Primeval conditions – what can we learn from them?

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In this paper I argue that prehistoric British forests and their avifauna were similar to those persisting in a near-primeval condition in the Białowieża Forest (Polish/Belarussian border). Therefore, observations in the Białowieża Forest may serve as a baseline against which effects of changes in the British woods can be assessed. The results of long-term (30 years) studies of the breeding birds in the Białowieża National Park are summarized. They reveal that the local avifauna shows some features (high species richness, low population densities, high nest predation and low production of young) regarded as typical for undisturbed tropical forests. It is proposed that high productivity, high population densities and sedentary habits found in many British populations are to a large extent a recent phenomenon, due to forest fragmentation, reduction of predator diversity and changes in forest structure. The necessity to preserve the whole Białowieża Forest – currently seriously threatened by ongoing logging – as a benchmark for future biological studies is underlined.

Some 6000 years ago in the Mesolithic period, Britain was almost completely covered by continuous forests, inhabited by numerous – now nationally extinct – species of large predators and herbivores (Table 1). Therefore, in the pristine state British woodland birds faced quite different living conditions from those experienced in the highly fragmented, island-like secondary woods of contemporary Britain. Which woodland species inhabited Britain then, how did they use these forests and what factors shaped their population dynamics? We do not know, because no patch of such forest has survived in Britain. Luckily, there is one location in Europe where the forests have retained their primeval features – the Białowieża Forest, situated on the Polish/Belarussian border. This forest can be used as ‘a window into the past’, through which one can gain insights into the ecology and adaptations of temperate forest birds in primeval conditions (Tomiałojć et al. 1984, Tomiałojć & Wesolowski 1990, Wesolowski 2003a, 2005). The question is whether the data collected in this distant location (c. 1500 km from Britain) are relevant to the British situation? After all, even without any human intervention, these two areas would differ in many respects. These natural differences, though, appear much less pronounced than one could envisage. As shown in Table 1, the pristine British woods were inhabited largely by the same species and shaped by the same processes as operating in the Białowieża Forest. Apart from Britain being an island the only major discernible difference is climatic; although the Białowieża Forest is situated at the latitude of England, it has much colder winters with long-lasting snow cover due to its more continental location (see below). Keeping this difference in mind, I believe that the similarities between the areas are strong enough to justify using the Białowieża data as a model representing past conditions in pristine British woods.

I begin the paper with a brief description of the Białowieża Forest and of the long-term ornithological studies there, continue with documentation of patterns of species richness and birds’ densities in a primeval situation, depict possible processes responsible for the recorded patterns and contrast these findings with the data from British woods. I conclude with the general presentation of a primeval forest syndrome. Last, but not least, I describe threats to this unique forest and underline an urgent need to preserve it.

THE BIAŁOWIEŻA FOREST

The Białowieża Forest is located at the border between central and eastern Europe, in the middle of
the vast European lowlands, approximately at the same latitude as London (the Białowieża village coordinates are: 52°41′N, 23°52′E). Part of the Forest (613 of 1500 km²) belongs to Poland and the remaining part to Belarus. Biogeographically, the area falls within the mixed forest zone containing some native Norway Spruce Picea abies in almost all types of tree-stands. The relief of this forest is flat, mostly between 165 and 170 m asl and the climate subcontinental. For more details and photos see Tomiałojć et al. (1984), Faliński (1986), Tomiałojć and Wesolowski (1990, 2004, 2005).

Most of the studies reported below were carried out in the best preserved 47.5-km² part of the forest, which has been strictly protected since 1921 within the Białowieża National Park (BNP, Fig. 1). Even before that date, this core area had never been subject to forest exploitation other than very local tree cutting, charcoal production or some cattle grazing. The BNP stands are distinguished among European temperate forests by features which seem typical of most rich primeval forests. These are:

- Large heights of trees – the maximum heights for Białowieża Norway Spruces are 55 and 57 m, and for some other tree species 42–45 m (Faliński 1968, 1991).
- Multistorey profile of stands – in particular those of Oak–Lime–Hornbeam forest can be subdivided into 5–6 layers. The emergents of tropical forest find here their corresponding components in huge spruces which rise 10–15 m above the main canopy.
- Diverse tree community. Białowieża stands harbour 26 species of trees and 55 shrub species (Faliński 1991). The Oak–Lime–Hornbeam stands alone may be composed of a dozen or so tree species. They are also strongly diversified as regards the age and size of trees. Several individuals are up to 500 years old.
- Large amount of dead wood and uprooted trees. There are many dead standing stems, stumps, freshly uprooted trees and fallen logs (on average 130 m³/ha in Oak–Lime–Hornbeam habitat, Bobiec 2002). There are many rootpads, discs of flat root systems belonging to fallen trees, chiefly spruces. These rise vertically up to 7.5 m, forming walls up to 10–20 m long, and constitute a special habitat intermediate between the ground and the tree-layers.

