. For some reason their numbers tend to change in parallel. Could interspecific competition account for these patterns? Are low densities caused by the proximate interspecific competition for limiting resources, such as the breeding season food supply or nest sites? These questions are explored below.

4. Food limitation and competition for food in the breeding season?

Birds collecting invertebrates from leaves and twigs form about 50% of bird assemblages in the BNP and leaf-eating caterpillars constitute a substantial part of their diet. Preliminary observations revealed that these caterpillars constituted 70% of Middle Spotted Woodpecker *Dendrocopos medius* nestling food (in 1978), 40-60% of food brought to Wood Warbler nestlings (in 1987-1988) (L. Jenni unpubl, R. Cisakowski unpubl), up to 80 % of Marsh Tit nestling food and 55% in the case of Nuthatch *Sitta europaea* (in 1998) (Rowiński & Wesołowski 1999). Tomiałojć (1994) observed that even for Blackbird, in which *Lumbricidae* formed the most important food source, the caterpillars still made up 14-32% of nestling diet in 1986-1989. Therefore, there are grounds to assume that variation in the caterpillar numbers should have a strong influence on the breeding birds. The defoliating *Operophtera brumata* caterpillars occurred usually in low numbers, their outbreaks, causing partial to total defoliation of deciduous trees, separated by 8-11 (Wesołowski & Tomiałojć 1997). However, in the intervening years smaller scale outbreaks of other species, providing alternative food sources, could occur (*e.g.* partial defoliation of *Acer platanoides* by *Ptilophora plumigera* caterpillars; Rowiński & Wesołowski 1999). If, as these observations suggest, apart from the few 'bonanza' years, food resources are relatively scarce for several successive years, we should expect to observe frequent food limitation in the breeding season, and signs of interspecific competition for food. These phenomena could find expression in:

1. Compensatory changes in numbers of would-be competitors.
2. Small clutches.
3. Frequent starvation of young.
4. Lack of resource defence polygyny.

Contrary to expectations, changes in numbers of birds in the BNP over the 25-year study period are mostly independent of variation in *Operophtera brumata* abundance, for numbers of but three of 13 crown insectivores were positively correlated with caterpillar abundance. Moreover, changes in numbers of congeners are most often independent of one another (*e.g.* Great Spotted *Dendrocopos major* and Middle Spotted Woodpeckers, Wood Warbler and Chiffchaff *Phylloscopus collybita*) or positively correlated (*e.g.* Pied *Ficedula hypoleuca* and

Collared Flycatchers, Blue *Parus caeruleus* and Great Tits, Blackbird and Song Thrush) (Wesołowski & Tomiałojć 1997, T. Wesołowski unpubl).

Starvation and strong brood reduction was found to be unimportant, even in the low-caterpillar years. The year-to-year variation in nesting success in the eleven primarily insectivorous species studied so far in the BNP was mostly due to predation (review in Wesołowski & Tomiałojć 1995, Wesołowski 2001, L. Tomiałojć unpubl, D. Czeszczewik unpubl). During a 12-year study of Marsh Tit, only in a single season, when cold and rainy weather arrested caterpillar development and the young were in nests ahead of maximum caterpillar availability, was a sharp increase in nest losses recorded that could be attributed to food shortage. However, even then, the impact of food shortage was only indirect (*e.g.* causing the young to beg louder), because in the main, broods were lost to predation or nest soaking and not to starvation (T. Wesołowski & P. Rowiński unpubl).

