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## Ecology and biology of birds in the Białowieża Forest: a 40-year perspective

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Abstract. The aim of this study was to review the most important results from the last 40 years of intense ornithological research conducted in the Białowieża Forest. Furthermore, we discuss the threats that may destroy the unique ecology and characteristics of this forest.

Studying the avifauna of the Białowieża Forest provides us with a good general knowledge about natural ecological conditions and relationships, which prevailed in temperate European forests in the past. The avifauna of the Białowieża Forest is characterized by features associated with primeval habitats such as the stability of communities over time, high species richness, relatively low densities, high proportion of hole-nesting birds, very high predation pressure and weak, insignificant competition interactions. This emphasizes the importance of predation, excess of nesting sites for cavity nesting birds, high abundance of food, especially for insectivorous species and fluctuation of bird population size due to rodent outbreaks (pulsed resources). The most severe threats for the avifauna of the Białowieża Forest are: rejuvenation of tree stands, removal of dead wood, fragmentation of old-growth stands, change of tree stand composition (reducing the proportion of some tree species).

In order to expand our ecological knowledge about birds, we should keep the Białowieża Forest fully protected for years to come. The main priority should be the maintenance of natural processes changing the forest's species composition.

Keywords: Białowieża National Park, temperate forests, predation, forest birds assembly, forest management

### 1. Introduction

Until recently, majority of research concerning ecology and biology of broods of forest birds was conducted in strongly changed forests of temperate zone (Tomiałojć et al. 1984). One of the exception is the Białowieża Forest (hereafter BF) where ornithological research has been conducted since 40 years. The BF was preserved as a compact forest complex, despite strong pressure on colonisation and deforestation on the lowlands of Europe. Presently, the BF is one of the last remnants of primeval, lowland European forest. Exceptional, amongst lowland forests in whole temperate zone of Europe and North America, preservation status of the BF results from its history. The BF was protected as hunting area until the beginning of the 20<sup>th</sup> century. In the 20<sup>th</sup> century, new legal forms of protection of the BF were developed (national park, reserve, Natura 2000, UNESCO, etc.). This allowed for preserving very old forest stands, which are unique on a global scale. They were preserved not only in the Białowieża National Park (BNP) and the reserves but also in part of the managed stands of the BF. Some stands of the BF (i.e. oak-hornbeam, ash-alder and alder fen stands) are the most primeval stands in whole temperate lowland zone of Europe. It does not mean that they are virgin forests or that they were not subjected to the influence of humans. Such forests no longer exist even in tropical rain forests in Asia, Africa or South America (Willis et al. 2004). Owing to those features, the BF exists as a natural laboratory in which we can investigate organisms under the conditions once prevailing in forests before transformation made by humans (Wesołowski 2007b). That is why the BF is one of few forests in the world where we can study evolutionary adaptations of birds associated with, for example, predation, competition, food resources or breeding sites. Division of

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the BF to zones of different conservation regime (national park, nature reserves, managed stands) enables to study the direct influence of anthropogenic factors (including forest economy) on avifauna. Diversity and functioning of breeding birds' communities and their primeval behaviour in the BF can be treated as a model in comparison to other European forests of temperate zone. In here, the functioning of primeval birds communities before intensive forest management can be experienced and understood.

The aim of this study is a summary of results of more than 40 years of ornithological research conducted in the BF. Recent threats to avifauna caused by human activity were also discussed.

### 2. The characteristics of breeding avifauna

Forest avifauna of the BF shows many primeval characteristics that are consistent with the features of rain forests. Those characteristics distinguish this avifauna from avifauna of forests strongly transformed by human (Tomiałojć, Wesołowski 2004). It can be assumed that avifauna of the BF is similar to that occurred once in the past in the European forests. The BF is, therefore, a reference point for the study of forest birds' biology (Tomiałojć, Wesołowski 2004; Wesołowski 2007b). Primeval features of avifauna of the BF are discussed in the following sections.

#### **Species richness**

More than 250 species of birds were recorded in the whole BF. Most of them are breeding species (Tomiałojć 1995) and nest in deciduous forests - in ash-alder and oak-hornbeam stands, especially on the edges of the forest (on this variety, the presence of few non-forest species and species breeding outside of the forest influences). In years 2010-2014, on one study plot (33 ha) that is located on the edge of the BNP, 55 species nested jointly, whilst inside of the forest, the number of species was lower (Wesołowski et al. 2015). Those differences are related mainly to different habitat structure and also with a degree of forests' naturalness. On plots that are located directly next to open areas, ecotone species are present. Such indirect influence of human activity on nature also causes certain disturbances in birds communities. For instance, common starling (Sturnus vulgaris), which can be rarely seen in the depth of the forest, on the edge of the forest was in some years the most numerous species (Wesołowski et al. 2015).

Significant differences were found between abundance, diversity and species richness indices, between the BNP breeding avifauna and managed stands and, between breeding avifauna of reserves and managed stands. There was no such differences between the BNP and reserves, and all those indices on protected areas were higher than those in the managed stands (Czeszczewik et al. 2015).