Most of the BNP area (Fig. 1) is covered by three types of old-growth stands: (1) Oak–Lime–Hornbeam forest, richest in tree species and structurally the most diverse, which covers the largest areas (44% of

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<tr>
<th>Feature</th>
<th>Białowieża NP</th>
<th>England</th>
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<tr>
<td>Predator diversity</td>
<td>&gt; 30 species of birds and mammals important as bird and/or nest predators, from Lynx Lynx lynx and Wolf Canis lupus to rodents (Tomiałojć et al. 1984)</td>
<td>Same set of carnivores and rodents (Yalden 1999), as well as of raptors, owls (judging from their current presence in parts of Britain: Fuller 1995)</td>
</tr>
<tr>
<td>Windfalls/tree uprooting</td>
<td>Major gap-forming factors in all forest types (Fuller 2000, Bobiec 2002)</td>
<td>The same (Peterken 1996)</td>
</tr>
<tr>
<td>Cyclical rodent uprooting</td>
<td>Every few years outbreaks following tree masting (Pucek et al. 1993)</td>
<td>Recorded in mature woodlands (Southern 1959 in Lack 1966)</td>
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total acreage); (2) swampy deciduous forests (riverine stands and Alder *Alnus glutinosa* carrs), with the highest amount of dead wood (coverage 22%) and (3) mixed coniferous forests, dominated by Spruce and Scots Pine *Pinus sylvestris* (coverage 28%). The remaining areas are covered by old meadows partially overgrown by secondary woods.

**BIRD STUDIES IN THE PRIMEVAL FOREST**

The project has focused on the ecology and behaviour of birds breeding in the primeval old-growth stands and started in 1975 (Tomiałojć *et al.* 1984). It combined long-term (> 30 years) studies of structure and dynamics of the whole breeding community with the long-term population dynamics of individual species. The long-term data originate from a territory mapping-based bird monitoring on seven permanent census plots in the forest, each 24–33 ha in size (Fig. 1) – see Wesolowski *et al.* (2002a) for description of methods. Along with the information on bird numbers, data on changes in environmental variables potentially important for birds, such as weather, numbers of leaf-eating caterpillars, tree seed crop, holes, rodents and presence of predators, were gathered (Tomiałojć *et al.* 1984, Walankiewicz 1991, 2002, Wesolowski 1994, 1996, 1998, Wesolowski & Tomiałojć 1995, 1997, Rowiński & Wesolowski 1999). Alongside these studies, shorter intensive population studies on the breeding ecology and behaviour of a dozen or so species, mostly passerines, were carried out (reviewed in Wesolowski & Tomiałojć 1995, 2005).

**RICHNESS OF THE BREEDING AVIFAUNA**

During the last century, 111 forest/forest edge species were recorded breeding in the Białowieża Forest. Most of them had already probably bred there before the human colonization began (Tomiałojć & Wesolowski 2004) and almost all of them still breed in the forest (Tomiałojć 1995, Wesolowski *et al.* 2003a, 2006).

The contemporary British avifauna constitutes an impoverished version of that in Białowieża – all but a few British breeding species (e.g. Scottish Crossbill *Loxia scotica*) also nest in the Białowieża Forest, whereas numerous species breeding in the latter area do not nest in Britain (cf. Fuller 1995, Tomiałojć 1995, Tomiałojć & Wesolowski 2005). However, were the original primeval British forests species-poor as well? It is possible that, due to the marginal/insular position of Britain, some species, like Red-breasted Flycatcher *Ficedula parva*, never colonized the area, and the number of breeding species, even with no human influence, was smaller than that in the Białowieża Forest (Fuller 1995, Tomiałojć 2000a). However, most of the missing species probably became extinct due to the impact of human activities: deforestation and/or persecution. This is documented for some species, such as Goshawk *Accipiter gentilis* or Hazel Grouse *Bonasa bonasia* (reviewed in Fuller 1995), but many more birds could have disappeared from Britain before ornithological records began, e.g. several woodpeckers and Collared Flycatcher *Ficedula albicollis* (Mikusiński & Angelstam 1997, Tomiałojć 2000a, 2000b). There are also no good geographical or biological reasons why large birds such as Cranes *Grus grus* or Black Storks *Ciconia nigra* could not have bred in pristine British forests. I suspect that, in due course, remains of these species will be found in British archaeozoological excavations.
Very high species richness occurs in the Bialowieża Forest, not only at the landscape scale, but also locally within individual forest patches. In a 24–25-ha Oak–Lime–Hornbeam old-growth plot, an average of 35 (29–41) bird species occur in a single season, and in a slightly larger (33 ha) and more diversified forest-edge riparian plot up to 52 species can breed in one year and 74 bred at least once during 30 years (Fig. 2, Tomiałojć & Wesolowski 2004, Wesolowski et al. 2006). The very high alpha diversity seems to result from a fine-grained diversification of pristine forest stands into patches of different tree species and age composition, from recently formed gaps to patches of huge trees (Faliński 1986, Bobiec et al. 2000), as well as from the ubiquitous presence of various microhabitats (snags, holes, rootpads, tiny water pools). Such habitat diversification apparently suits the requirements of numerous species (Tomiałojć & Wesolowski 2004).

