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# INTERSPECIFIC COMPETITION FOR NEST HOLES CAUSES ADULT MORTALITY IN THE COLLARED FLYCATCHER[1]

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*Abstract.* Interspecific competition for nest sites between tits (*Parus* spp.) and Collared Flycatchers (*Ficedula albicollis*) was responsible for the death of 23 flycatchers during one breeding season. Eighteen (78%) of the killed flycatchers were males, and nineteen (83%) of the kills took place in nest boxes occupied by Great Tits (*Parus major*), and two (9%) in boxes occupied by Blue Tits (*P. caeruleus*). The number of casualties in different plots increased with increasing proportion of nest boxes occupied by tits ($r = 0.76$), and decreased with increasing density of nest boxes ($r = -0.43$). The number of casualties equalled up to 17% of all flycatcher individuals breeding in a given plot, indicating that interspecific competition for nest sites may constitute a significant source of adult mortality in the Collared Flycatcher population studied.

*Key words: Adult mortality;* Ficedula albicollis; *competition;* Parus major; Parus caeruleus; *nest sites; nest boxes.*

## INTRODUCTION

The two general forms of competition are exploitation and interference competition (Maurer 1984, Minot and Perrins 1986). Exploitation competition occurs when individuals use the same resources but do not directly inhibit each other, and interference competition when competing individuals confront directly. Both exploitation competition over food resources (e.g., Minot 1981, Gustafsson 1987) and interference competition over nest sites (e.g., Slagsvold 1975, Gowaty 1984, Minot and Perrins 1986) seem to be common between different secondary cavity-nesting bird species. In fact, nest site availability has been demonstrated to limit the size of local breeding populations in many hole nesting passerines (von Haartman 1971, Holroyd 1975, Slagsvold 1975, van Balen et al. 1982, Gustafsson 1988).

Intensive competition for nest holes among tits (*Parus* spp.) and flycatchers (*Ficedula* spp.) has been documented in several studies (e.g., Slagsvold 1975, Gustafsson 1988). Because tits initiate their breeding before the arrival of the migratory flycatchers, many of the potential nest sites are occupied before the flycatchers have arrived at the breeding grounds. However, flycatchers may attempt to take over nest boxes occupied by tits by rapid nest building (Curio 1959, Löhrl 1950, pers. observ.) or direct harassment of tits (Creutz 1955, Slagsvold 1978). Such attempts are probably rarely successful (Creutz 1955, Tompa 1967, see DISCUSSION) and may lead to flycatchers being killed in tit nests (Drost and Schilling 1940; Poulsen 1944; Campbell 1949; Christiansen 1954; von Haartman 1951, 1957; Creutz 1955; Löhrl 1950; Curio 1959; Jansson 1960; Tompa 1967; Král and Bicik 1992; see also: Gowaty 1984 for similar evidence in other species). According to von Haartman (1957) and Löhrl (1957), interspecific competition for nest sites may be the major cause of adult mortality among adult Pied (*Ficedula hypoleuca*) and Collared (*F. albicollis*) Flycatchers during the breeding season. If so, this phenomenon may have evolutionary interest since lifespan (i.e., survival) is known to be a major determinant of life time reproductive success (≈ fitness) in both Pied and Collared Flycatchers (Sternberg 1989, Gustafsson 1989).

In the course of a population study of Collared Flycatchers and tits in Sweden, we have frequently encountered dead flycatchers in nest boxes occupied by tits. In this note, we will examine whether the risk of mortality among intruding flycatchers can be related to the degree of interspecific competition for nest sites.

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TABLE 1. Descriptive information on study plots.

| Plot | Size (ha) | Number of nest boxes | Box density (box/ha) |
|---|---|---|---|
| 1 | 18.8 | 67 | 3.57 |
| 2 | 8.9 | 35 | 3.95 |
| 3 | 16.5 | 51 | 3.09 |
| 4 | 6.1 | 36 | 5.91 |
| 5 | 10.2 | 67 | 6.56 |
| 6 | 20.9 | 156 | 7.46 |
| 7 | 14.5 | 110 | 7.59 |
| 8 | 66.0 | 159 | 2.41 |
| 9 | 6.8 | 30 | 4.44 |
| 10 | 7.4 | 62 | 8.39 |
| 11 | 7.8 | 54 | 6.97 |
| 12 | 12.5 | 161 | 12.87 |
| 13 | 20.4 | 120 | 5.87 |
| 14 | 5.2 | 10 | 1.92 |