About 85% of breeding bird species of the BF are native, typically forest species that were present here before human presence. Remaining species are birds of the forest edges and also birds inhabiting open areas on former fields and meadows. Second group of birds appeared in the BF after deforestation of river valleys and creation of clearings as a result of the development of agriculture (Tomiałojć 1995: Wesołowski et al. 2003). Lack of species such as tree sparrow (*Passer montanus*) or European magpie (*Pica pica*) that nest in fragmented forests in different parts of Poland proves weak synanthropisation (Tomiałojć 1990).

### Low density of individual species

Low density of majority of species (Tomiałojć et al. 1984; Tomiałojć, Wesołowski 2004) results from large territories and social behaviour of birds (Wesołowski 1981, 1983; Wesołowski et al. 1987). The habitat is not filled with birds, despite food richness and nest sites, and low productivity could be a result of strong predation pressure (Tomiałojć, Wesołowski 2005). For instance, the density of great tit (*Parus major*), pied flycatcher (*Ficedula hypoleuca*), common blackbird *Turdus merula*) and dunnock (*Prunella modularis*) in the BF is several times lower than that in the forests of western Europe. Some species, however, rare in other places, in the BF in some years may reach very high density. A collared flycatcher (*Ficedula albicollis*) can be an example of that – it breeds in density up to 22 pairs / 10 ha (Walankiewicz 2002b).

#### Stability of bird communities

Breeding birds were monitored for more than 40 years on permanent study plots in oak-hornbeam forests, ash-alder and spruce-pine forests of the BNP (Tomiałojć et al. 1984; Tomiałojć, Wesołowski 1994, 1996; Wesołowski et al. 2002, 2006, 2010, 2015). The avifauna of the BNP, despite certain changes in bird's density, over the past 40 years was characterised by high stability unlike in other parts of Europe that are highly transformed by human. The majority of species regularly nesting in the BNP showed long-term growth trends what was related probably with global factors (Wesołowski et al. 2010). Stability of the communities results from long-term stability of forest habitats of the BNP (despite certain changes on the local scale) what creates favourable conditions for reproduction for many years (Wesołowski et al. 2015). Owing to the lack of long-term quantitative studies of birds from the outside of the BF, it is hard to conclude about changes to which avifauna was subjected for many years in the managed part of the BF. However, the negative influence of intensive forest management on

the density of different bird species was proved more than once (Wesołowski 1995c; Wesołowski et al. 2003, 2005; Czeszczewik, Walankiewicz 2006; Czeszczewik et al. 2015).

#### Unusual nest sites

Birds in the BF often nest in places that are unusual for them in other forests. It is caused by large variety of places suitable for nesting in the BF. Over 80% of wren's (Troglodytes troglodytes) nests in the BF are located in the disks of uprooted trees (Wesołowski 1983). Beside this species, couple more species (dunnock, blackcap (Sylvia atricapilla), blackbird, robin (Erithacus rubecula), song thrush (Turdus philomelos)) sometimes use this structure as their nesting places. Blackbirds build nests in decaying or foraging black woodpecker cavities of spruce snags (Tomiałojć 1993). Swifts (Apus apus), known mostly as urban birds and nesting on the buildings, nest in the cavities of old tall trees in the BF. Some species of the so-called open-nesters also nest here in the cavities. This is common habit in the BF in case of, for example, robin (P. Rowiński, oral inf.) and also in case of blackbird in early spring before the development of leaves (Tomiałojć 1993). Furthermore, in BNP, red-breasted flycatcher (Ficedula parva) nests are regularly found in shallow holes (Mitrus, Soćko 2010). Other species such as wren, dunnock and song thrush nest in the same manner. Discs of uprooted trees, strongly decayed tree trunks and also various type of cavities are a natural and common element of Białowieża's landscape. Those elements are especially common in the BNP and much less likely to occur in managed forests (Tomiałojć et al. 1984).

#### Large proportion of cavity-nesters

Cavity-nesters are an important group of forest birds. These species nest in tree cavities. They are divided into two groups: primary cavity-nesters (they excavate their own cavities) and secondary cavity-nesters (they breed in already existing cavities). Some secondary cavity-nesters are model species in ecological and behavioural research, for example, pied flycatcher, collared flycatcher, great tit or blue tit (Cyanistes caeruleus). Amongst primary cavity-nesters are woodpeckers (exception is wryneck (Jynx torguilla), which does not excavate cavities) and two species of tits (willow tit (Poecile montanus) and crested tit (Lophophanes cristatus)). Marsh tit (Poecile palustris), which in other forests, because of its skill of pecking (or rather scooping) cavities in decaying trees, is assigned to primary cavity-nesters, in the BF is a typical secondary cavity-nester because it nests exclusively in already existing holes (Wesołowski 1999).

This is substantial part of avifauna as a joint number of birds nesting in the cavities in the BF counts around 30 spe-

cies. In deciduous forests of the BNP, cavity-nesters constitute 40%, and in coniferous forests, over 30% of all nesting birds are cavity-nesters (Czeszczewik et al. 2015; Wesołowski et al. 2015). On the other hand, in the managed part of the BF, the proportion of this group of birds was lower: 30 and 25%, respectively (Czeszczewik et al. 2015).