The avifauna composition, however, does not change much across different forest types. Only a few species are replaced when one moves from one forest type to another. There are some specialists found only in a single habitat type, such as Green Sandpiper Tringa ochropus (Alder carrs) or Pygmy Owl Glaucidium passerinum (breeding in conifers). However, most of the other species are fairly ubiquitous, breeding in the majority of primeval forest habitats (Wesolowski et al. 2003, Tomiałojć & Wesolowski 2004). In the BNP even such dramatic changes of the forest structure as the appearance of large treefall gaps (up to several hectares in area) after heavy storms do not result in their colonization by new species. The gaps are still inhabited by the subset of species of the old-growth assemblage (Fuller 2000). As a result of this high plasticity of individual species, the combined number of species breeding in all woodland habitats is only a third higher than their number in the single richest plot (33 ha, Fig. 2). Due to this high similarity of species composition across forest types, it is justified to claim that a single old-growth bird community inhabits all types of this primeval forest (Tomiałojć et al. 1984, Wesolowski et al. 2002a, 2006).

**BIRD DENSITIES**

Contrary to what one might expect, the coexistence of numerous species in BNP does not result in a high overall breeding bird density. Even during the peak years in the early 2000s, the overall densities ranged from about 50 pairs/10 ha in coniferous forest to 135 pairs/10 ha in the riverine plot at the forest edge (Fig. 3). They are thus no higher than in managed forests of Germany or England (Flade 1994, Fuller 1995), but several times lower than those found in fragmented English woods (e.g. 400 pairs/10 ha in a Somerset Wood or 195 (max. 252) pairs/10 ha in Wytham Wood near Oxford – Parsons 1976, BTO data). Moderate overall densities in BNP result from very low densities of the majority of the species. Only a few numerically dominant species breed regularly in densities exceeding 5 pairs/10 ha (Fig. 4). For example, Chaffinches Fringilla coelebs (> 20 pairs/10 ha in some cases) are only sometimes locally
outnumbered by Collared Flycatchers (Walankiewicz et al. 1997). The group of fairly abundant species consists also of Robins Erithacus rubecula and Song Thrushes Turdus philomelos (all habitat types), sometimes Wood Warblers Phylloscopus sibilatrix (mostly dry stands), Blackcaps Sylvia atricapilla (mostly swamy forest), Hawfinches Coccothraustes coccothraustes (Oak–Hornbeam habitat), Goldcrests Regulus regulus and Coal Tits Parus ater (coniferous forest) and Starlings Sturnus vulgaris (forest edge) (Tomiałojć et al. 1984, Wesołowski et al. 2002a, 2006). Most other birds breed at densities below 3 pairs/10 ha but such species constitute on average 58% of the breeding species list in the riverine and up to 71% in the coniferous forest (Tomiałojć & Wesołowski 2004). Remarkably, many of the species which occur at low density in BNP reach much higher densities in British woods (Table 2).

**POSSIBLE CAUSES OF LOW BIRD DENSITIES**

These observations, however, only show that, in comparison with secondary woodlands, undersaturation in the primeval forest could occur more frequently, and that some birds demand more space for reproduction there. They do not explain why these differences occur. Several different mechanisms could be involved. Numbers of birds could be limited by strong interspecific competition for scarce resources (such as food or nest-sites), productivity of local populations could be dampened by resource scarcity and/or heavy predation or their non-breeding mortality could be very high. The possible role of these mechanisms is discussed below.

**Table 2.** Population densities (pairs/10 ha) of some birds in primeval forest and in English woods. For BNP mean densities in the locally best habitat recorded during 30 years, and – in parentheses – maximum density recorded within a 24–33-ha plot in a single season are shown (extracted from Wesołowski & Tomiałojć 1997; Wesołowski et al. 2003, 2006). England: data from equivalent old-growth deciduous – mostly oak – woods; mean (maximum) values.

