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Author: Walankiewicz, Wiesław

Source: Acta Ornithologica, 37(2) : 91-106

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/068.037.0205

ACTA ORNITHOLOGICA
Vol. 37 (2002) No. 2

Nest predation as a limiting factor to the breeding population size of the Collared Flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland)

Wiesław WALANKIEWICZ

Department of Zoology, University of Podlasie, Prusa 12, 08–110 Siedlce, POLAND, e-mail: wwalan@ap.siedlce.pl

Walankiewicz W. 2002. Nest predation as a limiting factor to the breeding population size of the Collared Flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland). Acta Ornithol. 37: 91–106.

Abstract. This study is based on an analysis of nest-histories of 652 Collared Flycatcher nests found in natural tree cavities in the Białowieża National Park in 1988–1999. The secondary-cavity-nester Collared Flycatcher constitutes migratory single-brooded population breeding in high density in the primeval oak-lime-hornbeam (*Querco/Tillio-Carpinetum*) stands. Nest predation was the main reason of the breeding losses (240 nests) accounting for 91% (82%–100%) of them. Local production of fledglings was affected by nest predation caused by rodents, mustelids and Great Spotted Woodpecker. In this study a link between forest rodent cycles and the Collared Flycatcher fluctuations in number was documented. Number of produced fledglings depended on both, positively the number of the Collared Flycatcher breeding pairs in year N and negatively on the Yellow-necked Mouse density in year N. Rate of nest destruction is related to the density of the Yellow-necked Mouse recorded in BNP, while independent on the Collared Flycatcher density (nest predation limiting but not regulating). The predation pressure in some years keeps the Collared Flycatcher density at a level well below that of the potential the habitat resources (nest-sites, food). Local breeding density was shaped by fledglings productivity (breeding success) of the previous year. Earlier hypotheses concerning the Collared Flycatcher and other birds population limitation were also discussed.

Key words: Collared Flycatcher, *Ficedula albicollis,* nest predation, population dynamics, tree cavities, doomed surplus

Received — May 2002, accepted — Nov. 2002

INTRODUCTION

The role of predation in limiting bird density is still a controversial issue (Lack 1966, Nilsson 1986, Walankiewicz 1991, Martin 1993, Newton 1993, 1998) since predation is only one of several limiting factors acting on bird populations. While reviewing the impact of predation on birds, Newton (1993, 1998) concluded: "...with few exceptions (mainly game birds), predation seems to play a minor role in the direct limitation of bird breeding numbers...". This is not a new conclusion, as it is quite similar as proposed by Lack (1966). Rare but well documented exceptions where predation affected bird densities come mainly from open habitats of the European and North American ecosystems (Marcström et al. 1988, Willebrand 1988, Underhill et al. 1993). Such habitats harbour animal communities either originally composed of relatively few species, or secondarily impoverished by human activity.

Compared to other groups, (e.g. mammals: Newton 1994a), it is not an easy task to distinguish the influence of predation on bird populations from the impact of other agents. The reason behind this is that birds are very mobile and their behaviour may buffer breeding density changes, as the territorial behaviour may prevent some birds from breeding when the density increases (Brown 1969). Moreover, because many bird species winter far from their breeding quarters, they may also be limited in their winter quarters and during their migrations (Tate 1972, Rappole & McDonald 1994, Newton 1998). Separating the effect of predation from that of other limiting factors under natural conditions should be easier when the predation rate varies substantially from one season to another (Tomiałojć et al. 1984, Wesołowski 1985). The second condition should be that the current breeding density reflects the predation rate in the previous breeding season.

After half a century of studies on *Ficedula* flycatchers (model species of European ornithology) one of the main limiting factors — nest predation — is still regarded as unimportant to these secondary cavity nesters (Lundberg & Alatalo 1992, Newton 1994a, b, 1998). Results presented in this paper challenge such a conclusion.

The Białowieża population of the Collared Flycatcher is numerous and relatively easy to study. There are several features which make it a good subject for research.

1) Territorial behaviour, known among many bird species (e.g. Paridae) as an important factor moderating density, does not play a role in *Ficedula* species. Collared Flycatcher males when mated tolerate other singing males within a few metres range (Walankiewicz 1991). Up to five monogamous males may breed within 1 ha of an old-growth stand (Walankiewicz 1991, unpubl. author's data). Hence, it can be assumed that even in high density years no part of the Collared Flycatcher population is excluded from breeding because of aggressive territorial behaviour of males. As the number of suitable nesting sites in the Białowieża National Park (hereafter BNP) is very high, all males are able to find a suitable cavity for nesting (Walankiewicz 1991).

2) Socially dominant competitors to the Collared Flycatcher, such as the Great Tit *Parus major* and the Nuthatch *Sitta europaea*, breed in BNP at very low densities (Tomiałojć et al. 1984, Wesołowski et al. 1987), so they can not affect the density of the Collared Flycatcher by taking over the nest sites. Both these species in BNP have at their disposal at least three nest sites per pair in spring before the arrival of the Collared Flycatcher. Despite its very high densities, this species is not limited by the number of available nesting cavities either (Walankiewicz 1991). The still commonly accepted idea of a limited number of nest sites for secondary cavity-nesters results from the fact that earlier surveys were carried out in relatively young or intensively managed, chiefly coniferous, forests of Europe and the USA. Several recent works conducted in deciduous forests of the USA and Europe (Waters et al. 1990, Walankiewicz 1991, Sandström 1992) contradicts those earlier conclusions.

3) In the multi-species forest of Białowieża (composed of hornbeam *Carpinus betulus*, lime *Tillia cordata*, oak *Quercus robur*, maple *Acer platanoides*, elm *Ulmus* glabra, spruce *Picea abies*) the caterpillar biomass is much higher than in other deciduous temperate forests (Rowiński 2001, P. Rowiński personal inf.). In 1995–1999, despite very low numbers of the Winter Moth *Operophtera brumata* caterpillars (i.e. the most numerous species of moths), no symptoms of acute food shortage were recorded as various birds switched to an alternative source — abundant caterpillars of *Ptilophora plumigera* (Rowiński & Wesołowski 1999, Wesołowski et al. 2002). In BNP losses of the Collared Flycatcher nestlings, suggesting brood reduction due to starvation, were also low (ca. 5%, Mitrus 1998). Therefore, the Białowieża Collared Flycatcher population does not seem to be limited by food resources.

4) The Collared Flycatcher is a very numerous species of the lime-oak-hornbeam bird assembly of the BNP. In some years it is the most abundant bird, reaching a density of 22 pairs/10 ha (Walankiewicz et al. 1997a). Thus, this species constitutes an important part of the bird assembly and as such cannot be ignored as potential prey to local predators. For instance, half of all birds identified from the Pine Marten *Martes martes* scats were cavity-nesting birds (Jędrzejewska & Jędrzejewski 1998). The Pine Martens were responsible for ca. 25% of the Collared Flycatcher breeding losses in BNP (Walankiewicz 2002).

5) This species has a very short breeding season and therefore only few pairs have a chance to re-nest. I recorded no more than two re-nesting pairs in the study plot per year (< 2% of all breeding pairs). I included them into data on breeding success to be sure that the whole Collared Flycatcher rate of production was calculated. Newton (1993 p. 183) is aware that in some studies re-laying were omitted. So due to that, he strongly emphasises that actual production could be higher and the influence of nest predation could be less important than "bald figures", i.e. what the percent of robbed nests meant. His warning does not apply however to the Collared Flycatcher case.