## MATERIAL AND METHODS

The data for this study were collected in the southern part of the island of Gotland (57°10'N, 18°20'E), Sweden. Nest boxes (32 mm entrance) in 14 discrete plots were inspected at 4–5 day intervals from 29 April to the end of June 1993. Twelve of the study plots consisted of rich deciduous forest dominated by oak *Quercus robur* and ash *Fraxinus execelsior,* while the two remaining plots were coniferous forest dominated by pine *Pinus sylvestris,* with some birch *Betula pubescens.* The density of nest boxes in these plots varied between 1.9 and 12.9 boxes/ha (Table 1) and more information on study area can be obtained from Lindén (1990) and Pärt (1991). At each visit, nest contents were recorded and dead Collared Flycatchers were checked for rings, sex and age. Skull injuries, typical for birds killed by tits (pers. observ.), were used as evidence that the flycatchers had been killed by tits. Other causes of mortality (dead flycatchers without injuries) were not encountered during this study. Additional data about flycatcher casualties were obtained from three plots outside our main study area. However, these data could not be used in all comparisons because numbers of breeding tits in these areas were not known.

In addition to Great Tits, Blue Tits (*P. caeruleus*) and flycatchers, other species breeding in the nest boxes in the study area included Tree Sparrows (*Passer montanus*; 4 pairs), Coal Tits (*Parus ater*; 13 pairs) and Nuthatches (*Sitta europea*; 7 pairs). All these species initiate their breeding before the Collared Flycatchers and therefore limit the availability of nest boxes for flycatchers. However, since their total numbers were low, they were ignored in all analyses but all conclusions would, if anything, be strengthened if their presence were taken into account.

Statistical testing of all correlations was carried out by randomization tests to overcome problems arising from distributional assumptions and small sample sizes (Potvin and Roff 1993). Five thousand randomly selected permutations were used to assess the null hypothesis of no correlation. The reported *P*-values indicate the proportion of permutations with correlation coefficients as high or higher than the observed value (Cheverud et al. 1989).

TABLE 2. Timing of the Collared Flycatcher casualties in Blue and Great Tit nests.

| Species | Nest-building | Egg-laying | Incubation | Unknown[a] |
|---|---|---|---|---|
| *P. caeruleus* | 0 | 1 | 1 | 0 |
| *P. major* | 1 | 14 | 2 | 2 |
| *Parus* spp. | 2 | 0 | 0 | 0 |
| All | 3 | 15 | 3 | 2 |

[a] Exact timing not known; either egg laying or incubation.

## RESULTS

Twenty-three dead Collared Flycatchers were found in 18 different tit nests. Nineteen (83%) of them were found in boxes occupied by Great Tits, two (9%) in boxes occupied by Blue Tits, and two in boxes with an unidentified tit nest (Table 2). More than one flycatcher was killed in three nest boxes, the maximum number of casualties being four. Males were killed more often than females (18 males/5 females), and 14 (66%) out of 21 aged dead flycatchers were adults (Table 3). Different age classes of males were killed in proportion to their frequency in population ($\chi^2_1 = 0.057$, $P = 0.812$; Table 3), but the data for females were too few to allow for inferential statistics ($n = 5$). The number of casualties relative to number of flycatchers breeding on a given plot varied from 0 to 17%, with a mean casualty rate of 4.2% (Table 4).

### TIMING OF MORTALITY

The majority of the casualties occurred shortly after the arrival of the first Collared Flycatchers, when most of the tits had already initiated egg laying (Fig. 1). Fifteen (65%) killed flycatchers were found in tit nests at the egg laying stage, while three (13%) were killed both in the nest

TABLE 3. Age distribution and sex of the Collared Flycatchers killed by tits. Age category "≥ 1" refers to birds of unknown age.

| Sex | | $n$ | Age (years) | | |
|---|---|---|---|---|---|
| | | | 1 | ≥ 2 | ≥ 1 |
| Female | killed | 5 | 2 | 3 | 0 |
| Male | killed | 18 | 5 | 11 | 2 |
| | alive[a] | 274 | 80 | 180 | 14 |
| Both | (killed) | 23 | 7 | 14 | 2 |

[a] Only males in areas where kills occurred included.

building and incubation stages, respectively (Table 2).

