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Natural nest sites of the Collared Flycatcher *Ficedula albicollis* in lime-hornbeam-oak stands of a primeval forest

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Knowledge of habitat and nest site selection of secondary hole nesting birds under primeval conditions may aid in managing forests and in conservation biology. We studied location (n = 768) and dimensions (n = 624) of Collared Flycatcher nests in natural tree holes in a lime-hornbeam-oak stand of the Białowieża National Park, Poland. Collared Flycatchers bred most often in hornbeam *Carpinus betulus*, in holes that were on average 8.1 m above the ground in trees of a mean diameter at breast height (DBH) of 43 cm. The majority of nest holes were situated in tree trunks (79%), with most of these (87.9%) in living trees. Nest holes were either originally made by woodpeckers (17.4%), or created by natural decaying processes. The minimum diameter measurement of the entrance hole for all Collared Flycatcher nests was 4.6 cm on average. The average distance between the outer rim of the entrance hole and the floor of the nest cavity (danger distance) was 25 cm. The median floor area of the nest cavity was 96 cm^2. Differences between orientations of the hole entrances were insignificant.

1. Introduction

Secondary hole nesters that do not excavate their own nest cavity are limited by a shortage of natural tree holes in managed forests. Nest boxes provide nest sites at a local scale, but a much better large-scale solution would be to provide birds with natural holes within forests. Knowledge of natural tree holes is limited, but such information would improve the cultivation in forest stands of tree species which provide sufficient appropriate nest holes. In view of the widespread forestry activity which is currently underway in Eastern Europe, the knowledge of habitat and nest site selection of hole-nesting bird species would allow the identification of which tree species could be planted in order to provide nest sites for an entire hole-nesting bird assemblage. This would help both in managing forests in newly afforested areas, and also in conservation biology by providing high quality habitat for hole-nesting species, such as the Collared Flycatcher *Ficedula albicollis*, which may otherwise lack suitable nest sites in forested areas (Tomiałojć & Stawarczyk 2003).

Among the secondary hole nesters, natural nest sites of the Marsh Tit *Poecile palustris* (Wesołowski 1996), Pied Flycatcher *Ficedula hypoleuca* (Czeszczewik & Walankiewicz 2003), Nuthatch *Sitta europaea* (Wesołowski & Rowiński 2004), and some other species (e.g. Edington & Edington 1972, Rendell & Robertson 1989, Dobkin *et al.* 1995) are described in detail. The natural nest sites of Collared Flycatchers have been analysed by Maurizio (1987) in Switzerland and Sachslehner (1995) in Austria. Also, Wesołowski (1989) described some features of Collared Flycatcher nest holes in the Białowieża National Park (BNP), but hole characteristics were only assessed from the ground and did not include hole dimensions. Walankiewicz (1991) and Mitrus *et al.* (1996) analysed the breeding success of this species with reference to some dimensions of nest holes, while nest hole humidity has been studied by Wesołowski *et al.* (2002a).

In this paper, we comprehensively describe breeding holes and nesting trees of the Collared Flycatcher in the optimal habitat of the BNP. The Collared Flycatcher is one of the most numerous breeding bird species occupying natural holes in BNP, breeding in densities of up to 22 pairs/10 ha (Walankiewicz 2002b). We provide quantitative data on aspects of nest hole location (tree species, which part of the tree), as well as structural parameters (hole dimensions). This data provides information for forestry management and conservation biology; in particular, which kind of tree stand composition should be maintained in order to achieve a re-wilding of the managed stands and to comprise suitable habitats for the avian hole-nester assemblage.

2. Material and methods

This study was conducted in the strictly protected part of the Białowieża National Park (NE Poland), which has been protected since 1921. There are remnants of the primeval forest which have never been cut down. The forest structure is multi-age, multi-layer and multi-species. The lime-hornbeam-oak stand *Tilio-Carpinetum* is the most common forest type of the BNP. It consists mainly of lime *Tilia cordata*, hornbeam *Carpinus betulus*, oak *Quercus robur*, maple *Acer platanoides*, ash *Fraxinus excelsior*, elms *Ulmus* spp. and Norway spruce *Picea abies* (Tomiałojć *et al.* 1984). The Collared Flycatcher is one of the most numerous bird species in lime-hornbeam-oak stands and we have limited our observations to this habitat. We investigated tree holes used by breeding Collared Flycatchers within the study plot “W” described by Tomiałojć *et al.* (1984) (enlarged at the edges to a total of 36 ha), located near the main entrance of the BNP.