6) The Collared Flycatcher tend to return to previous breeding or natal grounds (Pärt 1991). Additionally, apart from the Białowieża there are no suitable habitats for this species within the range of a few hundred kilometres. Gotland Island in the Baltic Sea and the Niepołomicka Forest near Cracow (S Poland) or some forests in the Lublin region (E Poland) are the closest areas with large populations of the Collared Flycatcher. Hence, it can be assumed that migration of the species between those areas in subsequent sea-

sons is highly unlikely, and that local population dynamics reflect the influence of local factors.

7) The Collared Flycatcher winters in the tropics of Africa, avoiding the unstable conditions of the harsh sub-continental winters in Białowieża. I assume that losses during migration and wintering in Africa occur at a fairly stable rate on year-to-year scale. Such an assumption is based on the results of studies on the closely related Pied Flycatcher *Ficedula hypoleuca*, which, like the Collared Flycatcher, winters in Africa. After 21 years of study Järvinen (1989) concluded, that following a good breeding year, the species consistently has a higher density during the next breeding season. Also Svensson (1985) doubted that conditions in the African winter quarters of the Pied Flycatcher affect its breeding density.

The main purpose of present study was to determine the role of nest predation in shaping the fluctuation in breeding numbers of the Collared Flycatcher. This was achieved by:

— studying how the local production of fledglings is affected by nest predation,

— assessing how the local breeding density is shaped by fledglings productivity (breeding success) of the previous year.

STUDY AREA AND METHODS

The study was carried out during the years 1988–1999 in the Białowieża National Park (E Poland, 52°41′N, 23°52′E). The 36 ha study plot corresponded to plot W and its surroundings in Tomiałojć et al. (1984). It is covered by a primeval (sensu Tomiałojć 1990) oak-lime-hornbeam forest (Faliński 1986), where human disturbance is restricted to a few tourist paths and the scientists' activity. There are no nest-boxes, and all secondary cavity-nesting birds use only natural tree cavities created by either decay or excavated by woodpeckers.

The study plot was regularly searched for tree cavities by following Collared Flycatcher males during their settlement time. In 1989–1997 almost all nest cavities were found, as well as most of the cavities defended by males but not accepted by females (hereafter non-breeding males). The objective of that kind of activity was to assess the number of breeding pairs as well as of non-breeding males defending their cavities. Only males defending a cavity for at least two days were taken into account. In 1988 within plot W less intensive work was carried out, where only a portion of the Collared Flycatcher cavities were found. In the same year the 24 ha plot CM (Tomiałojć & Wesołowski 1994) was also searched for Collared Flycatcher nests. In all years and in all plots, the cavity content was checked using a lamp and a mirror attached to a flexible wire. All cavity trees were marked and checked many times from the ground for any bird activity. The goal was to determine whether the cavity was a breeding site or if it was a male's cavity, not accepted by a female. As breeding cavities were considered those in which at least one egg was laid and the nest had not been abandoned. By checking the cavity content, the breeding success and reasons of failure were estimated.

The objective of this work was to obtain data about the characteristics of cavities and to compare dimensions of the cavities in years of low Collared Flycatcher density with those used during high-density years. Since several papers mentioned that in high-density years some secondary cavity nesters are forced to use sites of poorer quality (Newton 1998), dimensions of breeding cavities were assessed.

The following characteristics of nest cavities were measured: two entrance diameters (vertical and horizontal) and maximum depth, i.e. distance between the lower rim of the cavity entrance and the centre of the nest bottom. From those two entrance diameters measured vertically and horizontally the smallest one was taken for calculation as excluding some potential predators. It has been proved that the size of the cavity entrance affects the safety of the Collared Flycatcher nests (Walankiewicz 1991). In the Białowieża population of Marsh Tit *Parus palustris* the chance of a nest being predated was influenced by the maximum cavity depth (Wesołowski 2002). This species breeds in BNP in cavities of dimensions similar to those used by the Collared Flycatcher. Because of difficulty in inspection, some (11%) cavities were not checked.

Losses incurred by predators were assessed by recording such clues as: broken shells or perforated eggs, killed nestlings by their damaged bodies, disappearance of nestlings or eggs in the period when they should still be in the nest.

Additionally, in the years 1989–1997, the age of the Collared Flycatcher males that had settled within the plot was determined by recording their plumage. Yearlings were distinguished from older males (hereafter "old males"), by the brown, rather than black, colour of their primaries (Svensson 1984). Males were observed under good light conditions using binoculars 10 x 50 mm. Depending on the year, it was possible to age 36–90% (mean = 71%) of the males breeding within the study plot (Table 1). Based upon the number of settled males within the plot, the number of yearlings was calculated by extrapolation. In all years the males were aged with the same effort.

Although the numbers of non-breeding males were probably overestimated (part of them changed the place of singing), the males were counted and checked consistently in all seasons with the same intensity. Thus, the numbers of non-breeding males obtained by this method properly reflected changes of their real numbers and changes in their proportion (%) to the numbers of breeding males.

In the years 1975–1999 a parallel monitoring was conducted, using the territory mapping method to census all birds on two other (CM — 24 ha and MS — 30 ha) plots within BNP (Tomiałojć et al. 1984; Tomiałojć & Wesołowski 1994, 1996, Wesołowski et al. 2002). Those extensive territory mapping data were used to test the assumption that population variation on a 36 ha plot (real densities) properly reflects the Collared Flycatcher fluctuations across the entire BNP area during 1988–1995. It has been proved that the territory mapping method properly reflects changes in the Collared Flycatcher breeding densities (Walankiewicz et al. 1997a).

Eventually the Collared Flycatcher breeding losses were analysed in relation to population density changes of the important nest predators, such as: the Yellow-necked Mouse *Apodemus flavicollis*, the Pine Marten and the Great Spotted Woodpecker *Dendrocopos major* (Walankiewicz 2002). Long-term data on the rodent density changes in oak-lime-hornbeam stands of BNP had been obtained from the Mammal Research Institute of the Polish Academy of Science (Pucek et al. 1993 and unpubl. data, Jędrzejewska & Jędrzejewski 1998); while densities of the Pine Marten during 1988–1996 from Zalewski et al. (1995 and unpub. data). This plot was covered by the same oak-lime-hornbeam forest association like plots W, CM and MS. The Pine Marten data came from a vast 10 km^2 plot mostly covered by the same forest association as plot W. The latter is located on the southern rim of the Mammal Research plot. The Great Spotted Woodpecker breeding densities from plot W (25 ha) are from Tomiałojć & Wesołowski (1994, 1996), and Wesołowski et al. (2002).

Additionally, a variation in indices of leaf-eating caterpillars from BNP was used to express changes in food availability. Indices of caterpillars were taken from Tomiałojć et al. (1984), Wesołowski & Stawarczyk (1991), Wesołowski & Tomiałojć (1997) and Wesołowski et al. (2002). Caterpillars (mostly Geometridae) were counted once a season, in May, depending on the stage of leaf development. Each time 50–120 standard twigs (0.25 m^2) from the lower parts of the hornbeam underconopy were searched. Jędrzejewska & Jędrzejewski (1998) strongly suggested that the Collared Flycatcher breeding losses in the BNP are negatively correlated to the caterpillars density.

All statistical procedures followed the formulas given in STATISTICA for Windows. All probability values in the text are two tailed.

Table 1. Basic data on the *F. albicollis* breeding performance and share of breeding and nonbreeding males by age (i.e. yearlings versus older than one-year old) within plot W in years 1989-1999. For some calculations also breeding success from 1988 year was used (35.3%, n = 17). Breeding success is expressed as % of nests from which at least one bird has fledged.

