Breeding Success and Timing of the Pied Flycatcher Ficedula hypoleuca Nesting in Natural Holes and Nest-Boxes in the Białowieża Forest, Poland

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Breeding success and timing of the Pied Flycatcher *Ficedula hypoleuca* nesting in natural holes and nest-boxes in the Białowieża Forest, Poland

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Abstract. Broods of Pied Flycatcher nesting in natural tree holes and nest-boxes in Białowieża Forest (E Poland) were compared. Natural holes in primeval stands of the Białowieża National Park were located by following singing males, then monitored several times during the season. Nest-boxes situated in the managed part of the forest were inspected weekly. Flycatchers breeding in natural holes started laying eggs on average two days later (15 May) and laid smaller clutches (6.4 eggs) than birds breeding in nest-boxes (13 May and 6.7 eggs). The predation rate was significantly lower in natural holes (av. 47%) than in nest-boxes (av. 65%). This result indicates that generalisations regarding the evolution of adaptations to predation by nest-box populations should be treated with caution.

Key words: Pied Flycatcher, *Ficedula hypoleuca*, tree holes, nest-boxes, Białowieża Forest, clutch size, predation rate, breeding biology

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INTRODUCTION

The biology of the Pied Flycatcher is well studied, but majority of these studies were conducted in managed forests, with nest-boxes. Only a few papers describe some of the breeding parameters of this species nesting in tree holes (Nilsson 1975, 1984, Alatalo et al. 1988, 1990, 1991). Even if birds breed in natural holes, in the forests where such studies were carried out, other important factors may be totally different to the primeval conditions in European forests in the past. For instance, potential predators are usually less frequent in forests modified by man than in natural ones. In the latter case predators can be responsible for most of brood losses among hole nesters, and breeding losses could reach even the level of two thirds of breeding attempts (Walankiewicz 2002a).

Because it is easy to attract the Pied Flycatchers to nest-boxes, this bird has become a model species in ecological studies. Some studies carried out on this species led to such generalisations that nest predation among hole nesters is low (e.g. Lundberg & Alatalo 1992). In this paper, I compare timing, clutch sizes and breeding success of the Pied Flycatcher in natural tree holes and nest-boxes in Białowieża Forest. I presumed that nest-boxes were better and broods in them would be layed earlier, larger, and breeding success would be higher than in natural holes, because the Pied Flycatcher usually prefers nest-boxes (van Balen et al. 1982, Lundberg & Alatalo 1992). I also discuss a difference between primeval and secondary conditions.

STUDY AREA

Data was collected in Białowieża Forest (E Poland). This is one of the best-preserved lowland forests in Europe. It is characterized by a high rate of primeval stands. Its most valuable central part is protected since 1921 as a strict reserve (recently it is a part of Białowieża National Park, hereafter referred to as BNP), but before it was protected for the last a few centuries as a hunting area of Poland' rulers. The primeval stands preserved in BNP are multi-storey, mixed-species, uneven-aged, composed of trees reaching unusual heights and contain a large amount of dead timber and uprooted trees. Detailed descriptions are in Tomiałojć et al. (1984) and Faliński (1986).

The Pied Flycatchers, which in strictly protected part of BNP bred exclusively in natural holes, were studied in three different forest types. Location and description of the study plots as in Tomiałojć et al. (1984):

1) oak-lime-hornbeam stands — plots: W (enlarged at the edges), CW, CM, MN, MS (total 138 ha);

2) riverine stands — plot K (33 ha);

3) coniferous stands — plots NE and NW (total 50 ha).

Additionally, data was collected in vicinity of plots, as well as along roads in BNP in these stand types.

The nest-box transect was located in managed part of the Białowieża Forest, about 12 km SW from BNP. Nest-boxes were fixed up on trees 2.5–4 m above ground along 13 km long forest roads surrounding eight forest units. Traffic was not intensive there (several cars at the most per day). This transect crossed various types of forests: coniferous stands (with Scots Pine *Pinus silvestris* and Norway Spruce *Picea abies* as dominant trees; 115 nest-boxes), ash-alder stands (with Alder *Alnus glutinosa* and Ash *Fraxinus excelsior*; 67 nest-boxes) and in oak-lime-hornbeam stands (with Oak *Quercus robur*, Hornbeam *Carpinus betulus* and Lime *Tilia cordata*; 8 nest-boxes). The stands were mostly 50–80 years old. All nest-boxes had the same dimensions: 10 × 10 cm of bottom area and 3.5 cm of entrance diameter.