## KILLS IN RELATION TO NEST BOX OCCUPANCY AND BREEDING DENSITIES

There was no association between number of casualties and local population density (pairs/ha) of tits (Great Tit: $r = -0.09$; Blue Tit: $r = 0.03$; combined: $r = -0.06$; for all comparisons: $n = 14$, $P > 0.36$). Further, no correlation was found between casualty numbers and absolute number of tit pairs in a given area (Great Tit: $r = 0.08$; Blue Tit: $r = 0.05$; combined: $r = 0.06$; $n = 14$, $P > 0.39$ in all comparisons). However, the number of flycatcher casualties in different plots decreased with increasing nest box density (boxes/ha; $r = -0.43$, $r^2 = 0.19$, $n = 14$, $P = 0.047$), and increased with proportion of nest boxes occupied by tits (Great Tit: $r = 0.51$, $r^2 = 0.26$, $P = 0.048$; Blue Tit: $r = 0.54$, $r^2 = 0.29$, $P = 0.025$; combined: $r = 0.76$, $r^2 = 0.57$, $P = 0.001$; Fig. 2).

## DISCUSSION

Despite the extensive literature dealing with interspecific competition between flycatchers and tits (Slagsvold 1978; Gustafsson 1987, 1988; Sasvari et al. 1987; see Slagsvold 1975 for review of earlier literature), only anecdotal notes of mortality of flycatchers in tit nests have appeared (Drost and Schilling 1940; Poulsen 1944; Campbell 1949; Christiansen 1954; von Haartman 1951, 1957; Creutz 1955; Löhrl 1950; Curio 1959; Jansson 1960; Tompa 1967; Král and Bicik 1992). This might indicate that casualties are incidental to the degree that they cannot constitute any significant source of mortality among flycatchers. By contrast, the results of this study show that killing by tits may be relatively frequent, leading to death of up to 17% of the Collared Flycatcher individuals breeding in a given area. Although

TABLE 4. Number of killed Collared Flycatchers in relation to the number of flycatchers breeding in a given plot.[a]

| Plot | Number killed | Number of breeders[b] | Killed/ breeders (%) |
|---|---|---|---|
| 1 | 5 | 30 | 17 |
| 2 | 4 | 28 | 14 |
| 3 | 3 | 38 | 8 |
| 4 | 2 | 34 | 6 |
| 5 | 2 | 26 | 8 |
| 6 | 1 | 124 | 0.8 |
| 7 | 1 | 68 | 1 |
| 8 | 1 | 86 | 1 |
| 9 | 1 | 32 | 3 |
| 10 | 0 | 30 | 0 |
| 11 | 0 | 46 | 0 |
| 12 | 0 | 132 | 0 |
| 13 | 0 | 100 | 0 |
| 14 | 0 | 6 | 0 |
| Mean | 1.42 | 55.7 | 4.2% |

[a] Only the 14 main study plots included.
[b] Number of breeding attempts·2.

this is an extreme value (mean for all study plots was 4.2%), even this study might have underestimated the actual frequency of kills for two reasons. First, some kills may take place outside the nest box, and tits may sometimes remove bodies from nest boxes. This is indicated by dead flycatchers having been found on the ground under nest boxes (von Haartman 1951, Creutz 1955, pers. observ.). Second, tits or other flycatchers may quickly assemble a nest on top of a killed flycatcher, in which case the kill may be easily overlooked (J. Merilä, pers. observ.; see also: Gowaty 1984). It is also worth emphasizing that the casualty rates reported in this study are not exceptional for the particular year (1993) when these data were collected, but dead flycatchers have been encountered frequently during other study years as well (L. Gustafsson pers. comm.; J. Merilä, pers. observ.). Thus, casualties caused by fighting may be more common than previous reports indicate.