#### Large number and diversity of tree cavities

There is a surplus of various cavities in the BNP and their number does not limit the presence of secondary cavity-nesters. Many cavities remain unoccupied every year (Walankiewicz 1991; Wesołowski 2011, 2012). Density of cavities in coniferous forests of the BNP amounts to at least 12.5/ha (Walankiewicz et al. 2014), and in deciduous forests, it's at least four times higher (unpublished data). Despite the fact that there are several times less cavities in the managed stands, still there are more cavities than the breeding pairs of cavitynesters (Walankiewicz et al. 2014; Czeszczewik et al. 2015). Competition for cavities in the BNP is, therefore, not an important issue for secondary cavity-nesters (Wesołowski 1989, 2003, 2007a; Walankiewicz 1991; Walankiewicz et al. 1997; Czeszczewik et al. 2012), unlike it was showed in forests transformed by humans (Newton 1998).

Some cavities can exists for many years while others deteriorate fast as a result of fall of trees or, in case of living trees, overgrowing of cavity (Wesołowski 1995b). Most durable cavities are those in large, living trees and not made by woodpeckers (they are formed in a different way, e.g. as a result of crack or a fracture of a part of a tree). Such cavities may last in good condition for a long time (several years, on an average) and be a nest site or a shelter for secondary cavity-nesters (Wesołowski 2011). In case of cavities excavated by woodpeckers in dead and/or thin trees, 'vitality' ends usually after a couple of years (Wesołowski 2012). In other forests, most of the cavities can be found usually in old and dead trees (Wesołowski 2012). Most of the cavities in deciduous forests of the BF were found in living trees (Wesołowski 1995b; unpublished data). Also secondary cavity-nesters in majority nest in the cavities of living trees (Wesołowski 1989, 1996, 2011; Czeszczewik, Walankiewicz 2003; Walankiewicz et al. 2007; Wesołowski, Rowiński 2004, 2012, 2014; Maziarz et al. 2015).

Woodpeckers as cavities 'producers' are known as a keystone or engineering species (Paine 1969; Jones et al. 1994). However, they do not play that role in the BF, despite their species richness and high density. Large number of cavities available in forests of various tree species composition did not come into existence as a result of excavating. These are, for instance, fissures, cracks in trunks or boughs, holes created as a result of a branch or trunk top's fracture and then their decay (Wesołowski 2007a). Secondary cavity-nesters who very often nest in woodpeckers' cavities, such as Eurasian pygmy owl (*Glaucidium passerinum*) and boreal owl (*Aegolius funereus*), or starling (60% of hollows). Remaining species generally nest in non-excavated cavities and rarely use woodpeckers' hollows as nesting places (Wesołowski 2007a). Stock dove (*Columba oenas*) nests in cavities excavated by black woodpeckers. The important role of woodpeckers, that is, regulating the number of insects (e.g. bark beetles) by accelerating the decay of dead wood, is not belittled.

Nest boxes are being mounted in forests strongly transformed by humans where only few cavities exist. Those artificial nesting places are often considered to be better than cavities (safe nesting places). However, that is not always the case as the results of the research conducted in the BF has shown. In tree cavities, very few nest parasites can be found, unlike in case of nest boxes (Wesołowski, Stańska 2001; Hebda, Wesołowski 2012). That results probably from the fact that in nest boxes, an old nest material can be found. In the cavities, on the other hand, this material is very rarely preserved till the next season (Wesołowski 2000; Hebda et al. 2013). Moreover, in managed forests stands of the BF, the nest boxes turned out to be an ecological trap because they also attracted predators that destroyed large part of birds' broods (Czeszczewik et al. 1999).

Most of the cavities were found on hornbeam (*Carpinus betulus*), and majority of them were found in the BNP in older, living trees with trunk diameter of 30–60 cm. Most of the cavity-nesters usually choose hornbeam as nesting place (Walankiewicz, Czeszczewik 2006), and this tree is the most common species in the BNP. Unfortunately, thicker hornbeams are less often seen in the managed part of the BF because of its cutting for fire wood.

#### Food is not a limiting factor

Most of the birds nesting in the BF are insectivorous. Even those species that feed on seeds also use animal food, for example, whilst feeding the brood. Owing to large diversity and abundance of invertebrates, more than 11, 000 species were recorded in the whole BF (Gutowski, Jaroszewicz 2001), so there is plenty of food for insectivorous birds. An important food of small passerines are caterpillars that appear after the development of leaves on trees and shrubs. They are a significant part of food for broods of many species. However, even amongst birds in which nestlings hatch after the peak of caterpillars' density (or in years of small number of caterpillars), they do not have any difficulties with feeding the brood (Walankiewicz 2006; Maziarz, Wesołowski 2010; Wesołowski, Rowiński 2014).

The base of some woodpeckers' diet (white-backed woodpecker (*Dendrocopos leucotos*), three-toed woodpecker (*Picoides tridactylus*)) are larvae of beetles living in decaying and dead trees that are very numerous in the BNP. Density of those trees is much lower in the managed part of the BF (Wesołowski et al. 2005; Czeszczewik, Walankiewicz 2006). Recently, after last outbreak of bark-beetle, the number of dead spruces has increased in the whole area of the BF what is very beneficial for the three-toed woodpecker (this species forages mostly on freshly killed or dying spruces) and, in the future, for white-backed woodpecker that feeds on decomposed trees, quite often on spruces (Czeszczewik 2009a).