In the whole of Białowieża Forest the following potential robbers of flycatcher broods were observed: Pine Marten *Martes martes*, Weasel *Mustela nivalis*, Red Squirrel *Sciurus vulgaris*, Forest Dormouse *Dryomys nitedula*, Fat Dormouse *Glis glis*, Yellow-necked Mouse *Apodemus flavicollis* and Great Spotted Woodpecker *Dendrocopos major*.

METHODS

Data from the natural holes was collected in 1989–1999; the most intensive period of study was conducted from 1994. Natural holes were localized by following the singing males. Next, the holes were checked several times in season, using a ladder or spurs, a mirror and a small lamp. The commencement of laying, clutch size and breeding success were determined. Nest-boxes were usually controlled once weekly, between the beginning of May and end of June in 1993–1997. In 1998 and 1999 nest-boxes were checked only three times per season.

As a full clutch were treated those nests where the number of eggs was the same during two consecutive controls, or when the eggs were incubated. Not all the nests were found at the beginning of breeding season, and sometimes date of laying at the base of hatching date or fledgling date and clutch size, or fresh-hatched young was calculated. I assumed that the females laid one egg per day, incubation took 14 days and nestling period was 15 days (Järvinen 1990). Successful broods were those where at least one bird fledged. Breeding success was measured as the rate of nests from which at least one bird fledged. Only first clutches were analysed. Calculations of the breeding success in natural holes were taken when broods were found no later than in an eggs laying stage.

In robbed nests every trace of predators were examined and the manner of robbery investigated. In many cases this allowed me to distinguish the kind of predator (Nowakowski & Boratyński 2000, Walankiewicz 2002a). The categories of nest robbers were as follows: Forest Dormouse, Yellow-necked Mouse, Pine Marten, Weasel, unidentified rodent, unidentified mustelids, unidentified mammal, woodpecker.

Climatic data were obtained from Mammals Research Institute in Białowieża. For statistical calculations Spearman rank correlation, MANOVA analyse and G-test (Sokal & Rohlf 1981) were used.

RESULTS

A total of 107 Pied Flycatcher broods in natural holes including 104 in deciduous and only 3 in coniferous stands of the BNP were recorded. In the managed forest, a total of 456 broods in nest-boxes including 207 in deciduous and 249 in coniferous stands were recorded. In nest-boxes females started to lay eggs on average two days earlier in deciduous stands (12 May on average) compared to coniferous ones (14 May on average) and the difference was significant ($F_{1,395} = 7.90$, $p < 0.01$). The clutch size was similar in both types of stands. Breeding success in nest-boxes was significantly lower in deciduous (30.6% on average) compared to coniferous stands (39.9%, G = 28.95, df = 5,

Table 1. Commencement of laying clutches (the day of May) in natural holes and nest-boxes (only broods from deciduous forests included). *1994–1999 for natural holes and 1993–1997 for nest-boxes.

Year	Natural holes				Nest-boxes			
	Average ± SD	Median	Range	N	Average ± SD	Median	Range	N
1993	–	–	–		10.2 ± 5.6	11	3–23	41
1994	14.1 ± 4.7	14	6–22	10	11.5 ± 5.2	11	2–22	39
1995	16.2 ± 3.5	16	13–23	6	12.5 ± 5.3	14	6–24	28
1996	12.3 ± 3.1	12	6–16	13	11.4 ± 2.9	12	4–24	36
1997	16.5 ± 1.9	17	13–20	16	15.6 ± 2.3	15	10–24	30
1998	8.5 ± 2.1	8	7–16	6	–	–	–	–
1999	16.8 ± 3.5	18	10–22	13	–	–	–	–
1993–99*	14.1 ± 3.2	15	6–23	64	12.2 ± 2.0	12	2–24	174

$p < 0.05$). For comparisons with data from natural holes only data from deciduous stands was used.