Observations were conducted between the end of April and the end of June in 1988–1999 and 2002–2005. During the latter period, only the eastern half of the study plot was included. Nest holes were located by searching for singing Collared Flycatcher males, and most of the holes were checked several times in a season. The hole was treated as occupied if it contained a nest with at least one egg and only holes with first clutches were analysed (re-nested broods among the Collared Flycatchers in the BNP is <2% of breeding pairs, Walankiewicz 2002b). The following parameters were recorded: tree species, the height of the entrance from the ground level, tree section (trunk or limb), orientation of the entrance (classified to the nearest 1/8 of the compass points), origin of the hole (woodpecker-made vs. natural, i.e. hole which appeared as a result of decaying processes after branch loss, cracks etc., which was easy to assess by the entrance shape), condition of the tree section containing the hole (live or dead) and slope of the part of the tree in which the hole was located (vertical, on the upper surface or under the sloping trunk/limb). Using tape, ruler and bendable wire the following measurements were made:

- diameter of the tree trunk at the breast height (DBH)
- diameter of the trunk/limb at the entrance height
- maximum and minimum entrance diameter
- hole depth (the vertical distance between the lower edge of the entrance and the middle of the hole floor, measured without nest)
- danger distance – the distance between the outer edge of the entrance and the middle of the cavity floor (this shows how deep a predator has to reach to the hole bottom)
- maximum and minimum diameter of the cavity

floor, measured at the level of the nest cup base.

On the basis of the cavity floor diameters we calculated the floor area (as an elliptic area). The cavity volume was calculated from the lower rim of the entrance to the bottom of the cavity, assuming the shape of the nest cavities to be a cylinder. Many holes were used by flycatchers in multiple years but due to hole dynamics (their measurements usually changed year by year) we treated them independently. In several cases two or three holes used by flycatchers (in different years) were located in the same tree.

The data on tree species composition were collected in July 1997 and repeated in 2003. All living and dead trees with DBH > 12 cm were counted within 24 squares (50 × 50 m), chosen randomly within the study area (total coverage 6 ha). Statistical procedures followed the formulae given in STATISTICA 7.1 and Sokal & Rohlf (1981). Presented values are means ± SD. All tests were two-tailed.

3. Results

3.1. Location of holes

We pooled data from all study years including the data used in an earlier paper (Walankiewicz 1991). Collared Flycatchers used tree species in a non-random fashion: there was a strong selection for hornbeams and maples in the study plot, although maple was not a common tree species. Spruce, lime and elm were largely avoided (G = 90.9, d.f. = 5, P < 0.001; Fig. 1). No significant storm demolitions occurred during the study period that could have destroyed a tree stand in the study plot, and the density of all tree species in 1997 and 2003 did not change significantly (χ^2 = 0.31, d.f. = 6, P > 0.05).

The nest holes were situated mostly in living trees (87.9%, n = 768), which closely reflected their frequency in the tree stand of 92.1% (G = 0.05, d.f. = 1, P > 0.05). The flycatcher nest holes were mostly located in tree trunks, with only 21% found in limbs. Only seven nest holes were located in a dead limb of a living tree. The holes were usually located higher in living trees than in dead ones (8.2 m ± 3.71, n = 675 and 7.0 m ± 3.52, n = 93, respectively; Mann-Whitney test Z = 3.53, P < 0.001). The tree species containing Collared Flycatcher nest holes differed significantly depending on whether trees were alive or dead (χ^2 = 77.97, d.f. = 6, P < 0.001); hornbeam was distinctly prevalent among the live trees containing utilized holes (83%), while only 62% of holes in snags were of this species, with 14% in dead maple and 14% in dead spruce.