<table>
<thead>
<tr>
<th>Species</th>
<th>BNP</th>
<th>England</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Wood Pigeon Columba palumbus</td>
<td>1.0 (3.4)</td>
<td>58</td>
<td>Parsons (1976) in Tomiałojć et al. (1984)</td>
</tr>
<tr>
<td>Tawny Owl Strix aluco</td>
<td>0.1–0.2*</td>
<td>0.6–0.7</td>
<td>Southern (1959) in Lack (1966)</td>
</tr>
<tr>
<td>Dunnock Prunella modularis</td>
<td>3.4 (5.8)</td>
<td>21.4†</td>
<td>Flegg and Bennett (1974) in Tomiałojć et al. (1984)</td>
</tr>
<tr>
<td>European Robin Erithacus rubecula</td>
<td>7.6 (11.8)</td>
<td>20 (27.5)</td>
<td>Gaston and Blackburn (2000)</td>
</tr>
<tr>
<td>Common Blackbird Turdus merula</td>
<td>3.2 (6.2)</td>
<td>32‡</td>
<td>Parsons (1976) in Tomiałojć et al. (1984)</td>
</tr>
<tr>
<td>Blue Tit Cyanistes caeruleus</td>
<td>3.2 (10.7)</td>
<td>12 (20)</td>
<td>Lack (1966)</td>
</tr>
<tr>
<td>Great Tit Parus major</td>
<td>3.4 (6.9)</td>
<td>17 (39)</td>
<td>Perrins (1965) in Lack (1966)</td>
</tr>
</tbody>
</table>

*Jędrzejewska and Jędrzejewski (1998).†Up to 50 pairs/10 ha in another study (Snow & Snow 1982).‡Up to 75 pairs/10 ha in urban parks (Lack 1966).
Food limitation and competition for food in the breeding season?

Birds feeding on invertebrates collected from leaves and twigs form about 50% of the bird assemblage in BNP (Wesołowski & Tomiałojć 1997, Wesołowski et al. 2006) and leaf-eating caterpillars constitute a substantial part of their diet, 55–85% of nestling food, depending on year and species (reviewed in Wesołowski 2003a). Thus, the variation in the caterpillar numbers should have a strong influence on the breeding birds. The defoliating winter moth *Operophtera brumata* caterpillars occur usually in low numbers, but their outbreaks, causing partial to total defoliation of deciduous trees, happen 8–11 years apart (Wesołowski & Tomiałojć 1997, Wesołowski & Rowiński 2006). However, in the intervening years, smaller outbreaks of other species, providing alternative food sources, can occur (e.g. Rowiński & Wesołowski 1999). As a consequence, the caterpillar supply remains adequate in most years. Actually, the caterpillar supply in BNP appears to be higher than in other deciduous temperate forests (Table 3).

Also, the bird data support the notion that food in the breeding season is usually superabundant. Interspecific competition for food in the breeding season does not play an important role and shortage of food does not limit reproduction (details in Wesołowski 2003a). This is supported by the following observations:

- changes in numbers of congeners are most often positively correlated (e.g. Pied *Ficedula hypoleuca* and Collared Flycatchers) (Fig. 5) or independent of one another (Wesołowski & Tomiałojć 1997, Wesołowski et al. 2006);
- birds in BNP lay clutches as large, or larger than the highest values recorded elsewhere (reviewed in Wesołowski 2003a);
- resource defence polygyny occurs regularly in several species in their high-density habitats (Wesołowski 1987);
- the year-to-year variation in nesting success is mostly due to predation (reviewed in Wesołowski & Tomiałojć 1995, Rowiński 2001, Wesołowski 2001, Walankiewicz 2002, Czeszczewik 2004). Starvation of young and strong brood reduction is found to be unimportant in all passerines (12 species) studied so far, even in the low-caterpillar years. Only in a few seasons, in which cold and rainy weather coincided with the nestling period of hole nesters (Wesołowski et al. 2002b), were higher losses observed. However, these may not be due to lack of food *per se*, but rather due to high-energy loss by nestlings in soaked nests.

Some signs of limitation of reproductive output by food resources are observed only in rodent specialists when rodents are unavailable. Buzzards *Buteo buteo*

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**Table 3.** Dry mass of caterpillar frass collected in different deciduous forests during seasonal peak of caterpillar availability. To enable comparisons the data presented in original graphs and tables were recalculated to g/day/0.25 m².