The clutch size of Białowieża birds was as large, or larger than the highest values recorded elsewhere (Wesołowski 1983, 1985, 1995, 2000; Piotrowska & Wesołowski 1989, Wesołowski & Stawarczyk 1991, Tomiałojć 1994); polygyny was found to be regular in several species in BNP habitats containing higher breeding densities (Wesołowski 1987). Usually 10-20% of bigamous males were recorded there, but in some years there could be up to 40% of bigamists (some even simultaneous trigamists) as found in a Wood Warbler oak-hornbeam area (plot C, 1978). Because none of the predictions has been confirmed, it seems justified to conclude that neither limitation by food shortage in the breeding season nor interspecific competition for food could be major forces shaping the structure and dynamics of insectivorous birds in this primaeval forest. It is not the equivalent of saying that food plays no role in shaping life of birds breeding there, but it stresses that food shortages alone cannot account for low overall breeding bird densities in the BNP.

5. Is competition for breeding holes important?

Secondary hole-nesters serve as a classic example of a group of species limited by shortage of nest sites, or interspecific competition (or both) (von Haartman 1971, Perrins 1979, van Balen *et al.* 1982, review in Newton 1994). The highest densities recorded in the BNP for this group were 30-40 pairs/10 ha (Tomiałojć & Wesołowski 1996, T. Wesołowski unpubl), values that are only just as high as those recorded for single species in nestbox areas, for example 40 pairs/10 ha for Pied Flycatcher (Tiainen *et al.* 1984) or 34 pairs/10 ha for Great Tit (Perrins 1979). Could low numbers in the BNP be due to shortage of holes and competition for this scarce resource? If so, then several phenomena should be visible:

1. Suitable holes are occupied every season.
2. Populations of potentially competing species change numbers in compensatory fashion.
3. Frequent interspecific aggression arises over holes and hole usurpation.
4. Only obligatory hole-nesters use holes.

By and large, the Białowieża results do not support these expectations. Different hole-nesting species changed their numbers in parallel or independently of each other (Wesołowski & Tomiałojć 1997). Furthermore, nest-holes are superabundant. Although, due to enormous technical difficulties (accessibility, safety) it has been impossible to produce data on hole density in the BNP, indirect conservative estimates of hole availability clearly indicate their excess. Collared Flycatcher, the most numerous species of hole-nesters in oak-hornbeam habitat (Tomiałojć & Wesołowski 1990), is the secondary hole-nesting species that breeds latest of all. In a detailed study carried out in 1989, Walankiewicz (1991) found that were at least 28 free holes/10 ha available for flycatcher selection. In other words, an average flycatcher female had at least two potential nest holes to choose from. Because all these flycatcher holes had been available to those species that had begun breeding earlier, early breeding species had at least 3 potential holes from which to select. These values represent minimum estimates because they include only the holes used by the birds in 1989 and it is known that birds are often irregular occupants of the numerous holes available (Wesołowski 2001, unpubl), even if one includes holes used by the facultative hole-nesters. Blackbirds breeding in holes were observed regularly in the BNP, almost 50% of their nests in oak-hornbeam habitat being in holes and semi-holes (Tomiałojć 1993). Moreover, Robin, Dunnock and Wren also used holes regularly.

Interspecific aggressive encounters and hole usurpation of one species by another were recorded in the BNP (Tomiałojć *et al.* 1984) but their frequency was quite low. For example, in a three-year study of Nuthatch based on over 160 broods (Wesołowski & Stawarczyk 1991) no case of hole-usurpation was recorded. Similarly no Collared (n=534) or Pied Flycatcher (n=159) males were killed while prospecting for holes. Hybridisation between Collared and Pied Flycatcher (though at only 0.4%, is nevertheless regular) is probably better understood in terms of competition for mates than as a by-product of competition for holes (Walankiewicz & Mitrus 1997, Czeszczewik & Walankiewicz 1999).

All these observations lead one to conclude that the low hole-nesting densities found in primaeval stands of BNP cannot result from limitation by the shortage of nest sites. Therefore, reports from other areas of the effects of nest hole shortages on limiting bird numbers and of strong interspecific competition for holes seem due mostly to by-products of human-induced habitat transformations, and not due to factors that are relevant in primaeval conditions.

