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Distribution, breeding density and nest sites of Hawfinches *Coccothraustes coccothraustes* in the primeval forest of Białowieża National Park

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Abstract. Long-term observations (1991–2002) have shown that Hawfinches breed throughout the extensive Białowieża Forest; they are only slightly less numerous in the forest interior than at its edge. Population size, habitat and nest sites were studied in two plots in the species-optimal habitat (continuous oak-lime-hornbeam old-growth). The true breeding density there was 4.0–8.4, reaching as much as 15.2 p/10 ha in some years, while, according to the combined territory-mapping method for the same period, it was, on average, 5.8 pairs/10 ha in oak-lime-hornbeam, 3.3 pairs/10 ha in riparian ash-alder, but less than 0.5 pairs/10 ha in mixed coniferous-deciduous or young deciduous stands (marginal habitats for this species). Being among the most numerous species in the Białowieża Forest bird community, Hawfinches hold small nesting territories that are sometimes loosely grouped. Nests are built at an average height of 18.1 (7–34) m in the tree canopy. Hornbeams are the preferred tree species for nesting in the oak-lime-hornbeam stands (also clumps of mistletoe in the continental maple), while black alders in the riparian woodland. Originally, the Hawfinch must have been a species of old, high forests. Its recent nesting elsewhere — low in bushes or, preferably, along woodland edges — is likely to be a secondarily acquired trait; it could also be due to a bias — Hawfinch nests are more easily discovered in such localities.

Key words: Hawfinch, *Coccothraustes coccothraustes*, population density, habitat choice, nest sites, pristine forest, Białowieża National Park

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INTRODUCTION

The Hawfinch is a passerine widespread across the whole Palearctic which, depending on the region, is a resident, short-distance migrant or summer visitor (Dementiev & Gladkov 1954, Cramp & Perrins 1994, Glutz von Blotzheim & Bauer 1997). It breeds commonly across the extensive Białowieża Forest. Though this east-Poland population largely winters in southern France and Italy, yet during some seasons considerable flocks stay for winter in the Białowieża Forest itself (Polish Bird Ringing Scheme data, Author's own observ.). In the most of Europe and Far East the species breeds typically in deciduous broad-leaved and, less frequently, in mixed deciduous-coniferous woodlands. Within its eastern-European part of range it settles also in the conifer-dominated stands, while in southern Siberia also happens in the mixed deciduous-coniferous "insular" woods of the forest-steppe transition zone (Dementiev & Gladkov 1954, Cramp & Perrins 1994). In the contemporary European anthropogenic landscape it widely, though in scarce numbers, occurs in woods, parks, orchards and several plantations of young trees, chiefly of poplars or birches (Bijlsma 1979, Krüger 1982, Knysh 1998).

The Białowieża Forest oak-lime-hornbeam undisturbed old-growth constitutes an optimal breeding habitat of the species, apparently very close to the pristine one. This habitat is quite different from the secondary tree-stands of fragmented west-European woodlands and park-lands, where the other studies of the Hawfinch biology were carried out (Mountfort 1957,

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Herroelen 1962, Bijlsma 1979, 1998, Krüger 1982, Newton 1985). Also recent studies in the orchards of western Poland (Kwiatkowska & Mroczkiewicz 1995), and in Ukrainian habitats (Knysh 1998) describe the secondary situation.

The aim of the present work was therefore to reveal the patterns of the "close-to-pristine" distribution, abundance, habitat and nest-site choice of the Hawfinch population in a little-disturbed extensive forest. A part of these results has been incorporated into the species section in the 14 volume of the "Handbuch der Vögel Mitteleuropas" (Glutz von Blotzheim & Bauer 1997), yet, the present paper is based on extended data set.

STUDY AREA

The field work was carried out in the very centre of the Białowieża Forest (= BF, ca. 1500 km^2, 30–40 km in diameter), situated on the Polish-Byelarus border. Though several parts of BF were subjects of the 19th and 20th century forest management, yet other fragments have retained the close-to-primeval woodland character (Faliński 1986, Jędrzejewska & Jędrzejewski 1998). The latter ones have been included into the Białowieża National Park (BNP thereafter) to remain under strict protection since 1921.

The BNP stands, as place of present study, are distinguished from managed woodlands by retaining features typical of rich primeval forests: multi-storey profile of stands, multi-species tree communities, high age and size of old trees, presence of young re-growth in between old timber and uprooted trees, high species richness of plants and animals (Tomiałojć et al. 1984, Faliński 1986, Jędrzejewska & Jędrzejewski 1998, Tomiałojć & Wesołowski 2005).

The intensive study plots

For the intensive study, two plots gridded 50 x 50 m have been selected in BNP (W = 31.5 and M = 30 ha). They are samples from the optimal for Hawfinch habitat, the ancient and never subjected to a direct human impact oak-lime-hornbeam *Tilio (Querco)-Carpinetum* old-growth with an admixture of mature spruces. Plot W represents the conditions typical of the 500 m wide forest-edge zone adjoining the Białowieża Glade, while plot M those of the forest interior, 3.5 km from the Białowieża Glade and 8 km from extensive agricultural landscape. This habitat is formed of a mostly deciduous, multispecies and multi-layer tree-stand, with its emergents (spruces, oaks, ashes) reaching the height of 40–45 (57) m. The tree stand in both plots is very similar to each other, differing only in a slightly higher share of old spruces in plot W than in plot M. Besides permanent census plots, some patches of much younger stands were checked each year in search for Hawfinch nests. These were: an area of 12 ha in BNP with the 20–50-year-old successional regrowth of the hornbeam-lime-ash (in a few windfalls) and a 7 ha patch of 20–30-year old aspen-birch-hornbeam stand on the former field in front of the forest wall (at the plot W). Additional observations were carried out in a habitat that is suboptimal for the species, a less dense and slightly lower pristine ash-alder riparian stand, and, sporadically, in a marginal habitat — mixed coniferous-deciduous stands (details in: Tomiałojć et al. 1984, Jędrzejewska & Jędrzejewski 1998, Tomiałojć & Wesołowski 2005).