The height of the nest hole above the ground did not depend on the hole origin (Mann-Whitney test Z = –0.45, P > 0.05) but depended on tree species – the highest holes were found in oaks and ma-

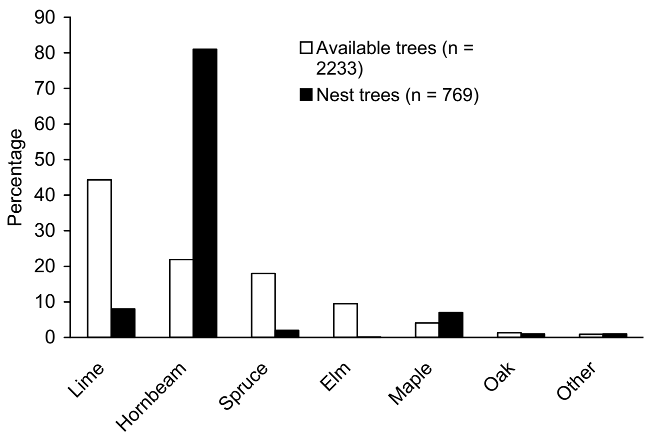

Figure 1. Tree species containing Collared Flycatcher holes in relation to tree availability within plot W.

Table 1. Dimensions of all Collared Flycatcher nest holes.

Variable	N	Average ± SD	Median	Range
Entrance height (m)	768	8.1 ± 3.71	8	0.5–23
Entrance smallest diameter (cm)	617	4.6 ± 1.87	5	1.5–17.5
Floor area (cm^2)	610	96.0 ± 72.26	79	18–491
Hole depth (cm)	623	21.2 ± 9.0	20	1–62
Danger distance (cm)	624	25.0± 7.96	24	4–62
Volume (dm^3)	610	2.0 ± 1.89	1	0.1–13.4

Table 2. Comparison of natural and woodpecker-made holes used by flycatchers.

Variable	Natural	Woodpecker-made	U-test	p
Entrance height (m)	8.0 ± 3.68	8.4 ± 3.59	–0.45	>0.05
Entrance smallest diameter (cm)	4.5 ± 1.99	4.8 ± 1.10	–3.13	<0.01
Floor area (cm^2)	97.8 ± 75.43	85.5 ± 48.73	0.35	>0.05
Hole depth (cm)	21.9 ± 9.14	17.1 ± 4.92	5.11	<0.001
Danger distance (cm)	25.4 ± 8.06	22.1 ± 4.90	3.73	<0.001
Volume (dm^3)	2.1 ± 2.00	1.5 ± 1.00	2.87	<0.01

ples and the lowest were in limes (Kruskal-Wallis ANOVA $H_{4,754}$ = 88.29, P < 0.001). The DBH of the trees containing nest holes ranged from 12 to 121 cm (43.0 cm ± 14.16, n = 204), and the diameter of the trunk or limb at the level of the hole entrance ranged from 10 to 75 cm (30.8 cm ± 10.31, n = 360).

Although orientation of hole entrances were classified to eight compass directions, it transpired that the main cardinal points (N, S, E, W) were significantly more frequent than intermediate ones (χ^2 = 62.90, d.f. = 7, P < 0.001). To avoid an error we reclassified the number of all intermediate expositions and added them to the cardinal directions. Hole entrances were orientated more or less evenly to the south, east and west (25–28%), only a northern orientation was less frequent (21%), but these differences were not significant (χ^2 = 4.32, d.f. = 3, P > 0.05). More than half of all hole entrances (56.4%) were situated in a vertical plane, with 36.1% inclining upwards and only 7.5% downwards. One hole was of a chimney-type.

Only 17.4% of Collared Flycatcher nest holes were woodpecker-made. Almost half of them (48.1%) were situated in a dead section of a tree, as opposed to non-woodpecker-made holes which accounted for only for 5.3% in dead wood (significant differences, χ^2 = 181.33, d.f. = 1, P < 0.001).