Moreover, experimental research indicates that birds in the BNP rarely use winter supplementing feeding what suggests that food resources are sufficient for many birds to survive the winter (Wesołowski 1995a). This hypothesis finds confirmation in quantitative research of avifauna wintering in the BNP, which proved that number of wintering birds does not differ from the number of the same birds species during breeding season (unpublished data).

In forests transformed by human where diversity of both invertebrates and plants is much smaller than that in the BF, the food is one of the most important factors limiting the productivity and density of birds (Newton 1998). Different situation was found in case of the BF (Wesołowski, Tomiałojć 2005; Wesołowski 2007a). Smaller density of the whole group of insectivorous birds in the managed part of the BF in comparison with the BNP indicates the difference in food resources for those birds. This was confirmed by Wesołowski and Rowiński's (2006) research.

#### Heavy predation pressure

Predation is the main cause of brood loss in the BF. It was proved to be one of the most important factors limiting the density of the most numerous cavity-nester – collared flycatcher (Walankiewicz 2002b, 2006). A list of species robbing broods is long and still open. These animals are mustelids (mainly marten (*Martes martes*)), rodents (yellow-necked mouse (*Apodemus flavicollis*), forest dormouse (*Dryomys nitedula*), squirrel (*Sciurus vulgaris*)) and great spotted woodpecker (Walankiewicz 1991, 2002a; Wesołowski 2002; Czeszczewik 2004; Wesołowski, Rowiński 2012; Maziarz et al. 2016). Open nests, especially those located low, because of easier access are exposed to more predators. Loss in their broods is usually very high. For example, even over 80% of wood warbler (*Rhadina sibilatrix*) is being destroyed (Wesołowski, Maziarz 2009).

It is assumed that cavities as nesting places are safer in comparison to open nests, that are, placed on the ground, in low vegetation, shrubs or trees' branches (Wesołowski, Tomiałojć 2005). In some years, however, the loss in cavitynesters' broods is very high and was one of the highest in Europe (Wesołowski, Stawarczyk 1991; Wesołowski 1985, 2002; Walankiewicz 2002b; Czeszczewik 2004; Wesołowski, Maziarz 2009; Maziarz et al. 2016). It has been shown that the fluctuation in numbers of the collared flycatcher depends on the density of forest rodents (Walankiewicz 2002b, 2006).

Basic strategy allowing for successful rear of the brood is the hiding of the nest from predators as best as possible. Different characteristics of cavities are solid walls of living trees, higher location on a tree, small entrance hole, large bottom, appropriate depth. Those features impede the access to the cavity for some bigger predators and make the broods safer. Locating the nest in non-excavated cavity reduces the risk of finding it by great spotted woodpecker, which may rob both eggs and nestlings (Walankiewicz 1991, 2002a; Wesołowski 1996, 2002; Wesołowski, Rowiński 2004, 2012; Mitrus, Soćko 2010; Maziarz et al. 2016). Chosen cavities are characterised by the combination of characteristics, such as appropriate light, microclimate and protection against flooding, allowing for safety and minimal requirements for the rear of the broods (Maziarz et al. 2016).

Additional behaviour of birds (e.g. mixture of saliva and rotten-wood that reduces the size of entrance of a nuthatch's cavity, locating the nest far from the entrance, covering of eggs by parids and nuthatch) and behaviour such as avoiding inessential activity near the nest or tit's hissing in the nest at the sight of an intruder increase the safety of the nest (Wesołowski 1998; Wesołowski, Rowiński 2004, 2012). Active deterrence of an intruder may be a line of defence in case of an attack. A contact with a predator is always a risk what is confirmed in dead adult that can be found in cavities (Wesołowski 2002; Czeszczewik et al. 2008). Red-breasted flycatcher often occupies semi-cavities that are usually open from the front side what helps the incubating female observing the surroundings and in case of danger allows for escape. Even when the eggs are robbed by a predator a female still has a chance for a second brood (Mitrus, Soćko 2010). Avoiding predation from small predators such as rodents that can easily climb to any cavity seems impossible. An occupation of large territories and low density can be a part of anti-predation strategy for some species, for example, tits or wren (Wesołowski 1981; Wesołowski et al. 1987).

A research on wood warbler showed its amazing anti-predation adaptation. As a result of that adaptation, this species has become a nomadic species. It is very exposed to predator attack because of nesting on the ground. Its biggest threat are rodents, which are very numerous in some years – on a hectare of a forest, even 70 individuals of a yellow-necked mouse may occur (Jędrzejewska, Jędrzejewski 2001). If, after arrival at the breeding ground, wood warblers find high density of rodents, they move to another location (yet unrecognised). Since 1975, many warblers that were singing in the BF in early spring was observed several times. Then, they disappeared without nesting because of high density of rodents. Eleven times more wood warblers than in previous year nested in one year when the density of the rodents was low (Wesołowski et al. 2009).