The breeding season conditions in BNP fluctuated between years in two respects: the weather and the caterpillar abundance. For the purpose of this paper, the former factor is especially important. Of all years with prevailing weather typical of the region, the most aberrant was the exceptionally warm season 1993 (between the 22 April and mid-May temperatures up to 24–28°C). This caused the Hawfinch to build nests during the advanced stage of leaf development, with consequences shown in the paper.

METHODS

Two kinds of field results on the species abundance have been analysed: 1) the territory mapping technique estimates and 2) the true density data. The first type of data (after Tomiałojć et al. 1984, Tomiałojć & Wesołowski 2005) reflects approximate Hawfinch abundance being extracted from the standard bird survey carried out with the application of an improved (combined) version of the territory-mapping technique. In the case of Hawfinch this method causes the underestimates constituting (68) 76–84% of true numbers (Tomiałojć 2004). The true Hawfinch abundance (and true breeding density) was obtained from two census plots surveyed with a much higher effort during the breeding seasons 1991–1994, 1996 and 1998 (and less completely for 1995, 1997 and 2002). Each year 12–18 half-day visits per one plot were made between mid-April and mid June. All observations were recorded on 1:1000 maps in

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order to draw the approximate limits of nesting ranges. The pairs were followed as long as possible to make simultaneous records of the neighbouring pairs and to enable repeat-searching of nests in all suspected sites. The total time effort was ca. 90–124 hours of work per plot and season, depending on the weather and current population size. Persistent observations of the Hawfinch distribution and behaviour, following movements of particular pairs and finding most nests resulted in 95–100% accuracy, which was checked by comparing the numbers assessed with the number of nests found after leaf fall (Tomiałojć 2004). The individual life histories of most Hawfinch pairs could be followed, though not of all of them, as there was no individual marking.

The nest search started after a few April surveys, when the steadily occupied activity ranges of particular pairs became known. During the late April and early May, before full leaf development in deciduous trees, Hawfinch nests under construction are quite conspicuous, so that usually 80–94% of them were found. When repeated search in a nesting range failed, attention was focussed on the territorial behaviour to eventually find most missing nests. The knowledge of nest locations enhanced the precision of the estimates of the nesting range numbers. A slight bias can be present only in the case of nests located in spruces, yet most of spruces were transparent enough and only some caused difficulties.

The active nests and the structures recalling the remnants of the previous-year nests were regularly checked from the ground by binoculars for occupancy or for signs of rebuilding them. A smaller sample of nest contents was checked by repeated climbing. As the Hawfinch nest constructions are solid enough to persist in dense forest for two-three seasons, so a presence of a few old nests in a tree served as an indication of a preferred site. The height of nest location was estimated by counting 2 m-long units, earlier marked at the tree-stem base; these estimates were from time to time checked by an altimeter used in forestry.

Owing to the absence of any overt advertising of the territories in this species, here only the number and an approximate size of its nesting ranges were evaluated. Therefore, there was no sense in more detailed measuring the size of individual nesting ranges, though some (those surrounded by other ranges, sometimes in small subcolonies) could be evaluated precisely. Two or three nests in a nesting range almost always resulted from replacement clutches (which could be judged from their relative timing), as there is no firm evidence for double-brooding in this population (Tomiałojć, in prep.).

To describe the Hawfinch nesting-tree preference, within plots W and M, 3279 live trees of diameter ≥ 15 cm were measured (W. Walankiewicz, unpubl. data). Under this procedure, 50 randomly selected sample areas of 0.25 ha each (12.5 ha in total) were investigated.

RESULTS

Breeding distribution and abundance of forest Hawfinches

Distribution across the BF. 25-year extensive observations have documented that Hawfinches inhabit various types of mainly deciduous old growth across the whole BF tract. In the BNP they breed preferably in the oak-lime-hornbeam stands and then in the riparian ash-alder old growth as suboptimal habitats. Intensive-study data confirm that the Hawfinch breeds not only along the forest edges. For comparable years the mean density was 8.5 p/10 ha for the forest-edge plot W and almost 7.0 for the forest-interior plot M (Table 1). Although this difference is statistically non-significant due to small sample (t-test, $p > 0.05$), yet it may be consistent in most years. Moreover, in forest-interior plot M also the span of density fluctuations was higher, suggesting a slightly less suitable character of this area. The figures for the two sample plots usually fluctuated in parallel (Table 1), sporadically (during unusual year 1993) displaying the opposite changes. The reason for the latter may be local, acting in plot M, where, in 1992, heavy nest destruction (82.3%, $n = 17$) by predators could force adult Hawfinches to move to other sites next season. In the marginal habitat type, the conifer-dominated plots, single pairs bred only during two caterpillar outbreak periods (1975 and 1992–1993), though not during the two other ones: 1982 and 1994.

In the BNP Hawfinches are strongly restricted to the old and medium-age woodland, only exceptionally breeding in young tree-stands. After realising this unexpected regularity, each year starting from 1993, before full leaf development I made comparative searches over two areas (12 ha in BNP and 7 ha of a re-growth in front of plot W). Only three remains of old nests from various years were found in the first area, and nothing in the second one.

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Table 1. True numbers of pairs and breeding densities in the oak-lime-hornbeam old growth of BNP.