	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	1988-1999
Pairs	48	61	36	41	81	68	77	79	63	53	45	59.3
% breeding success (n)	55.8 (43)	30.4 (56)	50.0 (32)	89.2 (37)	51.3 (78)	55.6 (54)	70.5 (61)	61.5 (65)	28.8 (52)	34.3 (35)	50.0 (28)	51.1 (558)
Share (%) of predation in losses	84.2	97.4	100	100	84.2	87.5	94.4	88	97.3	87	85.7	91.4
Females killed in the nest		2	1				1					3
Breeding yearlings	9	28	10	19	36	19	25	21	16	20	5	18.9
Breeding old males	39	33	26	22	45	47	52	58	47	33	40	40.2
Fledged birds	80	56	54	110	132	113	163	138	54	58	62	92.7
Non-breeding old males	25	18	13	25	21	26	14	19	19	12	17	19.0
Non-breeding yearling males	9	13	4	13	13	11	13	4	8	8	7	9.4
% of non-breeding males	41.5	33.7	32.1	48.1	29.6	35.9	26.0	22.5	30.0	27.4	34.8	32.9
Age of recognized males (%)	64.6	36.1	61.1	80.5	89.8	86.8	88.3	70.9	50.8	69.8	82.2	71.0

RESULTS

Nest predation and density changes

Nest predation was the main reason of 91% (82%–100%, 240 nests) of the Collared Flycatcher breeding losses (Table 1). Other reasons of the breeding losses, e.g. unfertilised eggs (18 nests; 3.3%), or fall of the nest tree (3 nests; 0.6%) were much less important. The total breeding losses varied much from year to year from less than 10% in 1992 to ca. 70% in 1990, 1997 and 1999 (Table 1).

Within the 36 ha plot the Collared Flycatcher breeding numbers varied more than twofold, i.e. from 36 to 81 pairs. The strong changes in the Collared Flycatcher breeding numbers were recorded twice within plot W (Fig. 1). The first change was between the 1990 and 1991, when after high nest losses (70%, n = 56) the Collared Flycatcher breeding densities strongly declined. The second occurred between the 1992 and 1993; the breeding density in 1993 doubled that of 1992, when only 11% of the broods were depredated. Number of breeding pairs in year N was correlated to breeding success in year N-1 (R = 0.816, p < 0.002, n = 11).

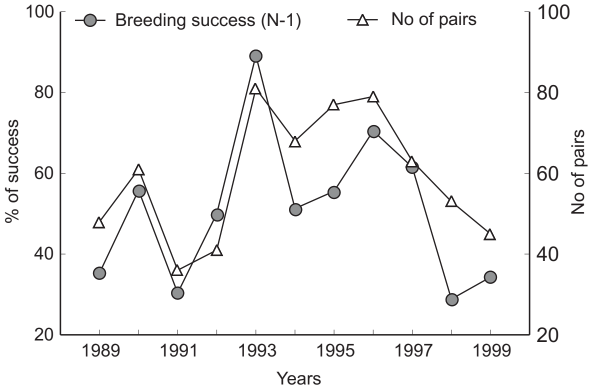

Fig. 1. Number of the Collared Flycatcher pairs in the year N in relation to the breeding success in the previous year (N-1).

Yellow-necked Mouse densities and the rate of destroyed flycatcher nests

The Collared Flycatcher breeding success was negatively related to the Yellow-necked Mouse density index expressed in number of individuals/100 trap nights ($r_s = -0.608$, p = 0.036, n = 12, Fig. 2). It suggests that the Collared Flycatcher breeding losses were heavier in high density years of the Yellow-necked Mouse. The Yellow-necked Mouse reached high densities only three times during this work, so the other robbers of the Collared Flycatcher broods could also have some influence.

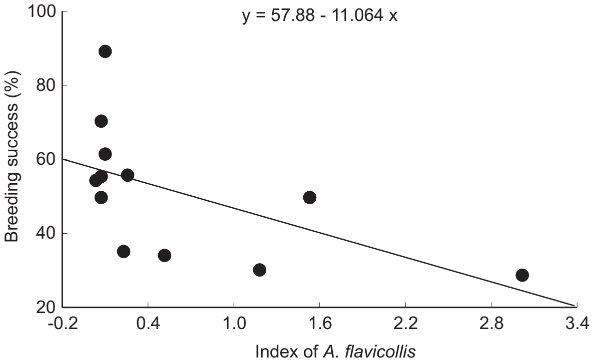

Fig. 2. Breeding success (%) in relation to the Yellow-necked Mouse density index in BNP.

Pine Marten and Great Spotted Woodpecker density and the Collared Flycatcher breeding success

The breeding success of the Collared Flycatcher has not been found to be related to the Pine Marten densities (R = 0.352, ns, n = 8, Table 2), nor to the Great Spotted Woodpecker breeding numbers ($r_s = 0.148$, ns, n = 12, Table 2).

Number of produced fledglings

Since the number of fledglings could be influenced by the number of breeding pairs and by nest losses caused by the Yellow-necked Mice, a multiple regression analysis of those two factors was done.

It has been found that the number of produced fledglings depends on both, the number of the Collared Flycatcher breeding pairs in the year N and the Yellow-necked Mouse index in the year N (R = 0.850). These two factors in multiple regression analysis explain 72% of variation in number of flycatcher fledglings produced in the year N (p = 0.006). Of these two factors, slightly more important was the number of breeding pairs (semipartial correlation coefficient, SR = 0.618, p = 0.011) followed by the negative influence of the Yellow-necked Mouse density (SR = -0.532, p = 0.021).

Joint number of breeding pairs and produced fledglings vs breeding density in the following year

Since the breeding population in the year N may consist of birds which bred in year N-1 and fledglings produced in the year N-1, both factors were analysed in relation to numbers of breeding pairs in the year N. Multiple regression showed that only the

Table 2. Pine Marten density in BNP and the Great Spotted Woodpecker density in the study plot. Marten density in years 1988–1996 come from Zalewski et al. (1995) and unpubl. data. Due to the 1990 weather condition it was impossible to collect data for that year. The Great Spotted Woodpecker breeding pairs within 25.5 ha plot W in years 1989-1999, obtained by territory mapping method (Tomiałojć & Wesołowski 1994, 1996, Wesołowski et al. 2002).

Years	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Martens/km^2	0.64	0.61	?	0.44	0.76	0.36	0.59	0.45	0.51	—	—	—
Woodpecker pairs/10ha	2	2.5	2.5	2	2.5	3.5	3.5	2.3	3	5	3	3

latter factor significantly influenced breeding population in subsequent year (R = 0.833, $p < 0.016$, n = 10, breeding pairs in year N-1, SR = -0.281, ns; SR fledglings in year N-1, SR = 0.982, p = 0.017, Fig. 3).

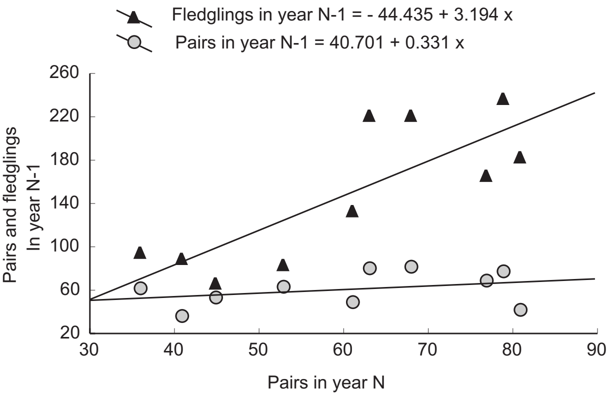

Fig. 3. Relation between both number of breeding pairs in year N-1 and fledglings produced in year N-1 versus breeding pairs in year N.

This means that breeding density does not depend on the number of pairs that bred within the study plot in the previous year but depends on the number of fledglings produced in the previous year.