<table>
<thead>
<tr>
<th>Locality</th>
<th>Habitat</th>
<th>Study years</th>
<th>Frass mass</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Netherlands</td>
<td>oak forest</td>
<td>1957–1966</td>
<td>0.12–1.89*</td>
<td>van Balen (1973)</td>
</tr>
<tr>
<td>Japan</td>
<td>mixed forest</td>
<td>1994–1995</td>
<td>c. 0.10</td>
<td>Seki and Takano (1998)</td>
</tr>
<tr>
<td>Switzerland</td>
<td>oak forest</td>
<td>1989–1991</td>
<td>0.05–0.08</td>
<td>Zandt (1994)</td>
</tr>
<tr>
<td>Switzerland</td>
<td>deciduous forest</td>
<td>1997</td>
<td>c. 0.06</td>
<td>Fischbacher et al. (1998)</td>
</tr>
<tr>
<td>Corsica</td>
<td>Quercus ilex forest</td>
<td>1987–1993</td>
<td>0.02–0.08</td>
<td>Barbura et al. (1994)</td>
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<td>NP</td>
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*Frassfall during a winter moth *Operophtera brumata* outbreak.

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**Figure 5.** Pattern of changes in numbers of Pied and Collared Flycatchers in BNP over a 30-year period (extracted from Wesołowski & Tomiałojć 1997, Wesołowski et al. 2006) – an example of similar changes in congeneric species.
and Tawny Owls switch to hunt mostly on birds, yet they are apparently unable to compensate fully for lack of their main prey. During the rodent crashes, they lay smaller clutches or fail to breed at all (Jędrzejewski et al. 1994a, 1994b, van Manen 2003).

Nest-holes in short supply?

Secondary hole nesters serve as a textbook example of population limitation by shortage of nest-sites and/or by interspecific competition for them (reviewed in Newton 1994). The highest densities of this group recorded in BNP (up to 47 pairs/10 ha – Wesolowski et al. 2006) are rarely as high as those recorded for single species in nestbox studies, e.g. up to 70 nests/10 ha in Collared Flycatcher on Gotland (L. Gustafsson pers. comm.), 40 pairs/10 ha in Pied Flycatcher (Tiainen et al. 1984) or 39 pairs/10 ha in Great Tit (Table 2). Could the low numbers in BNP be due to a shortage of nesting holes?

The Białowieża data lend no support to such an explanation. Although, due to enormous technical difficulties (accessibility and safety), it has been impossible to measure hole density in BNP, the indirect and conservative estimates of hole availability clearly indicate an excess. Numerous holes, despite being usable, are occupied by the birds only in some years and remain unused in the others (Wesołowski 1989, 2001, 2006). Collared Flycatcher is one of the latest breeding species and is in the most difficult position, because it can only use the holes left over by the earlier breeding species. Yet, it is the most numerous species in the Oak–Hornbeam habitat (Wesołowski et al. 2003). Prospecting males have on average at least two holes to choose from (Walankiewicz 1991). Later arriving young males secure holes of the same quality as the earlier settling older birds (Mitrus et al. 1996) and quality of holes does not deteriorate with increasing Collared Flycatcher population density (Walankiewicz 2002). Also, the low frequency of interspecific hole usurpation (Wesołowski 2003a), and frequent use of holes by the facultative hole nesters (e.g. Blackbirds Turdus merula in the Oak–Hornbeam forest placed almost 50% of their nests in holes and semi-holes, Tomiałojć 1993) show that holes are superabundant and that the low hole-nester densities found in primeval forest cannot result from the shortage of nest-sites. Therefore, the limitation of bird numbers by the shortage of holes and strong interspecific competition for holes reported from other areas seem largely to be by-products of man-made habitats and not factors which could have been important in the primeval conditions.

High mortality outside the breeding season?

Temperate zone birds are often limited by food resources during the non-breeding season and harsh winter weather. The numbers of resident forest birds in spring in Britain are strongly dependent on the severity of previous winter (reviewed in Lack 1966, Greenwood & Baillie 1991, Newton 1998). As winters in the Białowieża Forest are harsher (snow cover lasting up to 3 months, temperatures dropping below −20 °C) than in Britain, one would expect the resident Białowieża birds to be strongly affected by severe cold spells. This is only partially true. Most BNP birds, such as, for example, Chaffinches, Robins, Wrens and Starlings (c. 75% of breeding bird assemblage, Wesolowski et al. 2002a, 2006), avoid this problem altogether by moving to areas with a milder climate. It is possible their mortality rates are indeed higher than those of their more secondarily sedentary English counterparts (Lack 1943/44), which are likely to profit from the existence of vast areas of man-made habitats and frequent supplementation with extra food by humans, and avoid the risks associated with large-scale movements. However, as mortality rates of migratory birds remain largely unknown, it is impossible to answer this question at the moment.