Years	Census plot and size			
	Forest edge (W), 31.5 ha		Forest interior (M), 30 ha	
	N of ranges occupied	Density (p/10 ha)	N of ranges occupied	Density (p/10 ha)
1991	20	6.3	21	7.0
1992	21	6.6	16.5	5.5
1993	26.5	8.4	12	4.0
1994	23	7.3	23.5	7.8
1995	23.5	7.5	?	?
1996	48	15.2	35.5	11.8
1997	24	7.6	17.5	5.8
1998	45	14.3	?	?
2002	23	7.3	?	?
Average (for comparable years)	28.2	8.9 (8.56 ± 3.3)	21.0	7.0 (6.98 ± 2.7)

Breeding numbers and densities. During the 8-year period of the intensive study, the numbers of Hawfinches fluctuated roughly by the factor of two (Table 1), but without a clear trend.

In their optimal habitat, Hawfinch pairs are spread over the whole area, chiefly during the high-density years (Fig. 1), though not very uniformly. Consequently, active nests of different

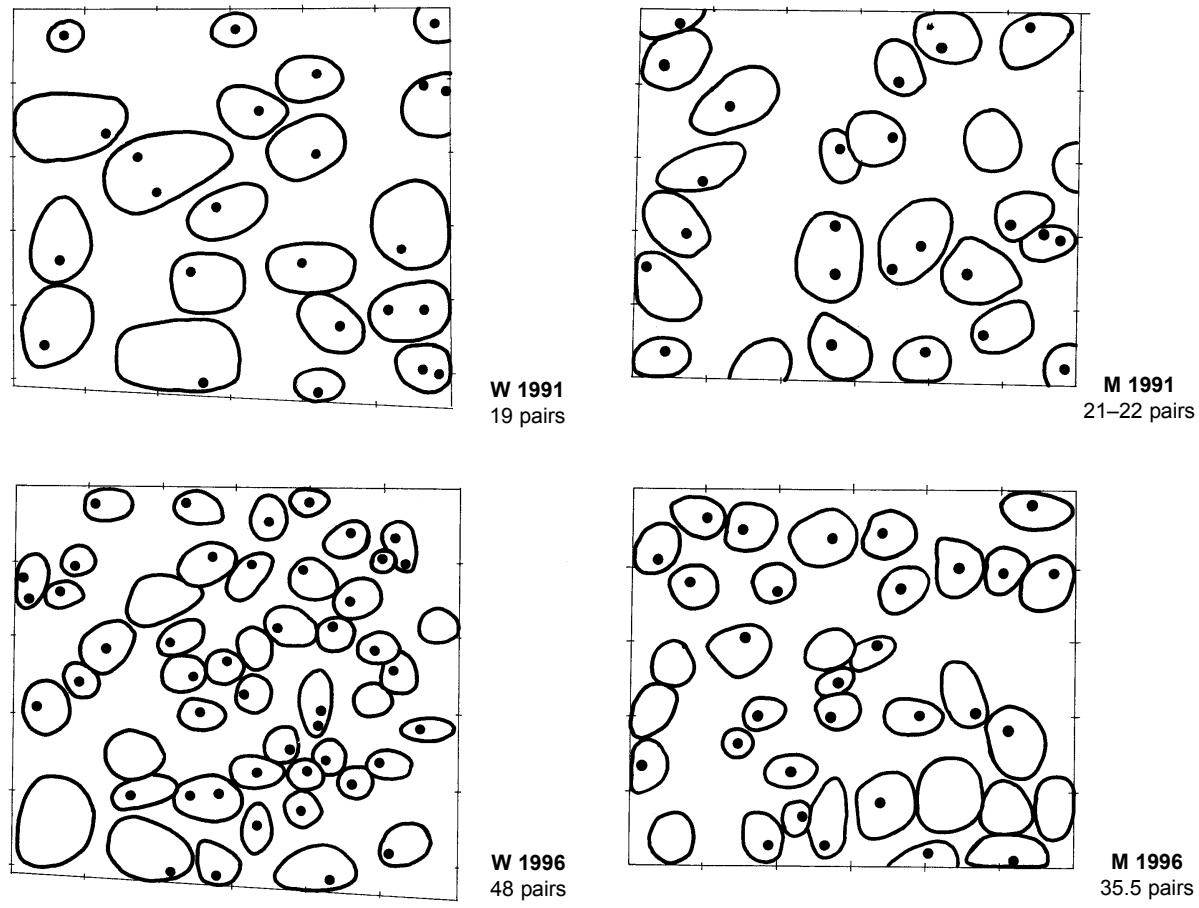

Fig. 1. Distribution of nesting ranges and nests found (dots) in two sample plots: alongside the south exposed forest-edge (plot W) and the forest-interior (plot M), both during low (1991) and high (1996) Hawfinch numbers. Two nests in a range denote replacement breeding attempts.

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pairs can be only 50–70 m apart, less often as close as 20, and once only 7 m from one another.

Though the birds were not individually marked, a considerable number of simultaneous records of neighbouring pairs whose movements were followed long enough and finding almost all nests allowed to estimate the approximate size of many Hawfinch nesting ranges (not "territories"). This approximate size varied between 1.5 and 2.0 ha, sometimes (in loose colonies of 3–5 pairs) were only 0.2–0.5 ha.

The nesting sites

Nesting tree choice. Oak-lime-hornbeam parts of BNP significantly differed in the utilisation of nest trees, depending the tree-stand composition (χ^2 = 133.27, df = 6, $p < 0.0001$) (Fig. 2). In the BPN the Hawfinches nest mostly in hornbeams and, then, in continental maples and limes. The results have been shown in two samples (Table 2): for several habitats searched extensively and for the intensively studied oak-lime-hornbeam stands alone (with almost all nests found), where true but local proportions have been reflected. The first sample suffers from a bias because during extensive observations some difficult nests must have been overlooked if located in less transparent sites, e.g. early in May even nests located high in bare (still leafless) oak branches might be obscured from below by dense crowns of hornbeams. So, proper proportions for the whole BNP may be intermediate between data from two columns in Table 2, though probably closer to those from the intensive period of study.