Relation between the number of fledglings and the number of old and young males breeding in the following year

The number of old males breeding within the study plot appears to be positively correlated with the number of fledglings produced in a previous year (Fig. 4). Multiple regression analysis of two factors, i.e. number of all breeding males in year N-1 and number of fledglings produced in year N-1, on number of adult males breeding in the year N revealed that this effect is independent of breeding population size in the previous year but is dependent on fledgling number produced in year N-1 (R = 0.820, $p < 0.020$, n = 10, pairs in year N-1, SR = 0.226, p = 0.444, and fledglings in year N-1, SR = 0.658, p = 0.050, Fig. 4). This means that more old males have a chance to mate after a high-breeding-success year. Interestingly, the number of young males breeding within the study plot is not related to the number of fledglings produced during a previous year (R = 0.411, ns, n = 10)

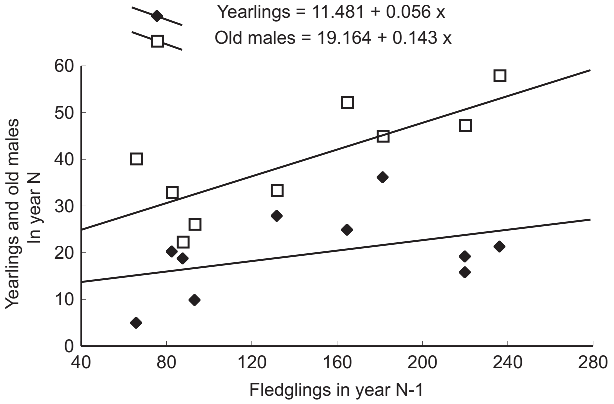

Fig. 4. Relations between the number of fledgling birds in year N-1 and the number of old and young males breeding in the following year N.

Breeding density and number of non-breeding males

In all study years a substantial surplus of non-breeding was recorded (Table 1). The number of non-breeding males did not increase with the increasing breeding density (R = 0.187, ns, n = 11, Fig. 5). This means that in high-density years (probably) more males have a chance to find females and number of non-breeding males do not increase.

Local or wider-range fluctuations?

The Collared Flycatcher density changes within the plot W have been proved to be synchro-

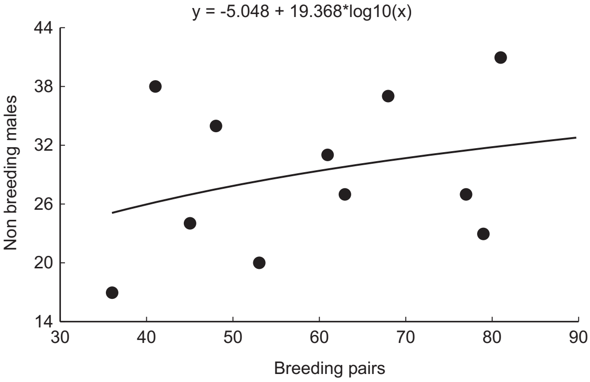

Fig. 5. Number of non-breeding males in year N in relation to breeding pairs in year N.

nised with those occurring in two other study plots (CM, MS) (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, 1994, 1996, Wesołowski et al. 2002), totally covering 54 ha in BNP (R = 0.625, p < 0.04, n = 10, Fig. 6). This suggests that data from plot W properly reflect the fluctuations of the Collared Flycatcher numbers within a wider area. Because all these plots (W, CM and MS) were located in oak-lime-hornbeam forest association of the BNP, it can be assumed that the data from the plot W, along with those from other plots form a sample reflecting the Collared Flycatcher dynamics in the all oak-lime-hornbeam stands of BNP which cover over 20 km^2. This type of tree-stand is the local optimal habitat for the Collared Flycatcher (Tomiałojć et al. 1984).

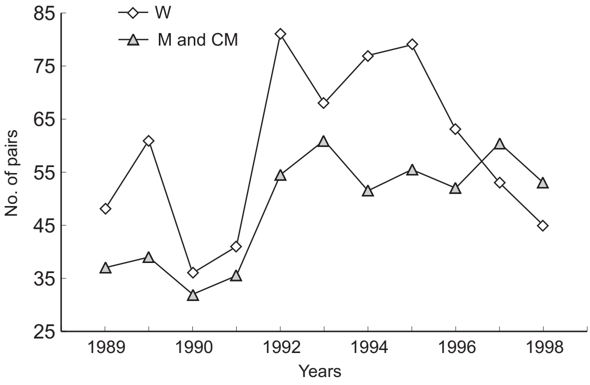

Fig. 6. Number of breeding pairs of the Collared Flycatcher on W plot in relation to pooled density within two study plots settled over BNP. Within those plots (CM, MS) the territory mapping method was used.

The Collared Flycatcher density and breeding success

The rate of the Collared Flycatcher breeding losses has appeared to be density independent (R = 0.573, p = 0.065, n = 11, Fig. 7). It means that predators were not intensifying their search for the Collared Flycatcher nests when these birds bred at higher density.

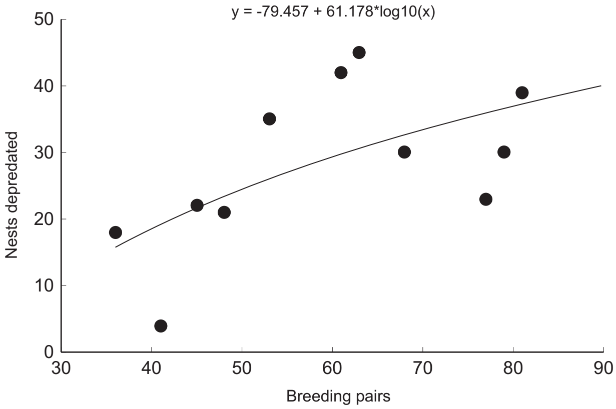

Fig. 7. Relation between breeding density and number of depredated nests.

Cavity quality in years of high and low Collared Flycatcher density

The median entrance diameter of the Collared Flycatcher breeding cavities in years of that species low density (1992) was not wider compared to the median diameter in very high density year (1993) (Mann-Whitney U-test, Z = -1.69, ns, n = 33). The

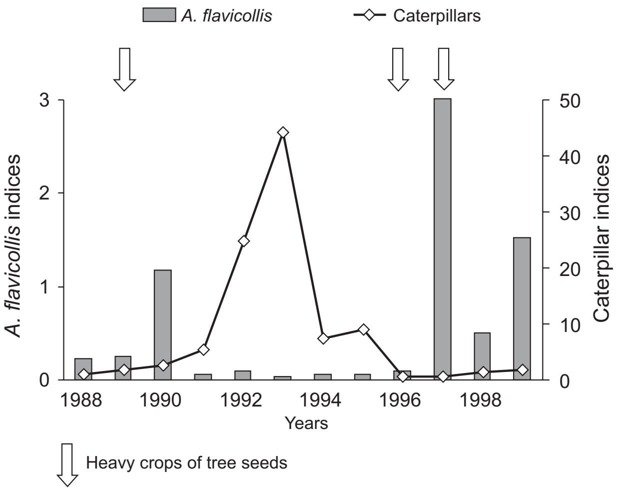

Fig. 8. Yellow-necked Mouse population dynamics in relation to leaf-eating caterpillars in BNP.

median cavity depth, i.e. the distance between the outer rim of the cavity entrance and the centre of the nest bottom, was not different between those two type of seasons, either (Mann-Whitney U-test, Z = -1.140, ns, n = 33). This means that under conditions of high Collared Flycatcher density, birds bred in as safe cavities as in years of low density. So, during high densities the Collared Flycatchers were not forced to breed in worse (less safe) cavities.