3.2. Dimensions of holes

The smallest hole entrance was 2.5 × 2.5 cm. Some of the entrance holes used by flycatchers were even narrower than 2 cm (Table 1). Slightly more than half of the hole entrances (51.4%) were circular or slightly oval (the ratio of the maximum and minimum diameters did not exceed 1.5), the rest were elongated. The woodpecker-made holes always had an approximately circular entrance. The danger distance, the smallest entrance diameter, depth and volume of the cavity depended on the hole origin – woodpecker-made holes were on average shallower, smaller and with a larger entrance (Table 2).

The depth of most nest-hole cavities (94%) ranged from 8 to 40 cm (Table 1). There was no relationship between tree species and cavity depth (Kruskal-Wallis ANOVA $H_{4,618}$ = 5.41, p > 0.05) but cavities located in the living sections of trees were on average deeper than in dead ones (Mann-Whitney test Z = 2.95, P < 0.01). Nest-hole cavities in maples had the largest floor area, while limes had the smallest. This is a result of the difference in the DBH of limes and maples (Fig. 2). The floor area of a cavity was correlated with trunk/limb diameter at the level hole entrance (r_s = 0.41, n = 357, P < 0.05). The volume of a cavity

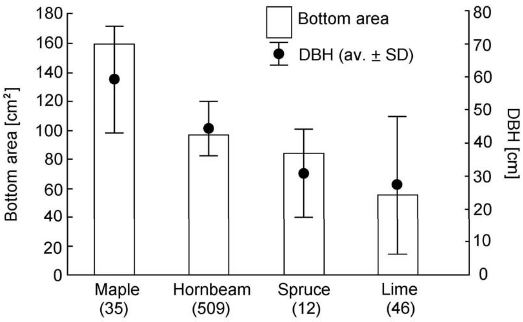

Figure 2. Floor area of Collared Flycatcher nest-hole cavities in relation to tree species DBH. Sample size given in parentheses.

was the result of other measurements: depth and floor area, these being very variable and having a median of 1.0 dm^3 (Table 1).

4. Discussion

Distribution of the Collared Flycatcher throughout Europe is patchy. Most research on this species has been done on nest-box plots (e.g. Alerstam *et al.* 1978, Gustafsson 1985, Merilä & Wiggins 1995). In fact, in Europe there are very few places with primeval or natural stands comparable to those in the Białowieża National Park. Our study was conducted in lime-hornbeam-oak stands of the BNP – this being optimal habitat for this species as indicated by recorded breeding densities being the highest there (Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1994, 1996, Wesołowski *et al.* 2002b, 2006). Because Collared Flycatchers in BNP still have a high surplus of natural tree holes even in years when they breed in high densities (Walankiewicz 1991, 2002b), we assume that they are not constrained in their choice of holes.

4.1. Location of holes

Collared Flycatchers appear to choose cavities for breeding by using hole parameters as cues, and not by distinguishing between tree species. The hornbeam, as the tree species with the highest number of holes, was overrepresented compared to other species, but especially compared to lime. Lime had the highest density among the tree species but was relatively rarely used for breeding. This was also found in BNP in the case of titmice *Paridae* (Wesołowski 1989, 1996), the Pied Flycatcher (Czeszczewik & Walankiewicz 2003) and the Red-breasted Flycatcher *Ficedula parva* (Mitrus & Soćko 2004). Our study thus shows that the Collared Flycatcher, in addition to other hole-nesters, benefits from the presence of older hornbeam trees in the stands. In another area (Vienna), where hornbeams were much less abundant, Collared Flycatchers prefer other tree species (Sachslehner 1995), but this finding probably is due to the smaller size of hornbeams in Sachslehner's study compared to BNP. Walankiewicz and Czeszczewik (2006) showed that the frequency of hornbeams being occupied by the Collared Flycatcher according to DBH classes was related to tree stand resources: over 40% of holes were located in hornbeams of 40–50 cm DBH. When considering all tree species together, the average DBH of trees containing Collared Flycatcher nests in the BNP was similar to the average DBH of nesting trees (44 cm) in Austria (Sachslehner 1995).