### 3. Influence of human activity on avifauna

The BF is one of the few European forests where all European woodpeckers' species can be found. Joint density of woodpeckers in the BNP differs depending on the habitat and ranges from 1.6 pair / 10 ha in coniferous forests to 4.4 pairs / 10 ha in swampy stands (Wesołowski et al. 2015). Research conducted in different parts of the BF showed that intensive forest management influences negatively on woodpeckers density. The most important variable conditioning their occurrence (especially two rare species: white-backed and three-toed woodpecker) was the amount of dead wood (Wesołowski 1995c; Wesołowski et al. 2005; Walankiewicz et al. 2002, 2011; Czeszczewik, Walankiewicz 2006; Czeszczewik et al. 2013). The occurrence of three-toed woodpecker is conditioned by the presence of decaying and freshly dead spruces (Wesołowski et al. 2005). In case of white-backed woodpecker, the presence of various forms of dead wood (standing, lying) of different species and in more advanced stages of decomposition is very significant. The volume of dead trees as well as the presence of thick trees is also important (Czeszczewik, Walankiewicz 2006; Czeszczewik 2009a, 2009b).

In case of whole communities of birds, significantly more insectivorous birds were nested in the BNP and nature reserves than in the managed part of the BF. Similar situation was in case of cavity-nesters (Czeszczewik et al. 2015). The structure of forest stand significantly affected the communities of birds in different parts of the BF. Basal area of living trees was positively correlated with the number of all birds, whilst the density of living trees was negatively correlated with both the number and species diversity of communities of birds. Moreover, in the managed part of the BF, the number of insectivorous birds and cavity-nesters was visibly smaller than that in the BNP with similar habitats and the most sensitive to changes caused by forest management turned out to be community of birds inhabiting coniferous stands (Czeszczewik et al. 2015).

It was shown that for many species of forest birds, natural gaps in forest stand with lying trees are very important. Those gaps are preferred as nesting or breeding spaces, for example, blackcap, chiffchaff (*Phylloscopus collybita*), and dunnock (Fuller 2000). In the BNP, the gaps, after certain amount of time, overgrow mostly with deciduous trees. In the managed part of the BF, the forest is much more dense and the gaps are usually managed by establishing one- or two-species planta-

Type of activity	Effects for the avifauna	Species or group of species	Source*
Reducing age of tree stands and remo- val of old trees	Shortage of cavities, dead wood and simplification of habitat structure lo- vers species diversity of invertebrates (food)	Secondary cavity nesters, woodpec- kers, insectivorous	11, 12, 1, 2
Removal of dead trees including cut- ting the spruces related to spruce bark beetle gradation	Lack of breeding and foraging places	White-backed, three-toed, black, lesser spotted woodpeckers	11, 5, 6, 12, 3, 1, 2, 7
Fragmentation of old-growth stands	Depletion of the species composition, change the size of the home range, and settlement of birds of open habitats in the forest interior	Woodpeckers, birds of prey	11
Simplification the forest structure by creating even aged stands	Reducing the number of nest sites	Cavity nesters, insectivorous	2
Planting of the monoculture (oak, spru- ce, pine)	Shortage of cavities, reducing the variety of food, lack of multilayer structure of stands	Cavity nesters, insectivorous	14
Aforestration of natural gaps in nature reserves with monocultures	Dissaperance of habitats	Ground nesters, birds foraging near the ground	4, 13
Reducing the share of key tree species (Hornbeam, aspen <i>Populus</i> <i>tremula</i> )	Shortage of good quality of cavities or sites for excavation	Collared flycatcher, woodpeckers	8,9
Seconadary forest succesion of the farmland	Disappearance of foraging grounds	Lesser spotted eagle	10

Table 1. Classification of threats for forest avifauna in the Białowieża Forest

\* 1 – Czeszczewik et al. 2013; 2 – Czeszczewik et al. 2015; 3 – Czeszczewik, Walankiewicz 2006; 4 – Fuller 2000; 5 – Walankiewicz et al. 2002; 6 – Walankiewicz et al. 2011; 7 – Walankiewicz et al. 2014; 8 – Walankiewicz, Czeszczewik 2005; 9 – Walankiewicz, Czeszczewik 2006; 10 – Wesołowski et al. 2003; 11 – Wesołowski 1995c; 12 – Wesołowski et al. 2005; 13 – Wesołowski et al. 2015; 14 – Wesołowski, Rowiński 2006.

tions. Such simplification of forest structure reduces the attractiveness of habitats for many species of birds.

The most important threats for avifauna in the BF were summarised in Table 1.

### 4. Summary

The BF is one of the few places in the zone of temperate climate where near-primeval conditions are still present. This extremely valuable fragment of forest, which is a heritage of a few nations, should not be changed into managed stands because of the possibility of studying the ecology and behaviour of forest birds. The BF should be covered with the widest and permanent legal protection, especially because over 99% of all forests of temperate zone are transformed by human. The BF, despite significant transformations on its large part, which happened in the 20<sup>th</sup> century, still remains a unique natural resource on the global scale. The guarantor of preserving existing natural values and goods of local culture should be cautious and responsible in taking all decisions concerning fighting the effects of natural environmental processes such as insect infestation, gap creation and rapid meteorological phenomena.