Caterpillar abundance in relation to the Yellow-necked Mouse densities

The highest densities of the caterpillars occurred in years when the Yellow-necked Mouse reached the lowest densities (Fig. 8). The outbreak years of the Yellow-necked Mouse (1990, 1997, 1999) occurred after heavy crop of tree seeds (Pucek et al. 1993, Jędrzejewska & Jędrzejewski 1998, Hansson et al. 2000, Z. Pucek unpubl. data).

DISCUSSION

The breeding losses caused by predators in BNP are much higher than in other European populations of *Ficedula* spp. (Lundberg et al. 1981, Gustafsson 1985). The related Pied Flycatcher suffers similar nest predation in the Białowieża as the Collared Flycatcher population under study (Czeszczewik et al. 1999, Czeszczewik 2001).

Main predators on the Collared Flycatcher broods

The Collared Flycatcher breeding losses are caused mostly by nest predators like the Yellow-necked Mouse, the Great Spotted Woodpecker and the Pine Marten (Walankiewicz 2002). Among them, the Yellow-necked Mouse shows the strongest fluctuations in number (Pucek et al. 1993, Jędrzejewska & Jędrzejewski 1998, Z. Pucek unpub. data, Table 1 and 2, Fig. 8). Thus, this rodent probably affects the most the Collared Flycatcher fluctuations in breeding productivity. In years of the Yellow-necked Mouse high density, this rodent destroys many nests of the Collared Flycatcher. High breeding losses lower the production of nestlings and, as a result, in the next year fewer females arrive and the species breeds at lower densities. The rodents are not the only nest robbers however, and, during 12 years of observation, they had only three years of very high densities (1990, 1997 and 1999, Fig. 8). Additionally, the rodent year 1999 was the last year of my observations. So, its impact on breeding density in the following year could not be measured since there are no data on the 2000 Collared Flycatcher density.

Other important Collared Flycatcher brood robbers, i.e. the Pine Marten and the Great Spotted Woodpecker, showed less pronounced fluctuation in numbers (only twofold, Table 2), so their impact on the Collared Flycatcher nest destruction seems to be more constant. Although in a 1991 year of very low rodent density, 50% of the Collared Flycatcher nests were depredated.

Density independent predation

One could speculate that in a year of high density the Collared Flycatcher may use cavities of lower quality (less safe), which would lead to higher breeding losses. Nests at high density would also attract more predators. Two strong facts from this study exclude the occurrence of such a situation in BNP. Firstly, the breeding losses are not heavier during high Collared Flycatcher density years (Table 1, Fig. 7). Thus, predators do not intensify their search for nests when flycatchers are common. Secondly, the quality (i.e. safety expressed as the width of a cavity entrance) of nest sites in high Collared Flycatcher density year (in 1993) was the same as in a year of low density (in 1991)(see Results).

Nest predation on the Collared Flycatcher broods has appeared density independent. It is obvious when the Collared Flycatcher broods are destroyed by three very different groups of predators, i.e. rodents, woodpeckers and the Pine Marten (Walankiewicz 2002). None of them fully relies on the Collared Flycatcher eggs or nestlings. They either switch among different kinds of animal food (Pine Marten), or forage mostly on insects (Great Spotted Woodpecker in May and June) or have a primarily vegetarian diet (rodents and Great Spotted Woodpecker in winter and early spring).

Summing up, the fluctuations and limitation of the Collared Flycatcher numbers in BNP appears to be associated with: 1) the presence of generalist predators able to switch rapidly between various prey groups when the abundance of particular prey species change; 2) mustelids and rodents able to climb up to tree tops (Borowski 1963); 3) a high number of the two small forest rodent species (Yellow-necked Mouse and Bank Vole *Clethrionomys glareolus*) which are the main prey for the mustelids (Pine Marten); 4) woodpecker skills which could get into cavities with a wider entrance or enlarge openings of other cavities. Woodpeckers may play an important role as a factor causing Collared Flycatcher breeding losses. For instance, in 1990 in one plot within BNP, five out of nine unsuccessful Collared Flycatcher nests were destroyed by woodpeckers (Walankiewicz 1991). In 1997–1998 within plot W and CM woodpeckers predated 20% of the Collared Flycatcher nests (n = 112) (Walankiewicz 2002). It seems that the only true nest robber among woodpeckers is the Great Spotted Woodpecker.

Causes of population fluctuations

In his review of literature, Newton (1998 p. 221) classifies effects of predation on bird populations into the following categories: no effects on breeding numbers of prey, reducing the breeding numbers, oscillations/fluctuations in the bird numbers, annihilation of the prey species.

Collared Flycatcher population in Białowieża falls into the third category, i.e. nest predation caused oscillations in breeding numbers. This predation pressure is exerted mainly by two mammalian groups (rodents and mustelids) and one avian group — woodpeckers (Walankiewicz 2002). All three groups rely on different types of food throughout most of the year. Nests contents (eggs, nestlings) are important to them for a relatively short period — usually no more than six weeks. Interestingly, in Białowieża 50% of all birds identified from the Pine Marten scats were the cavity-nesters (Jędrzejewska & Jędrzejewski 1998).

Furthermore, rodents, when they are very numerous, also destroy substantial proportion of bird broods. In such years the Yellow-necked Mouse density could exceed 70 individuals per ha (2500 individuals within 36 ha study plot!) (Jędrzejewska & Jędrzejewski 1998). At the same time on average only 1–2 pairs of the Collared Flycatcher might breed within 1ha (Walankiewicz et al. 1997a). Clearly, in such a situation the probability that a Collared Flycatcher nest may be found by a Yellow-necked Mouse is very high. In a year of high rodent density the Weasel *Mustela nivalis* also may destroy some of the Collared Flycatcher broods, since it climbs trees up to a few meters above the ground in search of prey. But this carnivore, relying mostly on rodents, only occasionally destroys nests (Jędrzejewska & Jędrzejewski 1998).

During following year, when rodents are scarce, and the Weasel almost disappears, a new effective predator, the Pine Marten, increases in number and may destroys flycatcher broods. This species has one-year-lag in reproduction after high rodent density (Zalewski et al. 1995).

The hypothetical mechanism of oscillations in the Collared Flycatcher density is different compared to that described by Newton (1998) for the northern game birds. There are two clear differences visible regarding the relation between the predator and prey.

Firstly, heavy breeding losses of the Collared Flycatchers begin in a year of high rodent density. Mammalian carnivores (mostly the Pine Marten) destroy the Collared Flycatcher nests during the next year. The Pine Marten density is predominantly influenced by the change in forest rodent abundance to which martens respond with a 1-year lag (Zalewski et al. 1995, Jędrzejewska & Jędrzejewski 1998).

Secondly, eggs and nestling of the Collared Flycatcher eaten by predators are not a part of a population surplus (Errington 1946, Newton 1998) but potential next-year breeders. Like Errington (1946) also Newton (1998) doubts the influence of predation in shaping bird population fluctuations (i.e. "predators simply remove a variable doomed surplus formed of birds that are destined to fail in their breeding or die for some other reasons"). He agrees with Watson & Moss (1979) that the role of predators in the cyclic fluctuations of some grouse is not wholly proven, and predation cannot be an explanation that applies even to all grouse populations. Yet, also the Collared Flycatcher annual nest losses (Fig. 1) strongly resemble the range of nest losses variation of three species of northern ground nesting gallinaceous birds (Storaas et al. 1982, Angelstam 1983, Myrberget 1984, Newton 1998).

The decline of the several passerine birds was recorded in Scandinavian studies in the situation when generalistic predators switched into robbing bird broods when their usual prey (rodents) had became scarce (Järvinen 1985, 1990). This case was not considered by Newton (1994a, 1998).