Mortality of Nuthatches Sitta europaea, birds sedentary in BNP (c. 50%, Wesolowski & Stawarczyk 1991), is no higher than that of the majority of the British sedentary birds (Dobson 1990), or of the Nuthatches in the Belgian population (Matthysen 1998). Moreover, mortality of this species in BNP is not concentrated in winter, thus failing to support the idea that heavy winter mortality is controlling numbers (Wesołowski & Stawarczyk 1991). Other, indirect observations also indicate that harsh local winters are not as detrimental as one might think.

Changes in overall numbers of local residents in BNP are positively correlated with the temperature of the preceding winter (Wesołowski 1994, Wesolowski & Tomiałojć 1997) in only two residents, Goldcrest and Middle Spotted Woodpecker Dendrocopos medius, others either do not show any correlation (e.g. Great Spotted Woodpecker Dendrocopos major, Nuthatch, Treecreeper Certhia familiaris) or their numbers are only moderately correlated with winter temperatures (Great, Blue and Marsh Tits Parus palustris).
The wintering birds extensively use tree seeds as food, yet in contrast to other areas, the numbers of residents in BNP are not dependent on masting of either deciduous trees or spruce (Wesołowski 1994, Wesołowski & Tomiałojć 1997). The local birds also hardly use feeders supplemented with fat or seeds (Wesołowski 1995a). The birds in BNP appear, thus, to be less dependent on any particular type of food than elsewhere. In such a diverse forest, the birds can apparently switch to other food types if one fails, without their numbers being affected adversely (Wesołowski 1994, Wesołowski & Tomiałojć 1997).

Deep, long-lasting snow cover, however, by preventing access to the ground, can lead to food shortages for rodent-eating Tawny Owl, as suggested by the strong decline in numbers of this species after the unusually snowy winter of 1995/96 (Jędrzejewska & Jędrzejewski 1997). Heavy predation continues during the post-fledgling period when predators such as Tawny Owl, Pygmy Owl, Buzzard and Pine Marten Martes martes switch to hunting juvenile birds (Jędrzejewski et al. 1994a, 1994b, Zalewski et al. 1995, van Manen 2003). As a consequence of heavy predation, the production of young remains very low in BNP for most of the time, yet it seems adequate for the long-term maintenance of local populations. Assuming that the adult mortality rate was close to the passerine average (54% per year, reviewed in Payne 1985), the birds would have to produce > 2 fledglings/pair/season to make the local populations demographically self-supporting. This condition is fulfilled; even the least productive species rear on average 2.4–2.5 fledglings/pair/year (Blackbird – Tomiałojć 1994, Wood Warbler – Wesołowski 1985, Collared Flycatcher – recalculated from Walankiewicz 2002 and Mitrus 2003) and the most productive species – Nuthatch (Rowiński & Wesołowski 1999) and Marsh Tit (Wesołowski 2003b) rear up to 5 young/pair/season.

The relatively low productivity combined with low population densities results in low production of young per unit area, sometimes by an order of magnitude lower than recorded in other areas (Wesołowski 1983, Wesołowski et al. 1987, Tomiałojć 1994). The low productivity, even without heavy mortality in the intervening non-breeding season, leads to few potential recruits in the following spring, and in turn, could result in undersaturation and low breeding numbers. The small number of potential settlers could also facilitate possession and defence of large territories (see above), as the exclusion of a large number of contenders from an extensive area would not be economically feasible. The large territories themselves, by diluting potential prey in space, could act as one means of avoiding predation (Wesołowski 1981, Wesołowski et al. 1987).

The BNP results also show that high predator pressure and chronically low productivity seem to constitute an inherent feature of bird life in all rich

**Low production of young?**

Predator diversity in BNP is two to three times higher than in most other European forests (Tomiałojć et al. 1984). Breeding birds have to contend with the diverse assemblage of predators (over 30 species, see Tomiałojć & Wesołowski 2005), using different modes of nest detection and attack techniques. Many of them are dangerous not only for broods but for the parent birds, too.

Being responsible for 65–95% of nest loss in different species (reviewed in Wesołowski & Tomiałojć 2005), predators are the most important factor limiting productivity. Nest soaking becomes important only in rainy, cold seasons in some hole-nesting species (Wesołowski et al. 2002b). Year-to-year variation in nesting success is mostly related to varying predation rates, even in the years with few caterpillars (Wesołowski 1983, 1985, Piotrowska & Wesołowski 1989, Tomiałojć 1994, Walankiewicz 2002). Nests are mostly robbed during the nesting stage, making the losses especially costly, because it limits further nesting attempts. The nest mortality rates in BNP (Fig. 6) exceed or are equal to the highest loss rates recorded for the same species in human-transformed areas (reviewed in Wesołowski & Tomiałojć 1995).