Our data indicate that casualties are caused by interspecific competition for breeding sites. The frequency of flycatcher casualties per plot increased with increasing proportion of nest boxes occupied by tits (Fig. 2), and decreased with increasing nest box density, but no relationship was found between breeding density of tits and flycatcher casualties, indicating that the casualties are not related to tit densities per se, but to the availability of nest sites. This is in line with Gustafsson (1987, 1988), who found strong inter-

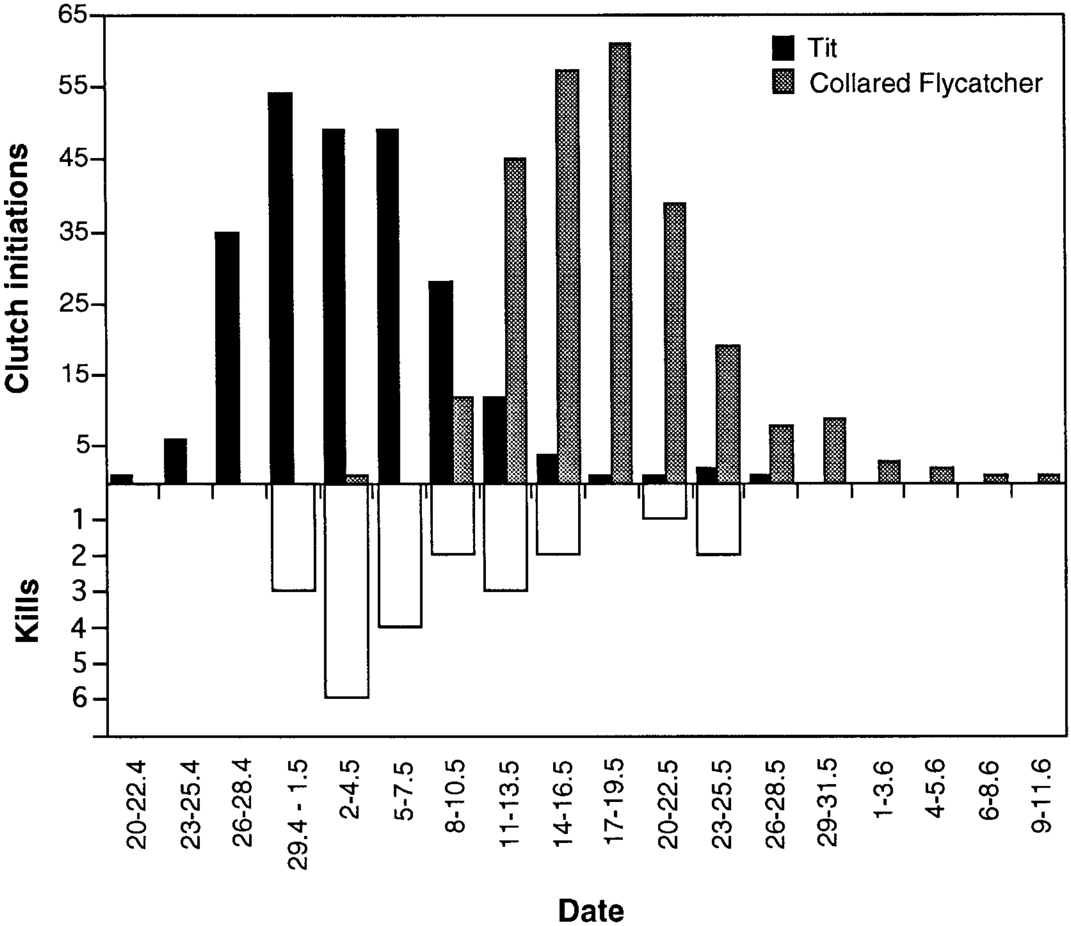


FIGURE 1. Timing of the Collared Flycatcher kills (below) in relation to clutch initiation dates of tits and flycatchers (above) in 1993. Tit = Blue and Great Tit combined.

specific competition for nest sites between flycatchers and tits in the same study plots. Thus, competition between tits and flycatchers may not only result in reduction of the breeding success of flycatchers (Gustafsson 1987, 1988), but in their death, i.e., loss of all future reproduction.