## **Conflict of interest**

The authors declare lack of potential conflicts.

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## References

- Czeszczewik D. 2004. Breeding success and timing of the Pied Flycatcher *Ficedula hypoleuca* nesting in natural holes and nest-boxes in the Białowieża Forest, Poland. *Acta Ornithologica* 39: 15–20.
- Czeszczewik D. 2009a. Foraging behaviour of White-backed Woodpeckers *Dendrocopos leucotos* in a primeval forest (Białowieża National Park, NE Poland): dependence on habitat resources and season. *Acta Ornithologica* 44: 109–118. DOI 10.3161/000164509X482687.
- Czeszczewik D. 2009b. Marginal differences between random plots and plots used by foraging White-backed Woodpeckers demonstrates supreme primeval quality of the Białowieża National Park, Poland. *Ornis Fennica* 86: 30–37.
- Czeszczewik D., Ruczyński I., Zięba-Schraven K., Wiśniewska J., Walankiewicz W. 2012. The Pied and Collared Flycatcher do not compete for microhabitats in the Białowieża Forest. *Belgian Journal of Zoology* 42: 131–135.
- Czeszczewik D., Walankiewicz W. 2003. Natural nest sites of the Pied Flycatcher in a primeval forest. *Ardea* 91: 221–230.
- Czeszczewik D., Walankiewicz W. 2006. Logging and distribution of the White-backed Woodpecker *Dendrocopos leucotos* in the Białowieża Forest. *Annales Zoologici Fennici* 43: 221–227.
- Czeszczewik D., Walankiewicz W., Mitrus C., Nowakowski W.K. 1999. Nest-box data of Pied Flycatcher *Ficedula hypoleuca* may lead to erroneous generalizations. *Vogelwelt, Suppl.* 120: 361–365.
- Czeszczewik D., Walankiewicz W., Mitrus C., Tumiel T., Stański T., Sahel M., Bednarczyk G. 2013. Importance of dead wood resources for woodpeckers in coniferous stands of the Białowieża Forest. *Bird Conservation International* 23: 414–425. DOI 10.1017/S0959270912000354.
- Czeszczewik D., Walankiewicz W., Stańska M. 2008. Small mammals in nests of cavity-nesting birds: Why should ornithologists study rodents? *Canadian Journal of Zoology* 86: 286–293. DOI 10.1139/Z07-139.
- Czeszczewik D., Zub K., Stański T., Sahel M., Kapusta A. 2015. Effects of forest management on bird assemblages in the Białowieża Forest, Poland. *iForest* 8: 377–385. http://www. sisef.it/iforest/contents/?id=ifor1212-007 [02.10.2014] DOI 10.3832/ifor1212-007.
- Fuller R. J. 2000. Influence of treefall gaps on distributions of breeding birds within interior old-growth stands in Białowieża Forest, Poland. *The Condor* 102: 267–274.
- Gutowski J.M., Jaroszewicz B. (red.). 2001. Katalog fauny Puszczy Białowieskiej. Instytut Badawczy Leśnictwa, Warszawa. 403 s. ISBN 83-87647-22-5.
- Hebda G., Pochrząst K., Mitrus S., Wesołowski T. 2013. Disappearance rates of old nest material from tree cavities: an experimental study. *Scandinavian Journal of Forest Research* 28: 445–450.
- Hebda G., Wesołowski T. 2012. Low flea loads in birds' nests in tree cavities. *Ornis Fennica* 89: 139–144.
- Jędrzejewska B., Jędrzejewski W. 2001. Ekologia zwierząt drapieżnych Puszczy Białowieskiej. Wydawnictwo Naukowe PWN. Warszawa. 461 s. ISBN 83-01-13533-6.