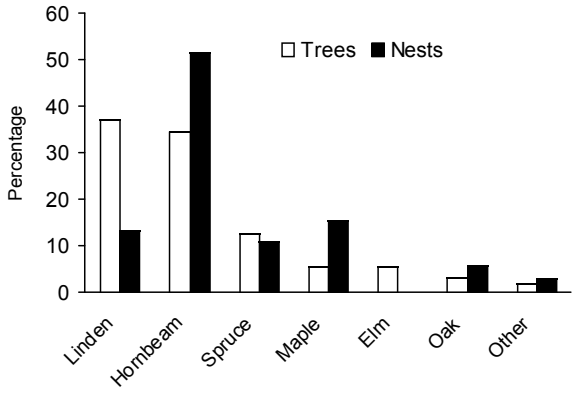

Fig. 2. Hawfinch nesting tree preference (N = 289 nests) in comparison with tree species share (N = 3279 trees) in the oak-lime-hornbeam parts of BNP.

Though most nests were found in hornbeams, yet Hawfinches showed the strongest preference (Fig. 2) for nesting in the continental maple, with the percentage of nests being 3 times as high as the share of that tree in the oak-lime-hornbeam community (15.6 versus 5.4%), then in pedunculate oak (5.9 versus 3.1%) and, lastly, in the most numerous tree, the hornbeam (51.5 versus 34.4%). High position of continental maples and, partly, of lime, both species being structurally unsuitable for Hawfinch due to scarce and smooth twigs, may be explained by the fact that a half of these nests were placed in the bunches of mistletoe *Viscum album*. These bunches, offering a support and a good cover under evergreen leaves, contained almost a half of 65 active nests found in these two tree species. Also the oak may be in fact not a preferred tree at all if one takes into account its large crowns, by volume equivalent to about three times as many other trees. Instead, another really preferred tree is the alder; its share as nesting tree among the oak-lime-hornbeam nests is low (1.7%), yet in riparian stands (where no maples and hornbeams) the alders constituted 56.6% of all nesting trees (n = 30), with the second position (26.6%) occupied there by spruces. The share of spruces in Table 2 may be slightly underestimated for the extensive study period, owing to a difficulty of finding nests in their dense crowns. Yet in oak-lime-hornbeam stands the spruce appears not to be preferred by Hawfinches even during the early spring, when a great majority of active nests was found by watching the owners and by turning special attention to scattered single spruces in

Table 2. Nesting trees with the active Hawfinch nests in BNP. Extensive study — 7 plots in three habitats (1975–1990, 1997), intensive — two plots in oak lime hornbeam (1991–1996, 1998). Details — see text.

Tree species	Number of nests (%)	
	Extensive study	Intensive study
Hornbeam *Carpinus betulus*	72 (49.3)	149 (51.2)
Maple *Acer platanoides*	12 (8.2)	45 (15.5)
Lime/linden *Tilia cordata*	24 (16.4)	38 (13.1)
Spruce *Picea abies*	15 (10.3)	32 (11.1)
Alder *Alnus glutinosa*	15 (10.3)	6 (1.7)
Oak *Quercus robur*	2 (1.4)	17 (5.9)
Birch *Betula verrucosa*	2	1
Ash *Fraxinus excelsior*	1	1
Aspen *Populus tremula*	0	1
Elm *Ulmus* sp.	1	1
Willow *Salix alba*	1	0
Hasel *Corylus avellana*	1	0
Totals:	146 (100)	291 (100)

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those ranges in which nests failed to be found earlier. On the contrary, the share of hornbeam nests among the old (from previous-year) nests was artificially high (69%, n = 92); this bias resulted from a higher conspicuousness of old nests when searched during the leafless period in April. The remaining tree species in BNP were accepted in proportion apparently slightly higher than is their share in tree community.

Height above the ground. The height of nest location did not change from year to year, hence, all the results from intensive study period have been pooled together. The mean height of active nests and of old (previous-year) ones, was also identical: 18.1 m (n = 433, span 7–33 m) for active, as well as 18.1 (n = 534, span 7–34 m) for the active and old nests combined. Only in one case a pair started to build their nest at the hornbeam stem 4 m above the ground, but deserted it because of the observer's presence.

Being located often in the upper parts of the crowns of the medium-sized or large trees, the Hawfinch nests might suffer from strong winds. Yet, in a dense and high old growth like that in BNP these apparently weak constructions tend to remain in trees for 2–3 seasons. A few cases of nests thrown down were inconclusive, whether this was caused by wind or by predators.

The Hawfinch nests in BNP are always placed in high and medium-size tree crowns. Of five types of nest location (Fig. 3), the four main are fairly similar structurally to each other. Most frequent (31%) are the nests at the main stem of a deciduous tree (often hidden in offshoots) or at a medium-size spruce crown. Three other locations are similarly frequent: in the mistletoe bunches, in uppermost vertical branches of old hornbeams and in branches of horizontally bent deciduous trees or on the lowest horizontal branches of huge spruces. Most exceptional (1.5%) are nests put Blackbird-like in a bifurcation of the bare main hornbeam stems, while the bush nests were not recorded at all. Disregarding described structural differences, the nests almost always were in sites with a free access from the air.