Most of the Collared Flycatcher holes in BNP were situated in live trees – this reflects their frequency in the tree stand. Dead sections of trees were used by Collared Flycatchers more often than by tits and Nuthatches (below 10%; Wesołowski 1989, 1996, Wesołowski & Rowiński 2004) and less often compared to Pied and Red-breasted Flycatchers (over 20%; Czeszczewik & Walankiewicz 2003, Mitrus & Soćko 2004). In BNP, 37% of the known nest holes occupied by all hole-nesting bird species were situated in dead substrate (Wesołowski 1995). In other forests, especially boreal, secondary hole nesters use breeding cavities located in snags more often than in BNP (e.g. Orell & Ojanen 1983, Saari *et al.* 1994, Bai *et al.* 2003). Although snags were plentiful (on average 30/ha, unpubl. data), and they usually contained numerous holes, they were not preferred by birds in BNP. This finding is probably a reflection of the situation in Białowieża primeval stands, where there are many old, living trees with plentiful holes of good quality.

The average height of the Collared Flycatcher nest-hole depended on tree species – the highest nests were found in oaks and maples. Indeed, oaks and limes are the tallest deciduous trees in BPN, but we had almost no recorded flycatcher nest-holes in the oldest (= tallest) limes. Compared to other secondary hole nesters in BNP the Collared Flycatcher bred at moderate heights – higher than Marsh Tit and Red-breasted Flycatcher, lower than Nuthatch and Starling *Sturnus vulgaris* and at a similar height to the Pied Flycatcher, Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major* (Wesołowski 1989, 1996, Czeszczewik & Walankiewicz 2003, Mitrus & Soćko 2004, Wesołowski & Rowiński 2004). The average height of Collared Flycatcher nest holes in BNP was similar to that found in Vienna (Sachslehner 1995), but much lower than in chestnut tree groves of the submontane zone of Switzerland (Maurizio 1987).

Despite a relatively high number of woodpeckers in the BNP (on average 2.5 pairs/10 ha in deciduous forests, Tomiałojć *et al.* 1984, Tomiałojć & Wesołowski 1994, 1996, Wesołowski *et al.* 2002b, 2006) holes created by natural decay are most common (Walankiewicz 1991). Woodpeckers and other excavators are regarded as the main hole producers in most of the managed forests of Europe or North America (e.g. Alatalo *et al.* 1988, Aitken & Martin 2004, Remm *et al.* 2006). However, Bai *et al.* (2003) in primeval Mongolian forest showed very similar rates of usage (17.7%) of woodpecker-made holes occupied by secondary hole nesters as in BNP. Woodpecker-made holes used by Collared Flycatchers in BNP were most often located in oaks and spruces. These tree species do not offer many holes formed by decay processes, but in the dead ones or in their dead/dying parts woodpeckers can excavate holes (Wesołowski & Tomiałojć 1986). Conversely, hornbeams provide numerous holes created by natural decay, as opposed to those solely created by woodpeckers.

4.2. Dimensions of holes

The minimum entrance diameter for a nest hole depends on the bird's size. Avoiding holes with wider entrances can prevent competition with larger species and decrease the risk of predation (van Balen *et al*. 1982). The Collared Flycatcher breeding holes were similar in size to cavities used by the closely related Pied Flycatcher (Czeszczewik & Walankiewicz 2003). They differed only in volume and floor area (Collared Flycatcher cavities were smaller) and in the smallest entrance diameter – Collared Flycatchers chose, on average, entrances that were 1 cm wider. Compared to Marsh Tit nest-holes in BNP, Collared Flycatcher holes were deeper, with wider entrances and larger floor areas (Wesołowski 1996). Contrastingly, Nuthatches occupied holes which were much shallower than those of Collared Flycatchers, but with very large floor areas (Wesołowski & Rowiński 2004). Compared to other European passerines, the Collared Flycatchers in BNP occupied larger holes than titmice in the Netherlands (van Balen *et al.* 1982) but smaller than most secondary hole nesters in Estonia (Remm *et al.* 2006). Natural cavities of different hole-nesting passerines in Sweden had similar depth (average 14–21 cm; Nilsson 1984) but in the Netherlands the Great Tit and the Blue Tit used shallower natural nest sites (van Balen *et al*. 1982).