6. Other possible mechanisms

As shown in the previous chapters, breeding bird densities in the BNP usually remain below levels set by food or nest site availability. Furthermore, proximately acting interspecific competition is of rather minor importance. Therefore, the Białowieża data, do not offer much support to the idea of equilibrial, saturated, strongly competitively interacting bird communities (Lack 1971, MacArthur 1972). The Białowieża breeding bird community seems to be better described by the 'individualistic' community model (Wiens 1989, McIntosh 1995). If not shortage of resources, then what keeps densities low in the BNP? Several mechanisms can be involved, such as:

1. Undersaturation, or too few birds settling in spring to occupy all the available space.
2. Density limitation by territorial exclusion.
3. Low productivity due to high nest predation.
4. The effects of events outside the Białowieża Forest.

Undersaturation can be common among breeding birds in BNP. It is possible that most of scarce and irregular breeders are permanently unable to fill space, though it is impossible to prove that the unoccupied areas really are suitable for them (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990). The year-to-year changes in distribution of territories, without any corresponding change in habitat structure, demonstrate this phenomenon much better. For example, densely packed Wood Warbler territories filled plot C in 1978 (21 territories), whereas in 1983 this area was almost empty (3 territories) (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1994). Similarly Great Tit in the low number years (Wesołowski *et al.* 1987) and Nuthatch, even in years of relatively high numbers (Wesołowski & Stawarczyk 1991), were not numerous enough for their territories to fill all the available space.

Saturation of habitats at low densities resulting from birds defending large territories is also clearly demonstrated in the BNP. Even birds as small as Wren, Chiffchaff or Marsh Tit can occupy territories covering 8-10 ha, their territory size in oak-hornbeam habit averaging up to 5 ha (Wesołowski 1983, Piotrowska & Wesołowski 1989, T. Wesołowski unpubl). The large territories in this habitat can to some extent reflect the distribution of necessary requisites, such as fallen logs (Wren) or canopy gaps (Chiffchaff), but the size can also improve males' chance of attracting a mate and, by spreading nests in space, can serve as antipredator device (Wesołowski 1987, Wesołowski *et al.* 1987).

Repopulation of plots after the experimental removal of territorial males (Wren, Great Tit and Wood Warbler) (Wesołowski 1981, Wesołowski *et al.* 1987, Wesołowski & Tomiałojć 1995) shows that if some males can be prevented from establishing territories, limitation of numbers by territorial defence can produce densities as low as 1.5 territories/10 ha.

For the majority of birds studied in the BNP so far (Wesołowski 1983, 1985, 1995, 1998; Piotrowska & Wesołowski 1989, Wesołowski & Stawarczyk 1991, Walankiewicz 1991, Walankiewicz *et al.* 1997, Tomiałojć 1994, Jędrzejewski *et al.* 1994), the overall nest loss rate amounted to 50-70%, occasionally rising to 76% (Wood Warbler) or dropping to 15% (Marsh Tit). For every one of these species, the Białowieża loss rates are equal to or higher than the highest values recorded for this species in other areas more transformed by human activity. Predation is responsible for at least 70-95% of nest losses. The impact of predation is greater if the timing of nest destruction is at a late stage of breeding, as is the case in the BNP, where they are destroyed mostly during the nestling period (Wood Warbler, Chiffchaff, Wren, Nuthatch, Marsh Tit), when the majority of energy investment necessary for rearing a brood has already been input, and when much of the time which otherwise could have been devoted to rearing a replacement brood had been wasted. In other areas, the maximum rate of nest predation does not occur during the nestling period. In consequence of the heavy predation pressure in the BNP, the production of young per breeding pair (and especially the production of young per unit area) is usually very low, sometimes being an order of magnitude lower than recorded in other areas (Wesołowski 1983, Wesołowski *et al.* 1987). The depressed productivity, even without heavy mortality in the intervening non-breeding season, translates into fewer potential recruits each following spring. In turn, this could result in undersaturation and low breeding numbers.