- Jones C. G., Lawton J. H., Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.
- Maziarz M., Wesołowski T. 2010. Timing of breeding and nestling diet of Wood Warbler *Phylloscopus sibilatrix* in relation to changing food supply. *Bird Study* 57: 540–552.
- Maziarz M., Wesołowski T., Hebda G., Cholewa M. 2015. Natural nest-sites of Great Tits (*Parus major*) in a primeval temperate forest (Białowieża National Park, Poland). *Journal of Ornithology* 156: 613–623.
- Maziarz M., Wesołowski T., Hebda G., Cholewa M., Broughton R. K. 2016. Breeding success of the Great Tit *Parus major* in relation to attributes of natural nest cavities in a primeval forest. *Journal of Ornithology* 157: 343–354.
- Mitrus C., Soćko B. 2010. Breeding success and nest-site characteristics of Red-breasted Flycatchers *Ficedula parva* in a primeval forest. *Bird Study* 55: 203–208.
- Newton I. 1998. Populations limitation in birds. Academic Press. 597 s. ISBN 9780125173667.
- Paine R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91–93.
- Tomiałojć L. 1990. Ptaki Polski rozmieszczenie i liczebność. Warszawa. PWN, 464 s. ISBN 83-01-09080-4.
- Tomiałojć L. 1993. Breeding ecology of the Blackbird *Turdus me-rula* studied in the primaeval forest of Białowieża (Poland). Part I. Breeding numbers, distribution and nest sites. *Acta Ornithologica* 27: 131–157.
- Tomiałojć L. 1995. The birds of the Białowieża Forest additional data and summary. Acta Zoologica Cracoviensia 38: 363–397.
- Tomiałojć L., Wesołowski T. 1994. Die Stabilität der Vogelgemeinschaft in einem Urwald der gemässigten Zone: Ergebnisseeiner 15jährigen Studieausdem Nationalpark von Białowieża (Polen). Der Ornithologische Beobachter 91: 73–110.
- Tomiałojć L., Wesołowski T. 1996. Structure of a primaeval forest bird community during 1970s and 1990s (Białowieża National Park, Poland). Acta Ornithologica 31: 133–154.
- Tomiałojć L., Wesołowski T. 2004. Diversity of the Białowieża Forest avifauna in space and time. *Journal of Ornithology* 145: 81–92.
- Tomiałojć L., Wesołowski T. 2005. The avifauna of the Białowieża Forest: a window into the past. *British Birds* 98: 174–193.
- Tomiałojć L., Wesołowski T., Walankiewicz W. 1984. Breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland). Acta Ornithologica 20: 241–310.
- Walankiewicz W. 1991. Do secondary cavity nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? *Natural Areas Journal* 11: 203–211.
- Walankiewicz W. 2002a. Breeding losses in the Collared Flycatcher *Ficedula albicollis* caused by nest predators in the Białowieża National Park (Poland). *Acta Ornithologica* 37: 21–26.
- Walankiewicz W. 2002b. Nest predation as a limiting factor to the breeding population size of the Collared Flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland). Acta Ornithologica 37: 91–106.
- Walankiewicz W. 2006. Czynniki ograniczające zagęszczenia lęgowe muchołówki białoszyjej *Ficedulaalbicollis* w pierwotnych grądach Białowieskiego Parku Narodowego (z krytycznym

przeglądem wcześniejszych hipotez). Akademia Podlaska. Siedlce.

- Walankiewicz W., Czeszczewik D. 2005. Wykorzystanie osiki Populus tremula przez ptaki w drzewostanach pierwotnych Białowieskiego Parku Narodowego. Notatki Ornitologiczne 46: 9–14.
- Walankiewicz W., Czeszczewik D. 2006. Znaczenie grabu zwyczajnego Carpinus betulus dla dziuplaków w Białowieskim Parku Narodowym. Chrońmy Przyrodę Ojczystą 62: 50–57.
- Walankiewicz W., Czeszczewik D., Mitrus C. 2007. Natural nest sites of the Collared Flycatcher *Ficedula albicollis* in lime-hornbeam -oak stands of a primeval forest. *Ornis Fennica* 84: 155–162.
- Walankiewicz W., Czeszczewik D., Mitrus C., Bida E. 2002. Znaczenie martwych drzew w lasach liściastych dla zespołu dzięciołów w Puszczy Białowieskiej. *Notatki Ornitologiczne* 43: 61–71.
- Walankiewicz W., Czeszczewik D., Stański T., Sahel M., Ruczyński I. 2014. Tree cavity resources in spruce-pine managed and protected stands of the Białowieża Forest, Poland. *Natural Areas Journal* 34: 423–428. DOI 10.3375/043.034.0404.
- Walankiewicz W., Czeszczewik D., Tumiel T., Stański T. 2011. Woodpeckers abundance in the Białowieża Forest – a comparison between deciduous, strictly protected and managed stands. *Ornis Polonica* 52: 161–168.
- Walankiewicz W., Mitrus C., Czeszczewik D., Jabłoński P. M. 1997. Is the Pied Flycatcher *Ficedula hypoleuca* overcompeted by the Collared Flycatcher *Ficedula albicollis* in the natural forest of Białowieża? *Acta Ornithologica* 32: 213–217.
- Wesołowski T. 1981. Population restoration after removal of wrens (*Troglodytes troglodytes*) breeding in primaeval forest. *Journal* of Animal Ecology 50: 809–814.
- Wesołowski T. 1983. The breeding ecology and behaviour of Wrens *Troglodytes troglodytes* living under primaeval and secondary conditions. *Ibis* 125: 499–515.
- Wesołowski T. 1985. The breeding ecology of the Wood Warbler *Phylloscopus sibilatrix* in primaeval forest. *Ornis Scandinavi*ca 16: 49–60.
- Wesołowski T. 1989. Nest-sites of hole-nesters in a primaeval temperate forest (Białowieża National Park, Poland). Acta Ornithologica 25: 321–351.
- Wesołowski T. 1995a. Birds from a primaeval temperate forest hardly use feeders in winter. Ornis Fennica 72: 132–134.
- Wesołowski T. 1995b. The loss of avian cavities by injury compartmelization in a primeval European forest. *The Condor* 97: 256–257.
- Wesołowski T. 1995c. Value of Białowieża Forest for the conservation of white-backed woodpecker (*Dendrocopos leucotos*) in Poland. *Biological Conservation* 71: 69–75.
- Wesołowski T. 1996. Natural nest sites of Marsh Tits Parus palustris in a primaeval forest (Białowieża National Park, Poland). Die Vogelwarte 38: 235–249.
- Wesołowski T. 1998. Timing and synchronisation of breeding in a Marsh Tit *Parus palustris* population from a primaeval forest. *Ardea* 86: 89–100.
- Wesołowski T. 1999. Marsh Tits (*Parus palustris*) are not excavators. *Ibis* 141: 149.