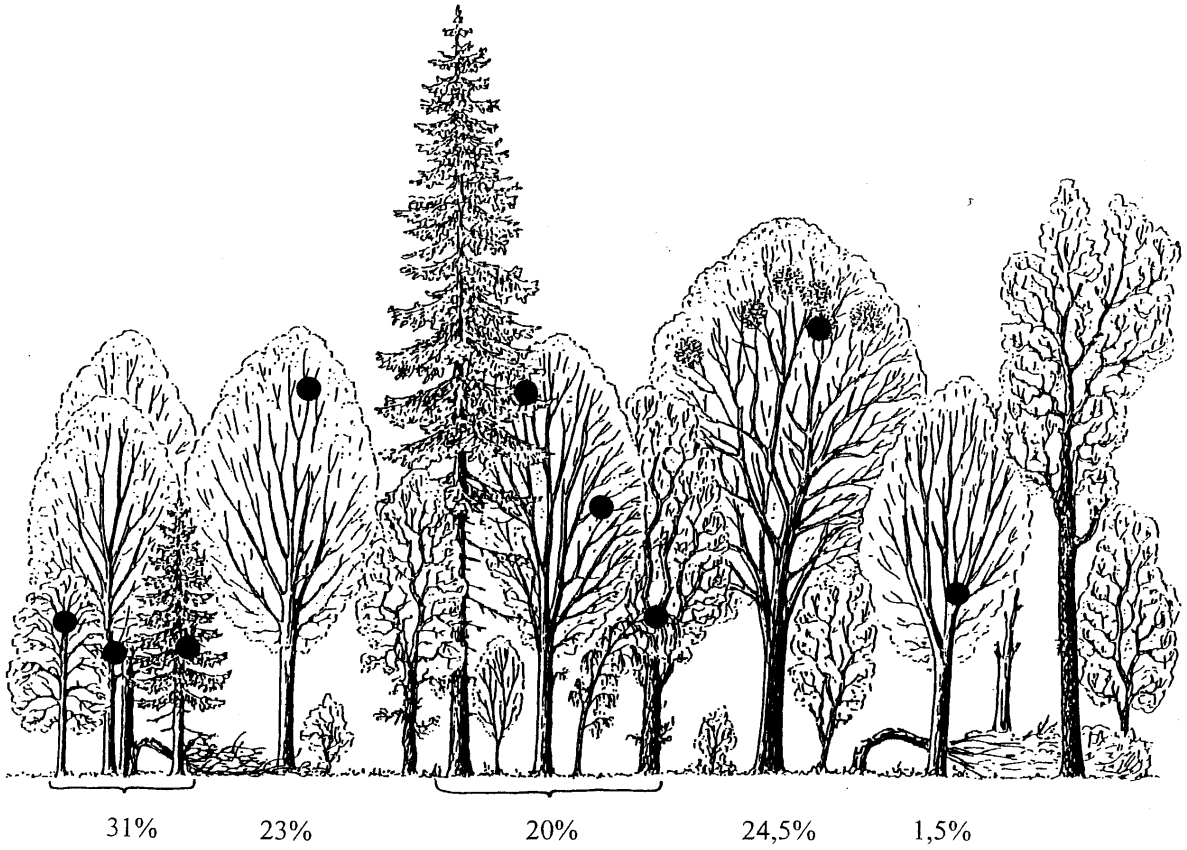

Fig. 3. Main types of the Hawfinch nest location in a high oak-lime-hornbeam forest of BNP. The illustration reprinted with the editors permission from Glutz von Blotzheim & Bauer (1997), but up-dated on larger material, N = 424 nests.

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DISCUSSION

Primeval and secondary features in the Hawfinch habitat choice and distribution

The breeding distribution and current population size. The spring-time distribution of Hawfinches in the Białowieża Forest can be estimated with ascending accuracy at three scales: for the whole BF, for the BNP area which is especially rich in the preferred close-to-primeval deciduous old growth, and for the study plots within the optimal habitats. At the first scale, Hawfinches settle to breed over the whole extensive BF, even in its innermost fragments 7–15 km distant from any larger open area. The forest interior, if containing the patches of optimal habitat, is being inhabited with average densities similar or perhaps only slightly lower than those along the forest edge (Table 1). The total Hawfinch population in the BF is not known because of difficulties in censusing this species (Tomiałojć 2004). Using the accurate density values as well as the incomplete relative estimates from the territory-mapping data for an extrapolation, it can only be roughly guessed that in the Polish BNP (within its old boundaries, 47 km^2), i.e. in the area covered in ca. 44% with the oak-lime-hornbeam old-growth, the remaining parts under mixed-coniferous-deciduous and ash-alder riparian stands, its local population may fluctuate between c.1000 pairs in low-density years and some 3000 during the peak numbers. Consequently, in the whole BF some 3 000–8 000 pairs may occur, which is equivalent to the whole British population estimated at 3 000–6 500 pairs (Stone et al. 1997).

Habitat choice. Within the BF Hawfinches show a strong preference to deciduous stands. According to averaged long-term mapping technique, the "relative breeding densities" (uncorrected, cf. Tomiałojć 2004) in oak-lime-hornbeam old growth are on average 3.9 p/10 ha, in old riparian ash-alder three times lower (1.6) while in the mixed coniferous-deciduous ones — occupied not every year — only locally and below 0.1 p/10 ha (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1994). The last figure explains why in the eastern (Byelarusian) part of BF, with its mainly coniferous tree-stands, the species is listed among regular but scarce breeders (Gavrin 1953, Dackevich 1998). E.g. also in our conifer-dominated plots, single pairs bred only during two (1975 and 1992–1993) Geometridae caterpillar outbreak periods, though not during the two other ones: 1982 and 1994 (Tomiałojć & Wesołowski 1996). As in optimal habitats the former years were not characterised by the highest Hawfinch densities, this excludes a possibility of an overspill from best habitats. The Hawfinches seem to penetrate marginal habitats randomly, settling in them when there is more food.

Breeding densities

The true breeding densities in BNP (Table 1), in best sites and years in the ancient oak-lime-hornbeam forest, are usually between 4.0–8.0, exceptionally even 13–15 p/10 ha. This makes Hawfinch the third or fourth most numerous breeder in the local bird community (Wesołowski et al. 2002). In spite of this, during the second-half of May, an observer less acquainted with this species may fail to notice the presence of even a single Hawfinch.