In 1994–1997 the Pied Flycatcher females started laying eggs on average two days later in natural holes compared to nest-boxes ($F_{1,176} = 8.44$, $p < 0.01$, Table 1). On average, the commencement of laying depended on the year ($F_{6,231} = 10.31$, $p < 0.001$). Generally, the Pied Flycatchers bred earlier in warmer years — average commencement of laying was related to air temperature in last 10 days of April (Fig. 1). There was no relation between commencement of laying and precipitations of this time ($r_s = 0.36$, $p > 0.05$).

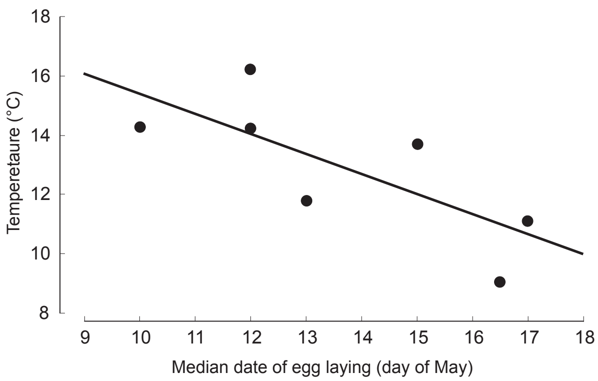

Fig. 1. Annual median date of clutch commencement in relation to mean ambient temperature in the last ten days of April (r_s = - 0.89, $p < 0.01$, n = 7 years). Data 1993–1999.

Pied Flycatcher females laid on average 6.4 ± 0.84 (n = 48) eggs in natural holes compared to 6.7 ± 0.84 (n = 183) in nest-boxes ($F_{1, 229} = 7.26$, $p < 0.01$). The number of eggs declined through the season, on average 0.08 egg/day. When the number of eggs in the nest-boxes was modified, taking into consideration the earlier date of the first commencement (minus 0.08 egg to multiply by two days), the difference between natural holes and nest-boxes was not significant ($F_{1,228} = 2.10$, $p > 0.05$).

Breeding success in natural holes was higher than in nest-boxes (on average 46.8 and 30.6%, respectively). Almost all breeding losses were due to predation. Predation rate reached from 15.4% in 1996 in natural holes to 85% in nest-boxes in 1994, and differed significantly between breeding sites (G = 41.14, df = 5, $p < 0.05$; Table 2). Among recognized robbers, rodents, and mustelids predominated in natural holes. In nest-boxes flycatcher's broods were robbed mainly by the Pine Marten

Table 2. Frequency (%) of successful (S) and predated (P) broods of the Pied Flycatchers in natural holes and nest-boxes.

Years	Natural holes			Nest-boxes		
	N	S	P	N	S	P
1993	8	37.5	50.0	39	28.2	66.7
1994	17	41.2	41.2	40	12.5	85.0
1995	11	36.4	63.6	28	67.9	28.6
1996	13	84.6	15.4	50	44.0	46.0
1997	21	52.4	47.6	31	19.4	80.6
1999	14	28.6	64.3	17	11.8	82.4
1993–1999	84	46.8	47.0	205	30.6	64.9

Table 3. Categories of nest robbers which destroyed flycatcher broods.

Predator category	Natural holes		Nest-boxes	
	N	%	N	%
Forest Dormouse	3	8	20	19
Yellow-necked Mouse	2	5	2	–
Unidentified rodents	6	16	–	2
Pine Marten	7	19	84	78
Weasel	–	–	1	1
Unidentified mustelid	1	3	–	–
Unidentified mammal	17	46	–	–
Woodpecker	1	3	–	–
Total	37	100	107	100

(Table 3). Other reasons for breeding losses in natural holes were: flooding with water (one nest), filling by rotten wood (one), rebuilding of the Pied Flycatcher nest with eggs by other species i.e. Collared Flycatcher and tit *Parus* sp. (2 nests with eggs). Only in one nest were all eggs found infertile. Another reason of breeding losses but predation in nest-boxes was nest desertion (6 broods).

DISCUSSION

In papers comparing the breeding parameters in natural holes and nest-boxes usually holes were reported as worse sites for breeding (e.g. Nilsson 1975, van Balen et al. 1982, Alatalo et al. 1990). Only a few papers showed no significant differences between natural holes and nest-boxes (Robertson & Rendell 1990, Mitrus 2003).