- Wesołowski T. 2000. What happens to old nests in natural cavities? *The Auk* 117: 498–500.
- Wesołowski T. 2002. Antipredator adaptations in nesting marsh tits *Parus palustris* – the role of nest site security. *Ibis* 144: 593–601.
- Wesołowski T. 2003. Bird community dynamics in a primaeval forest – is interspecific competition important? *Ornis Hungarica* 12–13: 51–62.
- Wesołowski T. 2007a. Lessons from long-term hole-nester studies in a primeval temperate forest. *Journal of Ornithology* 148: 395–405.
- Wesołowski T. 2007b. Primeval conditions what can we learn from them? *Ibis* 149: 64–77.
- Wesołowski T. 2011. "Lifespan" of woodpecker-made holes in a primeval temperate forest: a thirty year study. *Forest Ecology* and Management 262:1846–1852.
- Wesołowski T. 2012. "Lifespan" of non-excavated holes in a primeval temperate forest: A 30 year study. *Biological Conservation* 153: 118–126.
- Wesołowski T., Czeszczewik D., Hebda G., Maziarz M., Mitrus C., Rowiński P. 2015. 40 years of breeding bird community dynamics in a primeval temperate forest (Białowieża National Park, Poland). *Acta Ornithologica* 50: 95–120.
- Wesołowski T., Czeszczewik D., Mitrus C., Rowiński P. 2003. Ptaki Białowieskiego Parku Narodowego. Notatki Ornitologiczne 44: 1–31.
- Wesołowski T., Czeszczewik D., Rowiński P. 2005. Effects of forest management on Three-toed woodpecker *Picoides tridactylus* distribution in the Białowieża Forest (E Poland): conservation implications. *Acta Ornithologica* 40: 53–60.
- Wesołowski T., Maziarz M. 2009. Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primeval forest: a thirty-year perspective. *Acta Ornithologica* 44: 69–80.
- Wesołowski T., Mitrus C., Czeszczewik D., Rowiński P. 2010. Breeding bird dynamics in a primeval temperate forest over thirty -five years: variation and stability in the changing world. *Acta Ornithologica* 45: 209–232.
- Wesołowski T., Rowiński P. 2004. The breeding behaviour of the Nuthatch *Sitta europaea* in relation to natural hole attributes in a primeval forest. *Bird Study* 51: 143–155.
- Wesołowski T., Rowiński P. 2006. Tree defoliation by winter moth Operophtera brumata L. during an outbreak affected by structure of forest landscape. Forest Ecology Management 221: 299–305.
- Wesołowski T., Rowiński P. 2012. The breeding performance of Blue Tits *Cyanistes caeruleus* in relation to the attributes of natural holes in a primeval forest. *Bird Study* 59:437–448.
- Wesołowski T., Rowiński P. 2014. Do Blue Tits *Cyanistes caeruleus* synchronize reproduction with caterpillar peaks in a primeval forest? *Bird Study* 61: 231–245.
- Wesołowski T., Rowiński P., Maziarz M. 2009. Wood Warbler *Phylloscopus sibilatrix*: a nomadic insectivore in search of safe breeding grounds? *Bird Study* 56: 26–33.
- Wesołowski T., Rowiński P., Mitrus C., Czeszczewik D. 2006. Breeding bird community of a primeval temperate forest (Bia-

łowieża National Park, Poland) at the beginning of the 21<sup>th</sup> century. *Acta Ornithologica* 41: 55–70.

- Wesołowski T., Stańska M. 2001. High ectoparasite loads in hole nesters - a nest box bias? Journal of Avian Biology 32: 281–285.
- Wesołowski T., Stawarczyk T. 1991. Survival and population dynamics of Nuthatches *Sitta europaea* breeding in natural cavities in a primeval temperate forest. *Ornis Scandinavica* 22: 143–154.
- Wesołowski T., Tomiałojć L. 2005. Nest sites, nest depredation, and productivity of avian broods in a primeval temperate forest: do the generalisations hold? *Journal of Avian Biology* 36: 361–367.
- Wesołowski T., Tomiałojć L., Mitrus C., Rowiński P., Czeszczewik D. 2002. Breeding bird community of a primeval temperate forest (Białowieża National Park, Poland) at the end of XX<sup>th</sup> century. *Acta Ornithologica* 37: 27–45.

- Wesołowski T., Tomiałojć L., Stawarczyk T. 1987. Why low numbers of *Parus major* in Białowieża Forest - removal experiments. *Acta Ornithologica* 23: 303–316.
- Willis K. J., Gillson L., Brncic T. M. 2004. How "Virgin" Is Virgin Rainforest? *Science* 304: 402–403. DOI 10.1126/ science.1093991.

# **Authors' contribution**

D.Cz. – concept of research, analysis of research results, literature review, writing an article; W.W. – concept of research, analysis of research results, literature review, writing an article.