Traumatic deaths caused by interspecific competition for nest sites are not restricted to interactions between flycatchers and tits only, but House Sparrows (*Passer domesticus*) are known to kill adult Eastern Bluebirds (*Sialis sialis*) in nest boxes in rather high frequencies (Gowaty 1984). However, in contrast to evidence from some other species (e.g., Zeleny 1984, Belles-Isles and Picman 1986, Quinn and Holroyd 1989), we have never observed that tits or flycatchers would destroy or remove each others' eggs or young when attempting a take over of already occupied nest box. Instead, a new nest is usually built over eggs of the previous occupant (Slagsvold 1975).

Most of the killed flycatchers were males. Other flycatcher studies (e.g., Campbell 1949, Curio 1959, Tompa 1967) found a tendency for the opposite, but sample sizes in these cases were low. Heavier mortality on males might also be expected since male flycatchers arrive at the breeding grounds ahead of females, and female flycatchers enter holes after intensive male display including males' visits into the nest box (Lundberg and Alatalo 1992). Therefore, it is likely that males suffer a greater risk of conflict with tits, at least before nest building starts. During nest building, females may be in greater peril

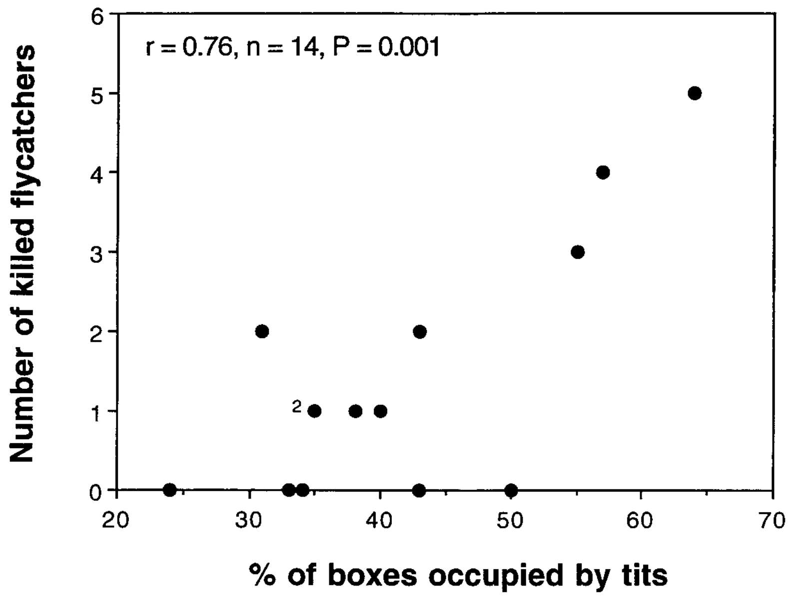


FIGURE 2. Frequency of Collared Flycatcher kills in different plots in relation to nest box occupancy by tits (% of all available boxes occupied by tits). 2 = two overlapping data points.

since they have to spend more time inside the nest box, but since most tits are already incubating at this time, females are less likely to come into direct contact with tits. Thus, more males may be killed due to their greater exposure to tits.

An important consideration is that, as in any other nest box study, the availability of high quality nest sites in this study might have been artificially high. Since natural cavities are abundant both in natural and managed forests (van Balen et al. 1982, Walankiewicz 1991, Sandström 1992), this might suggest that interspecific competition for nest sites in nature is less intensive. However, low breeding densities in "natural" situations (e.g., Lundberg and Alatalo 1992, Sandström 1992) together with observations that breeding densities can usually be increased by erecting boxes (von Haartman 1971) may indicate that high quality nest sites are indeed in scarce supply. If so, this might suggest that competition for nest sites in "nature" can cause similar levels of mortality among adult flycatchers as observed in this study. However, without any data on mortality in "natural" forests, this claim cannot be supported.

Finally, although flycatchers sometimes successfully manage to usurp tit nests (see Slagsvold 1975 for a review), successful takeovers are rare in our study area and are often suspected to be associated with desertion of tit nests for other causes (see Löhrl 1950, for similar observations).

In conclusion, the findings of this study indicate that interspecific competition for nest sites may constitute a significant source of adult mortality among Collared Flycatchers. Future studies on casualty rates should address the question of whether this mortality is dependent on individual differences in plumage coloration and body size. As shown by Gustafsson (1988), interspecific competition may increase the intensity of intraspecific competition, which then might translate to non-random mortality among Collared Flycatcher individuals differing in their phenotypic (and genotypic) characteristics.

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