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How nest-box data have led to erroneous generalizations: the case of the competition between Great Tit *Parus major* and *Ficedula* flycatchers

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Abstract. The Collared Flycatcher *Ficedula albicollis* population nesting in natural cavities in the Białowieża National Park was studied during 1988–1994. In none of the 534 cases, when a Collared Flycatcher was seen entering a natural cavity, was it killed. Additionally, in less than 2% (10/534) of observations did the male enter cavities owned by a different bird species. We suggest that competition for nest boxes should be interpreted very carefully because in parts of Europe where the experiments were carried out, many environmental characteristics have been profoundly altered by man.

Key words: competition, Great Tit *Parus major*, Collared Flycatcher *Ficedula albicollis*, Pied Flycatcher *Ficedula hypoleuca*, natural cavities, Białowieża National Park, nest predation, primaeval forest

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INTRODUCTION

Competition for artificial nest boxes between two *Ficedula* species (i.e. Pied Flycatcher *Ficedula hypoleuca* and Collared Flycatcher *F. albicollis*) and Great Tits *Parus major* has been analyzed in detail by Slagsvold (1975) and Kallander (1994). That such competition for nest sites between flycatchers and tits is a commonly accepted fact (see review by Newton 1994). The question then is whether this competition occurs in natural conditions or only in situations affected by human activities, i.e. forestry practices, additional food provisioning and low diversity of predators (Brush 1983, Walankiewicz 1991), which may have led to very high densities of flycatchers and tits in nestboxes. This question was not addressed in either Slagsvold's (1975) or Kallander's (1994) papers. We know of no studies in which competition for nest sites between Great Tit and flycatchers has been demonstrated in a forest area with only natural cavities. Moreover, recently published papers indicate that in most of Europe, titmice and flycatchers prefer old-growth deciduous stands, and that a large surplus of unused cavities exists. Walankiewicz (1991) found that every female of the Collared Flycatcher has at least two cavities in its disposal in old-growth forest of the Białowieża National Park. Sandstrom (1992) demonstrated that birds in a deciduous forest in Sweden use only about 5–10% of all available cavities.

According to many authors, Pied Flycatcher males try to usurp nest-boxes of the Great Tit, but the tits successfully chase off or even kill flycatchers. The death rate of the Pied Flycatcher males increases when Great Tits breed later in the season (see papers reviewed by Slagsvold 1975, 1978). The point is that, until now, all data on competition for nest sites between Pied or Collared flycatchers on the one hand, and Great Tits on the other, have been collected in nest boxes. Below we present new material to show that Collared Flycatcher males are fairly safe during their nest site explorations.

These data were collected in the primeval temperate forest of Białowieża National Park (hereafter BNP) and refer to natural cavities only.

METHODS AND STUDY AREA

In 1988–1994 we systematically searched for tree cavities by following Collared Flycatcher males during the period when they are settling, in a 36 ha plot in BNP (Poland, 52°41'N and 23°52'E). This plot corresponds to plot W and its surroundings described in Tomiałojć *et al.* (1984). It is covered by a primaeval (sensu Tomiałojć 1991) over mature oak-lime-hornbeam forest where human presence is very restricted and management is absent. There are no nest boxes, and all secondary cavity nesting birds use natural cavities created by decay or excavated by woodpeckers.

inspected their cavities many times. Observations of males only looking through into an entrance were excluded even if they stayed and sang by the cavity for a few days. The content of the visited cavities was subsequently checked using a lamp and a mirror. For more details see Walankiewicz (1991).

In 1989–1994, following this procedure, we found all nest cavities and most of the cavities defended by males but not chosen by females for nesting. In 1988, due to less intense work, only a portion of the Collared Flycatcher cavities were found.

RESULTS AND DISCUSSION

In none out of 534 cases, when a Collared Flycatcher male was seen entering a natural tree cavity, was he killed. Additionally, in less than 2% (10/534) of observations, did the males enter cavities owned by a

Table. 1. Number of the tree cavities inspected by *Ficedula albicollis* males; *one of three *P. major* nests was deserted with eggs.

[Tabela. 1. Liczba dziupli odwiedzanych przez samce muchołówki białoszyjej; *jedno gniazdo z jajami zostało opuszczone.]

	1988	1989	1990	1991	1992	1993	1994	1988–1994
F. albicollis nesting cavities	14	45	61	32	41	88	71	353
F. albicollis single male cavities	12	26	28	16	26	29	28	165
Nesting cavities of other species:								
Parus major	0	0	1	0	3	0	3*	7
Parus palustris	0	0	0	0	0	1	0	1
Parus caeruleus	0	0	1	0	0	0	0	1
Muscicapa striata	0	0	0	0	0	0	1	1
Erithacus rubecula	0	0	0	0	0	0	1	1
Total cavities inspected by *F. albicollis* males	26	71	91	48	70	118	104	521