The territory-mapping technique monitoring data for the whole 25-year period have revealed a significant though slow increasing trend in abundance of this species (Wesołowski & Tomiałojć 1997), which means that the present study described the population state higher than that from two earlier decades (Tomiałojć et al. 1984).

The averages of the "territory-mapping (incomplete) densities" from two 5- year periods (1990–1999) and from several plots were, accordingly: in the oak-lime-hornbeam stands (n = 6) 5.8 p/10 ha, in ash-alder and alder (n = 4) 3.3, while in mixed coniferous-deciduous stand — occupied not every year — below 0.5 p/10 ha (Tomiałojć & Wesołowski 1996, Wesołowski et al. 2002). However, the true density figures from mid-1990s obtained in two oak-lime-hornbeam stands were much higher, between 5.9 and 7.7 p/10 ha, and in exceptional years up to 15.5 p/10 ha (Table 1).

True breeding densities in oak-lime-hornbeam habitats of BNP are several times higher than in other European natural forests, though most data on the latter ones were based on the incomplete territory-mapping technique results (Mountfort 1957, Newton 1985, Flade 1994) and/or were obtained from a mosaic of suboptimal habitats (Bijlsma 1979, 1998). For western natural forests the highest figure usually was about 3.0 p/10 ha, and it was exactly the level found in BNP during the 1970s and 1980s (Tomiałojć et al. 1984, Glutz von Blotzheim & Bauer 1997), yet for the 1990s also our mapping data were higher almost by half: on average 5.6 p/10 ha in oak-hornbeam habitat (Tomiałojć & Wesołowski 1996, Wesołowski et al. 2002). However, high true densities found recently in the BNP may be not so exceptional, when the scarcity of comparable studies conducted in the

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deciduous old growth is taken into account. The only oak-hornbeam old growth patch from Holland (27 ha) similar to the BNP had exactly the density of 9.7 p/10 ha (Bijlsma 1998), though the site formed an inclusion amongst a more thinly populated secondary woodland. A few thorough investigations in fragmented anthropogenic landscape have revealed similar densities but from very small plots — up to 8.1 p/10 ha (Krüger 1982) or even 16.2 p/10 ha (Knysh 1998), the last result being an overestimation recalculated from 3.7 ha. Moreover, the latter two high densities were found in the habitats structurally very different from BNP stands — in the poplar plantations with a luxuriant bush layer or in old and low-tree orchards. Finally, a result comparable to BNP, with 12.8 p/10 ha, was reported from Germany, but from completely different conditions — an "insular" oak-hornbeam stand in which several attempts to increase the bird density were experimentally undertaken (Pfeifer & Keil 1958).

Forest-edge zone versus forest interior

It was suggested that the forest edge zone is preferred by Hawfinches for nesting (Krüger 1982, Knysh 1998). The BNP stands offer an opportunity to study the edge effect in an undisturbed forest, though the local southern edge has been made abrupt by humans, and only recently it redevelops a transition belt. My results allow to analyse this aspect at two scales. The first one, comparing Hawfinch densities in the forest-edge plot W and those from the plot M situated 3.5 km in forest interior failed to reveal a significant difference, although the density at the forest edge often was slightly higher (Table 1, Fig. 1). On the local scale, restricted to the plot W, within the first 200 m wide forest-edge zone, these birds also seem to occur in slightly higher numbers, but not very consistently from year to year. A spatial distribution pattern of their nesting ranges (Tomiałojć 2004 and Fig. 1) is only a little more stable along the forest edge than deeper inside (in the belt 200–500 m from edge). This pattern may result from the forest-edge line forming a barrier to the nesting range shifts under pressure of the neighbours. This would recall a fence effect, in an automatic way influencing density. Yet, the differences found are so small that they may hardly have any biological meaning for the Hawfinch population.

Do Hawfinches saturate BNP habitats?

The question should be split into two more detailed ones: 1) are Hawfinches distributed uniformly across the potentially suitable habitat? and 2) do they saturate the optimal oak-lime-hornbeam old-growth during high-density years? The distribution of nesting ranges as reflected on species maps (Fig. 1) shows some gaps left unsettled. Because most of these gaps were occupied in some years (a proof of suitability), this suggests that Hawfinches in the BNP do not saturate their optimal habitat, i.e. the number of physically suitable nesting sites and ranges exceeds the requirements. On the other hand, in both plots some fragments were occupied persistently with a greater density, while other ones with a lower density, indicating some microhabitat differentiation. E.g. the eastern half of plot W was always better populated than the western part (Fig. 1), sometimes in a proportion of 12 to 3 early-season occupied ranges. The western part is, in fact, more fragmented by windfalls, contains larger patches with unsuitable younger tree stands, and (which seems most important) has a lower share of the early-flowering forms of the old pedunculate oaks and of the continental maples, both trees being important for early spring foraging of Hawfinches. In spite of this, when compared to Dutch fragmented woodland (Bijlsma 1979, 1998), the distribution of breeding Hawfinches in the stands of the BNP is almost uniform (Fig. 1). Such a result adds a novel contribution to the knowledge resulting from the west-European studies in fragmented habitats (Mountfort 1957, Bijlsma 1979, 1998). Though, exact sizes of the Hawfinch breeding territories are hard to evaluate, the maps (Fig. 1) reveal only a very slight preference for some forest patches (i.e. occupied each year). So weak a preference fails to prevent from changes in location of small semi-colonies, which "move" from year to year even into opposite parts of the plot.