Heavy predation continues during the post-fledgling period when predators such as Tawny Owl, Pygmy Owl, Buzzard and Pine Marten Martes martes switch to hunting juvenile birds (Jędrzejewski et al. 1994a, 1994b, Zalewski et al. 1995, van Manen 2003). As a consequence of heavy predation, the production of young remains very low in BNP for most of the time,
primeval forests, independent of climatic zone (see below).

Why densities are low in primeval forest – summary

As shown above, the breeding densities of insectivorous birds in BNP remain usually below the level set by food or nest-sites, and interspecific competition is of minor importance. Only in the rodent specialists is production of young and adult survival sometimes influenced by food shortages. It remains to be seen whether mortality outside the breeding season is indeed higher in the largely migratory Bialowieża birds than in their sedentary British counterparts, but harsh winters in the forest do not seem to affect locally wintering populations severely. The chronically low productivity of birds in BNP combined with their high spatial requirements (large territories) emerge as potentially the most important factors in preventing the increase of local populations.

SECONDARY WOODS: HIGH DENSITIES COMBINED WITH HIGH PRODUCTIVITY

The birds in fragmented British woods, with an impoverished predator fauna, show an opposite suite of characteristics (Table 4). For example, Wrens in the BNP defend large territories, are infrequently polygynous and produce few young. British Wrens, despite living in crowded conditions, have very small territories and frequently attract several females, which reproduce much more successfully (Table 5). The higher production of young per female, combined with their higher density, results in a huge difference in the production/fledglings per unit area. The British Wrens may produce 10–20 times more fledglings than their counterparts from the primeval forest. Because British Wrens survive quite well (37%, Hawthorn & Mead 1975), their much higher productivity translates into many birds establishing territories in the following spring and high breeding densities. An identical sequence of events (human-induced weakening of predator pressure, increase in productivity, more would-be recruits, increased densities in secondary woods) has apparently led to an increase in numbers of Wood-pigeons _Columba palumbus_ (Tomiałojć 1976, 1980) and Blackbirds (Tomiałojć 1993, 1994) in small British woods. It seems that this is a general phenomenon. High productivity and high densities are observed when birds switch to breed in places devoid of, or inaccessible to, predators (islands, town interiors, and

| Table 5. Main differences between Bialowieża and British populations of the Wren _Troglodytes troglodytes_. Adjusted from Wesołowski (1983). |
|---|---|
| **Habitat distribution** | **Britain** |
| narrow, limited to some types of forest | very broad, preference for woodland types (Fuller 1995) |
| migratory | sedentary (Fuller 1995) |
| **Density (territories/10 ha)** | **0.5–0.8 (1.6) – Armstrong and Whitehouse (1977), Garson (1980a)** |
| mean 3–3.5 (max. 5.5) in the best (Ash–Alder) habitat | c. 50%, up to four females simultaneously (Armstrong 1955, Garson 1978) |
| mean 2.1 in the best habitat | c. 80–100 (Armstrong 1955, Garson 1980b) |
| **Frequency of polygyny (%)** | **5.9 (Garson 1980a)** |
| usually below 20, only bigamy, only in Ash–Alder Forest | c. 40 (Garson 1980a) |
| **Length of breeding season (days)** | mostly during egg-laying/incubation (Garson 1980b) |
| c. 80 | |
| **Mean clutch size in April and May** | 5.9 (Garson 1980a) |
| 6.8 | c. 40 (Garson 1980a) |
| **Nest loss (%)** | mostly during egg-laying/incubation (Garson 1980b) |
| c. 60 | |
| **Losses concentrated at:** | nesting stage |
when birds breed in colonies – references in Tomiałoń & Wesolowski 1989). The numbers of birds in such highly productive populations can increase up to some new limit set by food resources, nest-sites and/or interspecific competition for resources.

The current changes in British woods (increase in forest area, less intensive stand management, reduced gamekeeping, increasing predator diversity; reviewed in Fuller et al. 2005) are reversing the long-lasting trends, and moving the British woods again into the direction of the primeval state. This, in the long run, could result in a forest avifauna richer in species but with each occurring in lower densities.

**A PRIMEVAL FOREST SYNDROME**

A very high number of breeding species coupled with low to very low population densities are characteristic features of tropical rain forest bird communities (Haffer 1988, Thiollay 1990). This seems to be in sharp contrast to the situation in the temperate forests, which are usually inhabited by far fewer bird species (only c. 20% of the tropical values), but breeding in much higher densities (reviewed in Tomiałoń & Wesolowski 2004). However, the data used to form these generalizations originate from pristine forests in the tropics but from highly human-transformed woods in the temperate zone which could confound the results (Tomiałoń et al. 1984, Tomiałoń & Wesolowski 1990).