In calculating, we used only those cavities into which males were seen completely to enter. Multiple observations of the male singing by and entering the same cavity we included into calculations as one cavity inspected (some males acted in this way even for three weeks). We took into consideration only cases with males staying and owning a cavity at least for two days. Those males which sang by the cavity only one day were excluded. It means that all the Collared Flycatcher males which we included into our data

different bird species (Tab. 1). Therefore, it prompts the question: why were male Pied and Collared flycatchers killed in nest boxes by Great Tits during nest site searches in other study areas (Kallander 1994, Merilä & Wiggins 1995, Slagsvold 1975). Especially Merilä & Wiggins's (1995) study showed high *F. albicollis* mortality — 4,2% of breeders were killed. Although the study mentioned above was conducted in a different way (i.e. observers simply checked nest boxes while in our study observers followed *F. albicollis* males and

only then checked cavities) some comparisons are possible. If we compare numbers of Collared Flycatcher breeding pairs, there were 780 pairs in Merilä & Wiggins's plots in 1993 and ca 400 pairs in the Białowieża study (pooled data from 1988–1995,Walankiewicz 1991 and unpublished data). If in BNP the rate of killed flycatchers would be as in the Merilä & Wiggins's study, some 7–8 birds would be found. This did not happen, however. Not a single death has been recorded.

At BNP, flycatcher males, contrary to those nesting in nestboxes, Pied and Collared Flycatchers, have many more unoccupied cavities at their disposal, and competition with Great Tits is very low or absent (Mitrus *et al.* 1996, Tomiałojć *et al.* 1984, Walankiewicz 1991, Wesołowski *et al.* 1987). There is a very low probability for an *F. albicollis* male in BPN to visit a cavity containing a Great Tit nest.

We suggest that strong competition among tits, *Ficedula* flycatchers, and Starlings *Sturnus vulgaris* in Europe for nest boxes (Newton 1994) and among Starlings and native species in North America (e.g. Howell 1943, Zerhusen 1992) should be regarded as secondary phenomenon created or at least enhanced by long-term human activity, and not a natural character. Competition for nest-boxes should be interpreted very carefully because in parts of Europe where the experiments were carried out, many environmental characteristics have been profoundly altered by man. Some limiting factors have been eliminated ameliorated i.e. predation and others modified i.e. density, nestling survival rate, food in winter, attractiveness and safety of nest sites. For instance, for unclear reasons, nestboxes are more attractive to the Pied Flycatcher and many other animals than natural cavities (Balen *et al.* 1982, McComb & Noble 1981). So this preference alone could intensify competition. Furthermore, both tits and *Ficedula* flycatchers in western Europe breed at higher densities than it was in the past probably as a result of various factors like food provisioning in winter and lower density of predators, especially nest robbers (Tomiałojć *et al.* 1984, Wesołowski *et al.* 1987). Even at about two hundred km from BNP, in the vicinity of Warsaw, up to 60% of individually marked Great Tits breeding in a nonmanaged (since 1950's) oak-lime forest, wintered in close suburbias (J. Nowakowski personal inf.). In this way the wintering tits may have higher survival rates due to provisioning of additional food. Because tits and flycatchers breed in northern and western Europe mostly in nest-boxes, they have much higher reproductive rates than in natural cavities (Nilsson 1975, Walankiewicz 1991). In fact, the nestbox itself is designed to protect the nest against predators! Therefore, secondary cavity nesting birds may saturate relatively safer nestboxes up to the level in to which interspecific and intraspecific competition becomes secondarily very intense.

In conclusion, we do suggest that such artificially induced competition was uncommon under natural conditions once prevailing in the lowland deciduous forests of pristine Europe.

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STRESZCZENIE

[Jak dane zbierane w skrzynkach lęgowych doprowadziły do błędnych uogólnień: przypadek konkurencji pomiędzy bogatką i muchołówkami z rodzaju *Ficedula*]

W latach 1988–1994 na 36-hektarowej powierzchni grądowej Białowieskiego Parku Narodowego obserwowano zajmowanie dziupli przez samce muchołówki białoszyjej. Na powierzchni nie było skrzynek lęgowych. W żadnej z 534 dziupli do których wchodziły samce muchołówki nie znaleziono martwego samca (tab. 1). Tylko 2% dziupli (10/534) odwiedzanych przez samce muchołówki białoszyjej było wcześniej zasiedlonych przez inne gatunki (sikory — bogatka modra i uboga, rudzik). Wyniki te wskazują na małe prawdopodobieństwo odwiedzenia przez samca muchołówki wcześniej zajętej dziupli w warunkach naturalnego lasu białowieskiego. Podważają również powszechnie panujący od lat 50-tych XX w. wśród ekologów — ornitologów pogląd o istnieniu ostrej konkurencji o miejsca gniazdowe pomiędzy dziuplakami wtórnymi. Dlatego też wydaje się, że liczne przypadki zabijania samców muchołówek przez bogatki *Parus major* stwierdzone w Europie mogły zaistnieć tylko w warunkach eksperymentalnych oraz w sztucznie przegęszczonych populacjach i nie mogą stać się podstawą do tworzenia ogólnych praw ekologicznych.