Later breeding and smaller clutch size in natural nest holes compared to nest-boxes can result from: 1) more repeated broods in natural holes (Lundberg & Alatalo 1992), 2) older birds breed in nest-boxes (Enoksson 1993), or 3) better visibility of nest-boxes (Lundberg & Alatalo 1992). The first explanation is not the case in this study because I observed carefully all singing males on the study plots in BNP and only first broods were analysed. One-year-old Pied Flycatchers arriving later, start to breed with a delay, have smaller clutch sizes and brood fewer fledglings compared to older ones (e.g. Berndt & Winkel 1967). Lower rate of older Tree Swallows *Tachycineta bicolor* breeding in natural holes compared to nest-boxes was also shown (Robertson & Rendell 1990). I did not age birds in this study, but in BNP there exists a high surplus of nest holes (Walankiewicz 1991). Also on the nest-box transect, during each year of the study period, about one third of nest-boxes was unoccupied. So there is no reason to suppose that younger flycatchers could be excluded from breeding in both the BNP stands and in the managed stands of the Białowieża Forest.

Nest-boxes distributed along roads were more visible than tree holes and this could be main reason for the earlier breeding there. The Pied Flycatcher females usually check several potential nest sites before deciding on the most suitable (Slagsvold 1986). Numerous, evenly placed nest-boxes with many singing males in their vicinity (song attracts other males, Alatalo et al. 1982) could be easier to find by females. Breeding density of the Pied Flycatchers in BNP was low (Tomiałojć & Wesołowski 1996, Wesołowski et al. 2002). Therefore, some delay of breeding in natural nest sites could result from greater flycatchers' dispersion. Natural holes are less visible and more diverse compared to nest-boxes, and females could have more difficulties while selecting the proper nest site.

The clutch size of flycatchers can be smaller in natural holes compared to nest-boxes, because of the different bottom area (e.g. Nilsson 1984, Slagsvold 1987). In this study, only the commencement of laying influenced clutch size. Median of the bottom area of natural holes in BNP was about 100 cm² (Czeszczewik & Walankiewicz 2003), similar to nest-box bottom area.

Numerous studies showed much lower reproductive success in natural tree holes compare to nest-boxes (Nilsson 1975, Alatalo et al. 1990, Purcell et al. 1997, Mitrus 2003). Only Robertson & Rendell (1990) showed an opposite situation for the Tree Swallow. In central Sweden, in natural holes considered as less safe than nest-boxes, predators robbed 23–57% of Pied Flycatcher broods (compared to 15–64% in this study), while only 0–18% (29–85% in this study) in nest-boxes (Nilsson 1984, Alatalo et al. 1991).

Among other secondary hole nesters studied in BNP (Walankiewicz 1991, Wesołowski & Stawarczyk 1991, Walankiewicz 2002b, Wesołowski 1998), the Pied and Collared Flycatchers suffered the highest breeding losses due to predation. There is no other European forest where such a high rate of breeding losses of Pied Flycatchers was shown. But the fact is that some researchers do not publish study results if breeding losses in nest-boxes are heavy. There is a tendency to treat predators' activity as the intruders disturbing the study data, e.g. Winkel (1989) has treated one season with higher than usually predation rate as "abnormal" and excluded this year from the further calculations. Some unpublished data confirms that breeding losses in nest-boxes can be even higher than in the Pied Flycatcher populations, e.g. Goosanders *Mergus merganser* or Goldeneyes *Bucephala clangula* in Western Poland (inf. A. Mohr).

Pied Flycatchers, like Collared Flycatchers start to breed relatively late, during a time period when the Pine Marten intensively searches for bird nests (Walankiewicz 1991, Jędrzejewski et al. 1993, Walankiewicz 2002a, 2002b). Other species, which started breeding earlier (e.g. Marsh Tit *Parus palustris*) had a lower rate of breeding losses (Wesołowski 1998). Predators are sparse and play a relative small role in modified Western European forests. Also in Northern Europe potential predators of flycatcher's nests are usually limited mainly to the Weasel. But in the whole of Białowieża Forest there occurs a long list of nest robbers, which could play an important role in limiting breeding production and even densities the following year (e.g. Walankiewicz 1991, Wesołowski & Stawarczyk 1991, Walankiewicz 2002a, 2002b). Predation pressure on bird broods in Białowieża Forest is much higher than that found in other European forests. It resembles situations in the tropics (Skutch 1949). The nest-boxes considered commonly as safe and good nest sites, in the Białowieża Forest were not safer than natural holes. It is possible that, under the natural conditions of BNP, an antipredator strategy of the Pied Flycatchers could be breeding in low density, which could lead to the dispersion of nest sites.