For forest predators the Collared Flycatcher nest contents constitute the easiest and nutritious food source. During springtime it can create a time of plenty for predators. For instance, nearly 40% of biomass consumed in BNP by Pine Martens in June were birds (Jędrzejewski et al. 1993, Zalewski et al. 1995), and Pine Martens were shown to switch to eating birds. As a result of such a predator's feast, in the next year Collared Flycatchers, became much less numerous in the BNP (Table 1, Fig. 1), exactly like some small bird species in Scandinavia (Järvinen 1990).

Furthermore, a closely related species sharing the same nest predators — the Pied Flycatcher — in BNP fluctuates in a parallel way without any signs of compensation (Walankiewicz et al. 1997b).

Other factors (food, nest-sites)

Another question is: whether in good years the Collared Flycatcher approaches the level of the habitat carrying capacity either in nest sites or food resources? Under the Białowieża conditions food for insectivorous birds seems to be in surplus in the breeding season (Tomiałojć et al. 1984, Rowiński 2001, P. Rowiński pers. com.). There are no signs which would indicate that the average number of the fledged Collared Flycatchers per nest (only successful nests included) is substantially lower in the species high density year (6.0 fledged birds per nest in the low density 1992 year; 5.5 fledged birds per nest in the high density 1993 year, no statistically significant differences (Mitrus 1998, C. Mitrus unpubl. data). Despite more than seventy fold differences in the caterpillar densities in years 1992–1997 (Fig. 8) there were no significant differences in number of birds produced per successful nest (R = 0.089, ns, for young males; R = 0.400, ns for old males). In the same period time partial losses and clutch size of the Collared Flycatcher broods were not affected by the caterpillar abundance as well (after Mitrus 1998 and unpubl. data) According to new data (Rowiński & Wesołowski 1999, Wesołowski et al. 2002), in years of low Winter Moth densities, other abundant caterpillars of *Ptilophora plumigera* are available for birds in BNP. During 1996–1999 these caterpillars caused partial defoliation of maples (Wesołowski at al. 2002). So, in a breeding season food for insectivores birds breeding in BNP seems not to be a limiting factor.

Another limiting factor for secondary cavity nesters according to many researchers is the limited number of tree cavities. But, for BNP it has been shown with no doubt that nest sites (cavities) at least in oak-hornbeam stands are in surplus and every pair of the Collared Flycatcher has at least two good quality cavities at its disposal (Walankiewicz 1991, Mitrus et al. 1996). Shortage of nest sites may be experienced only in suboptimal (young, coniferous) or in simplified antropogenic habitats.

An apparent mechanism of cyclic fluctuations in the Collared Flycatcher numbers

The high nestling production in Collared Flycatcher population leads to: 1) higher breeding density during the following year; 2) high numbers of breeding old males (presumably enhancing the higher site fidelity).

This means that, after a year of high productivity more males (which always occur in excess in all study years, Table 1) have a chance to mate with females, which is reflected in higher breeding numbers and the lower rate of non-breeding males. Among the Collared Flycatcher older breeding males arrive four days earlier than one-year-old males (Mitrus et al. 1996). They also mate four days earlier (Mitrus 1998). Thus, for the Collared Flycatcher the number of males is not as critical as the number of available females. In all study years non-breeding (unmated) males singing within plot W constituted 22%–48% of all settled males. When after a year of high breeding success more females, presumably one-year old, arrive next spring, all of them have a chance to find mates. As a result the density of breeding pairs increases. This is why a high rate of production correlates with the next-year's high breeding density. Other facts supporting this explanation are: higher number of old males breeding within the plot area after high success year (Table 1, Fig. 3) and a lower rate of non-breeding males in years of high densities (Table 1, Fig. 5).

An apparent mechanism the Collared Flycatcher cyclic fluctuations is trigged indirectly by a heavy crop of oak and hornbeam seeds. In the winter following a heavy mast production of oak and hornbeam, two species of forest rodents (Bank Vole and Yellow-necked Mouse) can reproduce continuously for 1.5 year to reach very high numbers of 200–300 ind./1ha (Jędrzejewska & Jędrzejewski 1998, Hansson et al. 2000). Usually, a year of high rodent density is the first year of high Collared Flycatcher breeding losses caused presumably by the Yellow-necked Mouse (Walankiewicz 2002). A year later (the year of rodent crash) the Pine Marten increases its number, as this carnivore has a one-year lag in reproduction (Zalewski et al. 1995). Such a year is the second year of high breeding losses. In the third year, during low densities of both, rodents and martens, the Collared Flycatcher may have very high breeding success subsequently reflected in the following year by an increase in its breeding numbers.

Results of present study show not only that the Collared Flycatcher breeding numbers clearly depend on the level of nesting losses caused by nest plunderers in a previous year, but they also document a link between forest rodent cycles and the Collared Flycatcher fluctuations. In the BNP forests, unlike most studies carried out in the northern areas of Europe and America (Newton 1998), the highest breeding losses of the Collared Flycatcher can occur in two subsequent years (i.e. 1997, 1998) for two different reasons. The first is high rodent density year while the second one is when the Pine Marten has its highest density while rodents are scarce. Consequently, the mustelids switching to birds, destroys high proportion of broods (Jędrzejewska & Jędrzejewski 1998). This probably happened in 1991, when the Pine Marten, which is responsible for roughly one fourth of the Collared Flycatcher breeding losses (Walankiewicz 2002), occurred at high density and turned to robbing bird broods in May and June (Table 1 and 2). These months are usually a time of plenty for nests plunders. But, because at the end of June most passerine birds including flycatchers and are already fledged, the predators are forced to switch to other kinds of food. This is why the predator-flycatcher relationship cannot be density dependent (see Results). Furthermore, all three groups of predators searching for Collared Flycatcher nests seem to profit from both situations in years of high flycatcher density (2 pairs/ha) and in its low level (1 pairs/ha). The difference in prey abundance is only twofold and a brood of the Collared Flycatcher is worth searching in cavities, chiefly on the shortage of other prey.

The magnitude of the Collared Flycatcher fluctuations

Another question is, why the Collared Flycatcher increases in number so sharply after a year of high breeding success. The increase was particularly conspicuous after the 1992 high breeding success, (89%) when the species density increased the following year twofold: from 41 to 81 pairs. Theoretically, this means that all parents should return to the plot plus two yearlings produced per every pair as well. According to our knowledge, such a high returning rate of young and adult birds is very unlikely. There is another explanation, however. After a high breeding success, year old birds usually show higher fidelity, which is a well, known tendency of many birds (Pinkowski 1979, Herlugson 1981, Drilling & Thompson 1988). The Collared Flycatcher have a high natal fidelity even during their first return to breeding grounds (Pärt 1991), but when a clutch is destroyed the Collared Flycatcher females, and to a slightly lesser extent males, regularly abandon their territory (Löhrl 1951). The fact is that ca. 50 male yearlings (Table 1) and probably many young females as well settled within the plot in that particular year. So, probably all together these birds in 1993 alone formed a density of more than 20 pairs/10 ha in 1993 (Table 1).

The association between high nesting success and high densities of the Collared Flycatcher could result from more than one mechanism:

— site-fidelity of young and adults birds to the natal first breeding area (Pärt 1991);

— a greater tendency of adults to return to the same sites after successful breeding than after a failure (Bellrose et al. 1964, Pinkowski 1979);

— a greater immigration rate after a year with high quantity nestlings (public information hypothesis, Doligez et al. 2002, Withgott 2002);

— attraction of new breeders. In the closely related species the Pied Flycatcher singing males attract other new breeders (Alatalo et al. 1982).