The situation in the BNP as described above has been presented under the assumption that either there are no significant external inputs, or the changes of environmental factors in the Forest reflect their variability over larger areas. However, in spite of the BNP's relatively large area, birds breeding within it do not constitute fixed demographic units. Immigration of birds has contributed, at least in some years, to numerical increases in the highly variable Siskin *Carduelis spinus* and Wood Warbler, but its impact was discernible in some seasons on several other species whose rate of numerical increase in consecutive seasons could not always be accounted for by local production (Wesołowski & Tomiałojć 1997). One might expect emigration to occur in other years as well, though this would be more difficult to demonstrate. If events taking place outside the Forest were acting so strongly that the effects of local factors were swamped, the structure of the breeding community in the BNP could not be explained by analyses carried out solely within the BNP. This explanation seems scarcely to be applicable to Nuthatch (Wesołowski & Stawarczyk 1991) and other permanent Forest residents. But such species constitute only *c*10% of the breeding bird community in the BNP (Tomiałojć & Wesołowski 1996) and for the 90% of the population spending the winter outside the breeding areas, such a conjecture seems more plausible. However, if conditions in the non-breeding period were of the utmost importance for population dynamics, then one would expect species wintering in the same regions to have similar patterns of numerical change. This prediction, though, has not been corroborated (Wesołowski & Tomiałojć 1997). It would be premature to reject this hypothesis altogether, as migratory categories used in the analysis were quite broad, and species included in the same guild could have totally non-overlapping wintering ranges. Nevertheless, there is no evidence at the moment indicating that events in the non-breeding areas are the most influential in controlling bird numbers in the BNP (Wesołowski & Tomiałojć 1997).

7. Primaeval versus secondary forests

A comparison of features of bird communities from primaeval BNP stands with those in secondary forests shaped by human activities in other temperate areas of Europe reveals sharp differences between them (Tab. 1), yet both forest types are composed largely of the same tree species and are inhabited by the same bird species (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990,

Tab. 1. Major differences between primaeval and secondary temperate forests (modified after Tomiałojć *et al.* (1984), Tomiałojć & Wesołowski (1990).

	Primaeval	**Secondary**
Forest size	large, continuous	fragmented, isolated
Predator diversity	high	low
Availability of holes	excess	shortage
Species richness	high	low
Production of young	low	high
Density	low	high
Interspecific competition	seldom, insignificant	frequent, eminent

Tomiałojć 2000). The differences stem most probably from anthropogenic causes: in the secondary forests, a combination of fragmentation effects, a simplification of forest structure and widespread predator extermination. On one hand, the anthropogenic factors led to extinctions of more sensitive (large, specialised) species and thus to declining species richness. On the other hand they permitted the more productive populations of surviving species to burgeon, to increase numbers to a level at which limitation by resources and interspecific competition becomes important (Tomiałojć 1980b, 2000; Wesołowski 1983). The high productivity and high bird densities in the secondary woods seem to be characteristic of all habitats in which predator pressure is reduced (islands, colonies, some human settlements) and not characteristic features of temperate forest bird communities. As the Białowieża data clearly demonstrate, in the temperate zone and in pristine conditions, the forest bird communities have exhibited characteristics attributed usually only to tropical forests (high predation pressure, low densities, high species richness). This should be born in mind when one attempts large-scale intercontinental comparisons. For valid comparisons one should compare only the equivalent states. It seems best to avoid drawing conclusions if data from primaeval tropical forest is equated with those gathered in fragmented secondary European woods.

The results discussed here underline the vital importance of the preservation of reference areas in which conditions and processes characteristic of a pristine state can be preserved (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1990, Angelstam *et al.* 1997, Tomiałojć 2000). To ensure this, the whole Białowieża Forest should be preserved. Unfortunately, the BNP protects only *c*15% of the Polish part, the remaining parts being commercially managed. Worse still is that logging is concentrated in the last remnants of old-growth stands of natural origin.

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