Fortunately, the survival of BNP makes it possible to disentangle these factors. There were 86 species found breeding in all the monitoring plots in the BNP (1.9 km²) during 30 years, and 72–75 breeding in all the monitoring plots in the zone which could confound the results (Tomiałoń & Wesolowski 2004). Additionally, the distributions of species abundances in the BNP and in the tropics do not differ substantially. They are all highly skewed with rare species prevailing. The density of the median species in the BNP (0.5–0.8 pairs/10 ha), is quite similar to values from Panama (0.7 pairs/10 ha), though higher than in Peru (0.25 pairs/10 ha) – references in Tomiałoń & Wesolowski 2004.

These results indicate that the naturally existing differences in species richness and breeding bird community structure between temperate and tropical forests have been greatly exaggerated by human-created transformations of temperate forests. Also in the tropics, the typical ‘tropical’ structure of bird communities is recorded only from pristine forests. In secondary and logged tropical forests, as well as in semi-open habitats there, bird communities become more like the ‘temperate’ pattern (increased proportion of abundant and fewer rare species – Thiollay 1992).

Therefore, it seems justifiable to propose that a recognizable ‘primeval forest syndrome’ exists, i.e. that a combination of high species richness with low densities of individual species is a feature of all pristine forests, independent of climatic zone. Hence, it may be used as a yardstick of forest maturity, and absence of human-made disturbance (Thiollay 1990, 1999, Tomiałoń & Wesolowski 1990, 2004).

**BIAŁOWIEŻA FOREST – IS IT GOING TO SURVIVE?**

It has been possible to arrive at these conclusions, as well as at the majority of other generalizations presented here, only because the features of a primeval forest have been preserved in the Bialowieża Forest. Otherwise, our knowledge of pattern and processes shaping bird communities in European forests would remain highly biased. This fact shows the immense value of this forest as a reference site for biological science and justifies the urgent need for its preservation (Tomiałoń et al. 1984, Jędrzejewska & Jędrzejewski 1995, Bobiec 2002, Wesolowski 2005).
Unfortunately, less than 8% of the Polish part of Białowieża Forest has been excluded from any management. The remaining 92% is still open to logging and other forms of direct human intervention. The strictly protected part is too small to preserve features of the primeval forest and safeguard the continued operation of natural ecological and evolutionary processes. It is even too small to maintain viable populations of the majority of birds – over two-thirds of species occur there with populations of < 100 pairs (Wesołowski et al. 2003). There is enough space for only c. 30 pairs of White-backed Woodpeckers Dendrocopos leucotos (Wesołowski 1995) and c. 20 pairs of Three-toed Woodpeckers Picoides tridactylus (Wesołowski et al. 2005). Protection of the whole Forest and restoration of dead wood supply in the currently managed part would improve the situation substantially. This would provide breeding habitat for c. 350 pairs of White-backed Woodpeckers (Wesołowski 1995b) and for 260–320 pairs of Three-toed Woodpeckers (Wesołowski et al. 2005, unpubl. data).

The necessity to preserve the whole of Białowieża Forest as a national park is denied by the Polish authorities. Against all the evidence and legal obligations, logging is continuing. Most of the natural stands have been already replaced by – mostly coniferous – plantations (Tomiałojć & Wesołowski 2004, Wesołowski 2005), which are too young to be harvested. Therefore, the cutting operations are concentrated in the old-growth patches of natural origin, including within the nature reserves outside the strictly protected zone. These will result in continued loss of the natural forest remnants and, in consequence, loss of this unique benchmark site.

This scenario, however, need not become reality. If the Polish Government could be convinced that protection of this forest tract as a whole, with preservation of its unique natural heritage for future generations, is the only acceptable solution, far exceeding short-term benefits from timber extraction, then there would be some brighter prospects for the Białowieża Forest and its birds.

This review is based on work of more than 80 people who participated in the Białowieża bird studies for shorter or longer periods during the last 32 years. I am very grateful to all of them. It is impossible to name all of them here, but I would like to express special words of gratitude to L. Tomiałojć who has initiated the whole programme of bird studies in primeval conditions, and actively participated in its execution for over 25 years. I thank the BOU for the invitation and RSPB for making my participation possible at the BOU conference ‘Woodland birds: their ecology and management’ in Leicester. I also thank A. Amar and an anonymous referee for helpful comments on an earlier draft of this paper.

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Lessons from primeval conditions


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