These results suggest that breeding biology in nest-boxes differs slightly from natural holes, if other environmental conditions (i.e. occurrence of nest robbers) are not changed. In other areas, nest-boxes were much safer than natural holes (e.g. van Balen et al. 1982, Nilsson 1984, Robertson & Rendell 1990). Nest-boxes can be good nest sites, but only in forests changed by man where natural holes and predators are scarce. So, maybe this is why in BNP the Pied Flycatcher using natural holes have breeding losses which are lower than in densely distributed nest-boxes in the managed forest of Białowieża.

What affects the Pied Flycatcher broods more — nest sites or forest conditions? Unusually, predation pressure was higher in nest-boxes than in natural holes. There are two possible facts, which could lead to this situation. Firstly, nest robbers found it much easier to search nest-boxes than natural holes. Nest-boxes are densely distributed along roads and they were fixed up 2.5–4 m above the ground, while natural tree holes occupied by the Pied Flycatchers in BNP were on average 8.2 m above the ground (Czeszczewik & Walankiewicz 2003). Secondly, nest-boxes attracted the Forest Dormice and the Yellow-necked Mice as well as the Pied Flycatchers. The Dormice were recorded in nest-boxes ten times more often than in natural holes of BNP (unpubl. data). Białowieża Forest makes up large, close complex. Despite a century of management it still retains primeval features. For instance, the predator community is the same in both, managed and non-managed parts. Moreover, richness of invertebrates (potential food of flycatchers) is also high in managed stands.

Ornithologists working with nest-boxes often make an implicit assumption, which is: nest-boxes are not thought to affect the movements of breeding birds in or out of the study plot. This is too idealistic an idea. The studied nest-box Pied Flycatcher population formed a kind of "sink population" (Czeszczewik et al. 1999). Furthermore, in this study the presence of nest-boxes affected the movement of rodents (Dormice and Mice) into nest-boxes, which led to a higher predation rate than in natural holes. All this suggests that generalizations based on nest-box studies reflect man-made secondary conditions. Now, there is the great need to distinguish those results obtained under natural conditions in natural holes and those obtained in nest-boxes.

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STRESZCZENIE

[Sukces lęgowy i terminy przystępowania do lęgów muchołówki żałobnej w dziuplach i w skrzynkach lęgowych w Puszczy Białowieskiej]

Badania prowadzono w latach 1993–1999. Muchołówki gnieżdżące się wyłącznie w dziuplach badano w lasach liściastych ściśle chronionej części Białowieskiego Parku Narodowego. Powierzchnia skrzynkowa (ok. 190 skrzynek) znajdowała się w zagospodarowanej części Puszczy Białowieskiej, w drzewostanach iglastych i liściastych. Lęgi w skrzynkach zaczynały się wcześniej w lasach liściastych (średnio 12 maja) niż w borach (14 maja, $p < 0.01$), natomiast liczba jaj była podobna w obu środowiskach.

Początek składania jaj zależał od średniej temperatury powietrza w ostatniej dekadzie kwietnia, w latach ciepłych muchołówki wcześniej rozpoczynały zniesienia (Fig. 1). Muchołówki gnieżdżące się w dziuplach zaczynały składać jaja średnio o dwa dni później niż w skrzynkach w lasach liściastych (Tab. 1). Zniesienia w dziuplach były mniejsze niż w skrzynkach (odpowiednio 6.4 i 6.7, $F_{1, 229} = 7.26$, $p < 0.01$), co wiązało się z późniejszymi terminami składania. Dziuple naturalne okazały się bezpieczniejsze niż skrzynki (Tab. 2), odwrotnie niż to wykazano w Szwecji. Lęgi muchołówek najczęściej były rabowane przez kunę i koszatkę (Tab. 3). Średnie straty w lęgach muchołówki żałobnej spowodowane przez drapieżniki zarówno w dziuplach jak i w skrzynkach były najwyższe, jakie kiedykolwiek wykazano dla tego gatunku, jak również dla innych dziuplaków.