A tendency of "synanthropic" Hawfinches to form semi-colonies (Mountfort 1957, Bijlsma 1979, 1998, Knysh 1998) may partly reflect the mere fragmentation of the breeding habitat. In the BNP small aggregations of pairs occur only in a trace form, which may result from a structural uniformity of the deciduous old-growth. The function of such loose nest aggregations was thought to be anti-predatory (Bijlsma 1979, 1998). Also in the BNP the joint defence against Jay *Garrulus glandarius* were observed a few times, in which 4–5 birds, apparently 2–3 neighbouring pairs, were taking part. Yet, the better reproductive output of pairs in clusters in Bijlsma's case may result from the fact that under Dutch conditions the nests in

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clusters could also be in structurally better habitat patches, while scattered solitary nests (at least one km apart from each other) in the less safe ones. Applying Bijlsma's classification to my plots would make all nests belong to some "loose colonies". Therefore data from the BNP, though too restricted for a formal testing his hypothesis, allow to express some doubts concerning a part of the above explanation. In the BNP all the nests forming dense "clusters" (14 nests — those at a distance closer than 50 m from another nest) were eventually depredated, and the location of such clusters within plots was changing from year to year, suggesting absence of ties with a protective vegetation structure or food resources. Therefore, a modified explanation may be suggested: although the protective function of the clusters of nesting pairs may be inefficient to prevent robbing the nests (once the nest had been noticed by predator), yet it may still be of importance for mutual warning of the incubating or brooding females. This may be critical in habitats with a high diversity and abundance of predators dangerous to adult birds.

Pristine and secondary nest-site preferences

The BNP study findings contrast with most of European studies, including other Polish ones, with respect to the prevailing type of nest-sites chosen by Hawfinches (Table 3). This justifies a suggestion on what the pristine localisation of their nests was. The answer seems to be: it was forest tree crowns that originally provided most suitable nest location. In the dense forest of BNP all nests are high in live trees, with the average height above the ground (18 m) being four times that from Polish secondary habitats. Also in the Dutch natural woodland the mean nesting height is considerable (14 m after Bijlsma 1979). Low nesting happens in BF only exceptionally: three cases of the height between 1 and 3 m were reported (Gavrin 1953, Borowski & Okołów 1988, E. Pugacewicz — pers. comm.), always outside the old growth, in secondary habitats (forest plantations, village park). The data from national nest card schemes show, however, that this preference to nesting high is weakened and partly masked by a tendency to find mostly low nests, often in high bushes (Wesołowski & Czapulak 1986). Thus, it is far from certain that in the Polish countryside the average nesting height for Hawfinches is indeed 4.4 m (0.8–20 m, n = 154) (Glutz von Blotzheim & Bauer 1997, updated). Also the nesting tree selection is entirely different in primeval forests as compared with that in the other habitats. A clear numerical prevalence of the hornbeam-located nests in the BNP (Table 3) can be contrasted with the five times lower percentage of nests found in this tree in the country-wide Polish sample, which partly reflects a less numerous occurrence of this tree among cultural landscape, and partly a bias caused by searching anthropogenic habitats more frequently than woodlands. As in other European studies (Mountfort 1957, Bijlsma 1979, 1998, Krüger 1982, Newton 1985), in secondary Polish habitats the list of tree species selected for nesting is much longer, owing to a variety of habitats covered and different tree species composition. It contains parkland trees, domesticated orchard trees, as well as the poplar and birch plantations or high bushes (Krüger 1982, Kwiatkowska & Mroczkiewicz 1995, Knysh 1998). This is certainly a biased nest site choice owing to more frequent finding lower nests.

BNP Hawfinches clearly avoid the young woodland. This is a striking feature on the background of their high densities found elsewhere exactly in the young poplar or birch plantations and in orchards (Krüger 1982, Kwiatkowska & Mroczkiewicz 1995, Knysh 1998). It can be speculated that the forest population avoids breeding in young trees (in this case mostly in hornbeams, aspens and limes) because of their: a) poorer structural properties (smooth vertical branching with no horizontal twigs offering a support) and /or b) conspicuousness for numerous predators. Also nesting in high bushes has not been

Table 3. Difference in nesting tree choice between the various secondary habitats (Polish nest-record scheme data) and primeval forest of BNP (own results).

Tree species	Poland	Bialowieza NP
Hornbeam *Carpinus betulus*	14 (9.0%)	221 (50.6%)
Lime/linden *Tilia cordata*	2 (1.3%)	62 (14.2%)
Maple *Acer platanoides*	4 (2.6%)	57 (13.0%)
Spruce *Picea abies*	9 (5.8%)	47 (<ca.11.0%)
Alder *Alnus glutinosa*	7 (4.5%)	21 (4.8%)
Oak *Quercus robur*	8 (5.2%)	19 (4.3%)
Birch *Betula verrucosa*	9 (5.8%)	3 (0.7%)
Poplars *Populus* sp.	5 (3.2%)	1
Hasel *Corylus avellana*	1	1
Ash *Fraxinus excelsior*	0	2
Elm *Ulmus* sp.	1	2
Willow *Salix alba*	1	1
Elder *Sambucus nigra*	21 (13.5%)	0
Bird cherry *Padus avium*	13 (8.4%)	0
Hawthorn *Crataegus* sp.	3 (8.4%)	0
Pear *Pirus communis*	12 (7.7%)	0
Other 10 species	35 (1–3% each)	0
Total of nests	155 (100%)	437 (100%)
Species of trees	26	12

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confirmed for the BNP. This is mostly because the bushy plantations restored on clear-cut areas amongst managed forests have no counterparts in the pristine forest, except perhaps after fire. The course of forest regeneration on natural windbreaks in the BNP indicates that disturbed gaps in primeval forest do not pass through a high-bush thickets stage (Tomiałojć 1991).