Our data showed some differences in comparison with results collected in the BNP before 1989 (Wesołowski 1989). During this earlier period, more flycatcher holes were found in snags, made by woodpeckers, located in tree trunks and a much smaller number of holes under sloping trunks or limbs. Furthermore, the average height from the ground was lower in the earlier study. These differences probably resulted from a different method of data collection. Wesołowski (1989) considered data where a relatively small fraction of nests were found each year, mainly at the nestling stage (during feeding). Some holes are easier to find than others (e.g. in former woodpecker's holes, or in snags which have no branches). Some holes which are located relatively high up (e.g. 20 m high in the tree crown) or invisible from the ground could be easily missed. In our research, we spent a lot of time on the study plot mainly at the beginning of the season, when flycatcher males occupy new holes. Such holes were observed and checked many times and most of them were found before the trees had come into leaf. Using these methods, therefore, we could find different types of nest hole as well those which were easily visible from the ground (also, incidentally, for potential predators) as well those much better hidden; nest holes which are exposed to predation can differ in some parameters from the safer ones (Nilsson 1984, Rendell & Robertson 1989, Walankiewicz 1991, Wesołowski 2002, Czeszczewik & Walankiewicz 2003, Wesołowski & Rowiński 2004).

The Collared Flycatchers in our study also bred in trees with a greater DBH, on average, compared to those reported by Wesołowski (1989). Indeed, many holes which were occupied in the 1970s and 1980s were still being used by flycatchers in our study, and the DBH of those trees is greater now.

It was found that under Białowieża's primeval conditions the competition for holes is of relatively low importance (Walankiewicz 1991, 2002b) and the most important limiting factor in the Collared Flycatcher in BNP is nest predation (Walankiewicz 2002a, 2002b). A good method to avoid predation is to locate a nest in a hole with a small entrance surrounded by hard walls provided by a living tree. This model is typical for most of the studied hole-nesters in the BNP (Wesołowski 1996, 2002, Czeszczewik & Walankiewicz 2003, Wesołowski & Rowiński 2004). As we know the specifications of nest holes in years of high and low Collared Flycatcher density did not differ significantly (Walankiewicz 2002b), this means that under conditions of high Collared Flycatcher density birds could breed in similar holes as in the years of low density. Quality of the hole selected for breeding depends on many agents, but primarily on available resources, and this will require further study.

In summary, we have described in detail the nest holes and nest trees of the Collared Flycatcher under the primeval conditions of BNP. The hornbeam, once a widespread tree species in Europe, is the most important component of the primeval Białowieża stands in providing plentiful nest sites for the secondary hole nesting birds. Any attempts at protection or improvement of forest habitats should include this tree species as an important stand component. Forest management practices intended to conserve and to enhance forest bird assemblages must be informed by knowledge of habitat and nest site selection under primeval conditions.

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Sepelsiepon pesäpaikat alkukantaisessa lehtometsässä

Kolopesijöille suotuisien pesäpaikkojen ja pesintäympäristöjen tunteminen auttaa suojelupäätösten ja metsien hoitosuunnitelmien tekemisessä. Selvitimme 768 sepelsiepon pesän sijainnin ja mittasimme 624 pesäpuun ja -kolon ominaisuudet Bialowiezan kansallispuistossa Puolassa.

Sepelsiepot pesivät useimmin euroopanvalkopyökeissä oleviin koloihin, jotka olivat keskimäärin 8,1 metrin korkeudessa. Pesäpuiden ympärysmitta rinnakorkeudella oli keskimäärin 43 cm. Suurin osa pesäkoloista (79 %) oli puiden rungoissa. Näistä 87,9 % oli elävissä puissa. Pesät olivat joko tikkojen tekemissä koloissa (17,4 %) tai luonnonkoloissa. Pesäaukkojen pienin läpimitta oli keskimäärin 4,6 cm. Pesäaukon ulkokehän ja pesäpohjan välinen etäisyys oli keskimäärin 25 cm. Pesäpohjan ala oli keskimäärin 96 cm^2.

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