EARLIER HYPOTHESES CONCERNING THE BIRD POPULATION LIMITATION

After a half a century of studies on the *Ficedula* flycatchers (von Haartman 1957, Lundberg & Alatalo 1992), one of the potentially important limiting factor, i.e. nest predation, remains still underestimated or completely ignored while other limiting factors as the nest sites, competition or food resources are still regarded as more important (Newton 1994b).

Food

In accordance to this ideology, also Jędrzejewska & Jędrzejewski (1998) suggested, based on only five years of our survey on of the Collared Flycatcher breeding performance in BNP that, the food (Geometridae caterpillar abundance) positively influences breeding success. They analysed food abundance, rodent density and predation rate using the multiple regression analysis. Of these three factors, according to them, a positive influence of food resources, i.e. abundance of caterpillars, was the most important (semi-partial correlation squared, $SR^2 = 74\%$). My twelve-year data on the Collared Flycatcher breeding performance show however that the abundance of caterpillars has not influenced the breeding success of the Collared Flycatcher ($R = 0.171$, ns, $n = 13$). The explanation suggested by Jędrzejewska & Jędrzejewski (1998) is based on Martin's (1992) assumption that: 1) high density of insects allows the parents to have more time for guarding their nests and this way they may suffer lower nest losses, 2) during outbreaks of insects, predators on eggs and nestlings might shift to feeding on caterpillars as well. The first assumption is, however unfounded in Białowieża Forest the main Collared Flycatcher predators (Great Spotted Woodpecker, Pine Marten, Yellow-necked Mouse) are too strong to be chased off by this tiny bird. Additionally, two of them are nocturnal. So, this mechanism cannot work in the case of the Białowieża Collared Flycatchers. Moreover, calculations made by Jędrzejewska & Jędrzejewski (1998) were based on five-year data set obtained when the caterpillar outbreaks only coincidentally co-occurred with a low rodent density (Fig. 2). In spring 2002 the Winter Moth and the Yellow-necked Mouse in BNP had their outbreaks at the same time (T. Wesołowski, P. Rowiński and own unpubl. data) and in spite of this the Collared Flycatcher still suffered heavy nest losses (> 70%). Furthermore, the number of all foliage insectivores in BNP continued to increase in 1995–1999, despite very low numbers of the Winter Moth caterpillars (Wesołowski et al. 2002).

Nest sites and competition

The Collared Flycatcher has been a model species of European ornithology since the 1950s (von Haartman 1957, Lack 1966). For decades, the nest sites and competition for them have been regarded as the main limiting factor (von Haartman 1971, Slagsvold 1975, Alatalo et al. 1985). Also Newton (1998) considers the number of nest sites and competition with the stronger competitors (Paridae) to be the main limiting factors for *Ficedula* flycatchers. He admits that without nest-box provision large numbers of potential bird occupants (notably the Pied Flycatcher) would not presumably breed in Western-European forests (Newton 1998, p. 203). But, his point of view is based on nest-box studies where provision of new nest sites almost always led to an increase (often abrupt) following the year when boxes were installed. However, all of those experiments implicitly assume that: Nest-boxes do not affect between-year movements of breeding birds into or out of the study area, but this assumption is too idealistic (Czeszczewik et al. 1999). Nest-box plots are not isolated from surrounding areas so birds could move in and out freely. As a result, for example in our study plot situated in the managed Białowieża Forest, nest-boxes were populated in 1993-1997 by the almost stable Pied Flycatcher population despite the fact that 55%–75% broods were always destroyed and fledgling production was the lowest ever recorded for the species i.e. 1.74 ± 0.47 (Czeszczewik et al. 1999). This means that the nest-boxes year by year attracted new immigrant Pied Flycatchers, which makes this population of the "sink" type. Furthermore, in most studies, breeding density more than doubled, sometimes increased more than 20 times, after boxes had been provided (Swanson & Ryder 1979). Definitely, such safe nest sites produced many more fledglings than natural cavities and their own production populated the surrounding areas. The fact of high productivity of nest-boxes compared to natural cavities have for many years been well known (e.g. Nilsson 1975). So it is not understandable why it is still presented uncritically. The results based on nest-box experiments conducted in the forests of Western Europe should be treated with great caution. Even more, I suggest that many experiments with nest-box provision could lead to erroneous generalisations by exposing phenomena which rarely or never happen under natural conditions. As such biased conclusion serve the competition for nest sites between various cavity nesters, killings between cavity competitors, etc. (Walankiewicz 1991, Walankiewicz & Mitrus 1997, Czeszczewik & Walankiewicz 1999, Czeszczewik et al. 1999).

Newton (1998, p. 26) states "there is no reason to suspect that such nest-box studies mislead us on the general principles and mechanisms behind population limitation in birds". I believe it is a wrong conclusion. For example, there are very few studies on predation in nest-boxes in Western Europe. Researchers sometimes even admit that data from the years of heavy losses caused by predators were purposely not included in their analyses, thus, arbitrarily assumed unimportant (Winkel 1989). But we should keep in mind that nest-boxes are designed for the nesters (birds) safety (Frantzen & Winkel 1987).

So, this is why among such well-studied birds as the Pied and Collared Flycatchers or the Nuthatch, the impact of predation has not been well/sufficiently studied yet. There are only Nilsson's papers (1975, 1984) and the Białowieża data (Walankiewicz 1991, Wesołowski & Stawarczyk 1991, Walankiewicz et al. 1997a, Czeszczewik et al. 1999, Wesołowski 2002).

Recent generalisations on the role of predation are highly influenced by Newton's (1993, 1994a, 1998) opinion, summarised as follows: "predation seems to play a minor role in the direct limitation of breeding numbers" and "to reduce breeding or post breeding numbers the predation must be additive to other losses".

In her old review based on numerous studies of secondary cavity nesting species, Nice (1957) reported only four cases of fledgling success below 50%; the average breeding success was 66%. A relatively high breeding success among cavity nesters was once commonly accepted fact (e.g. Nice 1957, von Haartman 1971). Studies from Europe and North America have revealed a 70–90% success of birds breeding in nest-boxes (Bellrose et al. 1964, Bolen 1967, Bulmer & Perrins 1973, Dunn 1977, Nilsson 1984, 1986, Brawn 1987, Finch 1989). Today we know that such results reflect artificial situations. The nest-boxes can appear to be the "superleasers" (Hinde 1959) that allow birds to escape from predation pressure and unfavourable weather conditions. After heavy rains in Białowieża in 1988, for example, 16% (10 of 64) of the cavities were very wet or full of water (Walankiewicz 1991). Furthermore, East & Perrins (1988) recorded high breeding losses of Paridae caused by heavy rains. No such catastrophes have been reported for nest-box nests.

Thus, it is clear that most data on cavity nesters (Paridae and *Ficedula* spp.) breeding success came from nest-box studies and from parts of the world where woods are deeply transformed, and as such they could not properly reflect the importance of nest predation pressure as a limiting factor.

Cities and nest-box plots as safe islands

In view of the results obtained on the Collared Flycatcher breeding under natural conditions and situation of many birds breeding in cities, one more important category of the predation effects on bird populations by Newton (1998 p. 221) should be added: This is the creation of safe from nest predation areas, either in cities, or in nest-box plots. This effect of predation leads to an increase of bird densities in both urban and nest-box bird populations to an abnormal level. In this case predation influences bird populations not only directly through nest success, but it would influence their breeding density by attraction of birds to safe nest sites. Tomiałojć (1980, 1999) has proved beyond any doubt that the Woodpigeon production per unit area is 175 times higher in cities than in the adjacent rural areas (nest densities 450 times greater than in forests). These differences result from different predation pressure and not from varying food conditions. Humans have created a sort of "protective umbrella" above the urban Woodpigeons, which inevitably leads to extremely high densities (226 pairs/10ha). A similar situation occurs in nest-box plots, well known as areas of extremely high densities (e.g. Swanson & Ryder 1979), which usually play a role of "safe islands".