Nest location as possible defence against predation. Hawfinch nests in the BNP are located high in tree crowns (Fig. 3), yet almost always they are in sites with a free access from the air (the same was noticed in Ukraine by Knysh 1998). The most spectacular example of this was when BNP nests were in the mistletoes. Single bunches were clearly preferred while in crowns of some old limes densely covered with mistletoes the Hawfinch nest was usually at a side branch (never in the centre of dense crown). Checking nests by climbing caused females to leave high nests stereotypically by diving at the very last moment down in an injury-feigning flight that later turned direction 1–2 m above the ground. It is clear that such a mode of escape would be difficult from the nest in a dense part of the crown. In accordance to this, so many nests are located either in the outer parts of crowns or behind offshoots at the otherwise bare lower parts of tree stems (Fig. 3). A possibility of safe escape for incubating female may be the main reason.

What was the pristine habitat and nest site choice of forest Hawfinches?

A widespread distribution of Hawfinches in the highly fragmented forests might suggest that originally it was a species of the forest-edge zone. Yet, its persistent and numerous occurrence deep within the Białowieża Forest suggests that originally this finch had to be a true forest-interior inhabitant, more like the Chaffinch *Fringilla coelebs* or Siskin *Carduelis spinus* than like the forest-edge-bond Greenfinches *C. chloris* or Goldfinches *C. carduelis*. Given its very high breeding density in the oak-lime-hornbeam and ash-alder tree-stands, once widespread in the lowlands, the species must have been a numerous breeding bird in the primeval Central Europe (the area known to be covered largely by this type of woodland) while in Western Europe it had to be common in the beech-oak old growth (Mountfort 1957, Bijlsma 1998). It is likely that the carrying capacity of its past winter quarters (not of breeding grounds) set the upper population limit. Most of its original breeding habitat has been later turned into cultivated fields.

CONCLUSIONS

1. In the close-to-primeval conditions of high oak-lime-hornbeam stands of the BNP, the Hawfinch belongs to the most numerous bird species, with its true density reaching 4–15 pairs/10 ha. The species is distributed across the whole BF, with exception of purely coniferous stands. A very rough estimate for the old BNP (47 km^2) of its sharply fluctuating population size may be between 1000 and 3000 pairs and between some 3 000–8 000 pairs in the whole BF.
2. The pristine nesting conditions of the Hawfinch forest population can be characterised by the following set of features:
a) the species originally was a forest-interior dweller, as it still populates a continuous high forest, including forest interior;
b) it breeds high in mature tree crowns (18.1 m above the ground, which is probably the highest nesting among the European passerine birds) of mostly hornbeams; nesting in evergreen mistletoe bunches is also frequent, but not so in the evergreen spruces.
c) it almost permanently stays high in old forest canopy, where breeds, feeds and collects nest material;
d) it may occur in very high breeding densities, being a subdominant in a bird community.
3. The Hawfinch is a species that has probably evolved inside the fertile, humid and high forests of the lowland and submontane elevations. Its elsewhere observed preference for the forest-edge zone, to young woodland, as well as its wide occurrence in the open landscape, all seem to have been strengthened quite recently.

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STRESZCZENIE

[Rozmieszczenie, gęstość populacji i miejsca lęgowe grubodziobów w pierwotnym lesie Białowieskiego Parku Narodowego]

Wieloletnie obserwacje (1991–2002) wykazały, że grubodzioby osiedlają się na lęgi na niemal całym obszarze Puszczy Białowieskiej, w odpowiednich biotopach , w środku kompleksu leśnego będąc prawie tak samo licznymi jak w strefie przybrzeżnej (Fig.1). Gęstość zasiedlenia, sposób zajmowania biotopu i wybór miejsc lęgowych badano szczegółowo na dwóch powierzchniach próbnych (31.5 i 30 ha) wyznaczonych w optymalnym siedlisku gatunku, w pierwotnych i wysokopiennych drzewostanach grądowych. Kontrolowano je prawie co drugi dzień, lokalizując zapewne wszystkie rewiry lęgowe i wykrywając ponad 80% gniazd. Rzeczywista gęstość populacji wynosiła tam 4.0–8.4, a w niektórych latach nawet do 15.2 p/10 ha, podczas gdy niepełne wyniki uzyskane z pomocą kombinowanej metody kartograficznej wynosiły (średnia wieloletnia) 3.9 par/10 ha w starych grądach, 1.6 p/10 ha w łęgach jesionowo-olchowych oraz poniżej 0.1 p/10 ha i nie corocznie w marginalnym dla gatunku środowisku mieszanych borów oraz młodych i średniowiekowych drzewostanów liściastych. Leśne grubodzioby zajmują niewielkie rewiry lęgowe (nie "terytoria") rozmieszczone szeroko ale nie zawsze równomiernie, czasem tworząc luźne skupienia gniazd, najbliższe oddalone 7 m od siebie, choć znacznie bardziej równomiernie niż w mozaikowym krajobrazie Zachodniej Europy. Gnieżdżą się średnio 18.1 (zakres 7–34) m nad ziemią w koronach wielkich i średniej wysokości drzew tworzących sklepienie lasu (Fig. 3). W grądach (Fig. 2) najwięcej gniazd znajdowano w grabach (także kępy jemioły *Viscum album* są preferowane, zwłaszcza na klonach),

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podczas gdy w łęgach najczęściej zajmowanym drzewem była olcha. W BNP ujawnia się zupełnie inna wybiórczość gatunku drzewa lęgowego i wysokości gniazdowania od prawidłowości wykazanych dla całego kraju na podstawie materiałów z Ogólnopolskiej Kartoteki Gniazd (Tab. 3). Dowodzi się tu, że grubodziób pierwotnie był gatunkiem lęgowym zwartych i starych lasów liściastych i mieszanych. Jego obecne w innych rejonach kontynentu gniazdowanie albo głównie nisko nad ziemią, albo głównie w strefie brzegowej lasu wydaje się być cechami nasilonymi dopiero wtórnie, a w części nawet wynikiem wypaczonym przez łatwiejsze wykrywanie gniazd niskich i zlokalizowanych na obrzeżach lasów.

T. Cofta

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