Do vertebrate predators limit the population size of forest birds?

Very suggestive argument for predation limiting the numbers of birds comes from pristine forest of BNP (Tomiałojć at al. 1984, Wesołowski & Tomiałołojć 1997, Jędrzejewska & Jędrzejewski 1998). Most of 44 analyzed forest species in BNP showed visible lower breeding densities during two consecutive years, the outbreak and the crush of forest rodents (1978–1979, 1984–1985, 1991–1992). The magnitude of decline was the highest among ground nesters. In view of that predation seems to play a role in the direct limitation of breeding numbers reducing in some years breeding numbers of the Białowieża forest birds as it was proven in case of the Collared Flycatcher.

Although later Jędrzejewska & Jędrzejewski (1998) doubt in important influence of the predation stressing other factors (snow cover, interspecific competition and caterpillar abundance) as more important. Fact is, all their considerations are only correlative, i.e. with no full data on breeding success, homing rate etc. So, such conclusions should be treated with great caution.

Why the views of earlier researches do differ from the Collared Flycatchers results?

Although in his review Newton (1998 p. 26) admits, similar to Tomiałojć et al. (1984), that in some areas where studies were carried out, the predators could be scarcer than in natural habitats, yet he doubts that it is the common case in human-modified landscapes of Europe and Central and Northern America. Destruction of large predators is thought to have allow smaller ones to increase in number and exert a stronger pressure on prey population.

It seems that Newton's conclusions are unbalanced to some extent regarding the natural history of areas (Western Europe, Eastern North America) where most of the fieldwork on bird limiting factors was collected. For example, only 1.8% of the total mammal biomass in Great Britain is contributed by the wild species (Yalden 1999). This makes it clear how totally domestic mammals and humans dominate the British countryside and its ecosystems.

CONCLUSIONS

Under conditions of primeval forests (BPN) nest predation reduces the breeding success of the Collared Flycatcher population, leading to its lowered breeding density in the following year. This predation pressure in some years keeps the Collared Flycatcher density at a level well below that of the potential the habitat resources (nest-sites, food) would permit.

This study has shown that:

1) the Collared Flycatcher breeding losses may vary within the frames much wider (11% to 70%) than once recorded;

2) the main reason of nest failure under primeval forest conditions is nest predation (82%–100%);

3) rate of nest destruction is related to the density of the Yellow-necked Mouse recorded in BNP, while independent on the Collared Flycatcher density (nest predation pressure is density independent, i.e. limiting but not regulating);

4) the Collared Flycatcher breeding density positively depended on the number of fledged birds in the previous year while the number of fledglings produced negatively depends on the rate of destroyed broods;

5) high number of non-breeding Collared Flycatcher males was found (22%–48%) in all years of the study;

6) the Collared Flycatcher fluctuations in 36 ha study plot were parallel with the breeding numbers in other plots (54 ha) selected in oak-lime-hornbeam stands and scattered over the Białowieża National Park;

7) recent views on the role of predation in limitation of the bird numbers are influenced much by the fact that most of field studies on bird dynamics were carried out in deeply transformed areas of Western Europe or Eastern North America.

ACKNOWLEDGMENTS

I thank all the persons who helped me with field work, especially D. Czeszczewik, C. Mitrus, M. Stańska, A. Szymura, P. M. Jabłoński, R. Kuczborski, T. Stański, W. Jastrzębski, S. Michalak. I express my gratitude to D. Czeszczewik, C. Mitrus and P. Hamel for constructive help on previous drafts of the manuscript. The help of D. Czeszczewik with editorial rephrasing of drafts of this paper is gratefully acknowledged. K. Zub and P. Chylarecki provided statistical advice. R. Brasińska and G. A. Ricciardiello proof-read English. This work was supported by the University of Podlasie in Siedlce. The very kind cooperation of the Białowieża National Park administration is acknowledged as well.

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STRESZCZENIE

[Drapieżnictwo gniazdowe ogranicza liczebność lęgową muchołówki białoszyjej (z krytycznym przeglądem wcześniejszych hipotez)].

W latach 1988–1999 badano wpływ drapieżnictwa gniazdowego na zagęszczenie lęgowe muchołówki białoszyjej *Ficedula albicollis* gniazdującej w dziuplach naturalnych w grądzie Białowieskiego Parku Narodowego. Na 36 hektarowej powierzchni porośniętej pierwotnym lasem grądowym intensywnie wyszukiwano od momentu przylotu dziuple zajmowane i bronione przez samce. Dziuple te następnie wielokrotnie kontrolowano z ziemi oraz sprawdzano ich zawartość przy użyciu drabiny lub drzewołazów, w celu stwierdzenia czy są to dziuple lęgowe lub też dziuple samotnych nielęgowych samców. W dziuplach lęgowych sprawdzano wielkość i udatność lęgów oraz opisywano dokładnie przyczyny niepowodzenia lęgów (niezalężone jaja, upadek drzewa, zalewanie wodą, drapieżnictwo). We wszystkich latach badań poza rokiem 1988 udało się znaleźć prawie wszystkie dziuple lęgowe i określić los większości lęgów (Tab. 1). Znana jest też dość dokładnie liczba nielęgowych samców które broniły dziuple na powierzchni (ptaki nie były znakowane indywidualnie i część z nich zmieniała z pewnością miejsce śpiewu). Określano też w większości przypadków wiek samców (jednoroczne lub starsze dalej zwane odpowiednio młode i stare, Tab. 1).

Głównym powodem strat lęgowych (11%–70% zniszczonych lęgów w różnych latach) były drapieżnictwo gniazdowe powodowane przez łasicowate (kuna leśna), dzięcioła dużego i gryzonie. Poziom strat zależał od poziomu zagęszczenia myszy leśnej i nie był zależny od zagęszczeń innych w/w rabusiów lęgów (Fig. 2). Sugeruje to, że fluktuacje liczebności muchołówki białoszyjej w pierwotnym lesie białowieskim są wyraźnie powiązane z cyklami liczebności gryzoni leśnych (myszy leśnej) (Fig. 8).

Liczba par lęgowych zależała od produkcji młodych w roku poprzednim (Fig. 1, 3). Występował stały nadmiar (22%–48 %) samców. Zagęszczenia lęgowe na 36 ha powierzchni fluktuowały zgodnie z łącznym zagęszczeniem na dwóch innych powierzchniach grądowych (24 i 30 ha) w Obszarze Ochrony Ścisłej Białowieskiego Parku Narodowego.

W pracy ponadto szczegółowo przedyskutowano dotychczasowe poglądy na czynniki limitujące liczebność dziuplaków wtórnych. Po ponad 50 latach badań nad muchołówkami z rodzaju *Ficedula,* które są modelowymi obiektami badań europejskich, drapieżnictwo gniazdowe jest ignorowane i nie uwzględniane jako znaczący czynnik ograniczający. Pokarm, ilość dziupli i konkurencję ze strony innych dziuplaków uważa się nadal za znacznie ważniejsze niż drapieżnictwo. Wynika to z faktu, że większość badań dotyczących sikor i muchołówek przeprowadzono na powierzchniach ze skrzynkami lęgowymi, które wpływają na szereg parametrów lęgów i powodują przemieszczenia dużych części badanych populacji ptaków. Przy obecnym stanie wiedzy uogólnienia dotyczące roli drapieżnictwa w kształtowaniu zagęszczeń lęgowych ptaków wymagają dużej ostrożności.