Density Dependence in Reproduction of the Collared Flycatcher (Ficedula albicollis) at High Population Levels

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DENSITY DEPENDENCE IN REPRODUCTION OF THE COLLARED FLYCATCHER (*FICEDULA ALBICOLLIS*) AT HIGH POPULATION LEVELS

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SUMMARY

(1) We analysed density-dependent effects in the breeding phenology of a Central European population of the collared flycatcher (*Ficedula albicollis*) in a 4-year study. Different densities of breeding flycatchers were created experimentally, by providing nest boxes at different densities.

(2) Clutch size, number of hatched eggs and fledged young were density-independent. Flycatchers laid more eggs when the caterpillar supply was high.

(3) Reproductive success (hatching, fledging and breeding success) was density-dependent. Bad weather, especially in early spring, significantly reduced reproductive success.

(4) Flycatchers laying large clutches tended to produce smaller young at high population density.

(5) Great and blue tit density did not influence the reproduction of the collared flycatcher.

INTRODUCTION

The fluctuation in numbers of a bird population may be caused by density-dependent and density-independent factors. Both factors may operate in almost any season. The basic question of population ecology is which factor is essential or how these two related factors determine the population dynamics of a species.

Recently, Alatalo & Lundberg (1984) analysed the density-dependent effects in breeding success of pied flycatchers (*Ficedula hypoleuca* Pall.) using an experimental approach. Manipulation of breeding density of hole-nesters by provision of nest-boxes is possible, especially in flycatchers since they prefer artificial boxes to natural nest cavities (Lundberg *et al.* 1981). Alatalo & Lundberg created a high (two pairs per ha) and a low (less than one pair per ha) density population. They found that neither clutch size, nor hatching success was density-dependent but fledgling number, nestling weight and tarsus length were slightly affected in a density-dependent way.

We performed an experiment to find out whether breeding phenological traits are intraspecifically density-dependent in the collared flycatcher (*F. albicollis* Temm.), a close relative of the pied flycatcher. In addition, we analysed the effect of bad weather and food availability on flycatcher reproduction. Gustafsson's (1985, 1987) and Slagsvold's (1975, 1978) studies have indicated that interspecific relationships are also important in population regulation in flycatchers. We also discuss the effects of other hole-nesting species.

METHODS

The study was carried out in an oak forest 25 km north of Budapest. The dominant tree species was *Quercus petraea*. We set up two plots, both with 100 nest-boxes, in autumn 1981. The nest-boxes were placed in a grid system about 25 m apart. The box entrance was 32 mm in diameter and the bottom area was 110 cm^2. In 1982 an extra 100 boxes were added in one of the two study plots (A). Each new box was placed between two old boxes so that the area of the plot remained 9 ha but the box density was doubled and the distance between the boxes was reduced to about 12–15 m. We considered this plot (A) as the experimental plot and the other one (B) as the control plot. The vegetation structure and the age of the oak trees were the same in both plots as they were parts of a continuous forest.

The boxes were inspected regularly (every second or third day) and the date of the first egg, clutch size and the number of hatched and fledged young were recorded during the breeding seasons from 1982 to 1985. We measured the weight with a Pesola spring balance (to the nearest 0·1 g) and the tarsus length (to the nearest 0·1 mm) of the nestlings on day 13 in the last 2 years. The adult females ($n = 199$) were captured during the second half of the incubation period within a 5-day period. The size of females (measured by weight, bill length, tarsus length and wing length) did not differ significantly either between plots or between years (J. Török & L. Tóth, unpublished data).

To measure reproductive output of the collared flycatcher, we recorded the mean number of eggs, hatched young and fledged young as well as hatching, fledging and breeding successes. Hatching success is the number of eggs hatched divided by the number of eggs laid. Fledging success is the number of fledglings divided by the number of young hatched. Breeding success is the number of fledglings divided by the number of eggs laid.

Food samples were collected with the neck-collar method (Kluijver 1933; Török 1981) from nestlings aged 5–10 days. The caterpillar supply was estimated from the production of frass, using ten collectors (surface of each collector was 0·25 m^2) between 1983 and 1985.

The collared flycatcher usually has only one brood in a breeding season in early May, but lays repeat clutches in late May if the first one is destroyed by heavy rainfall or predators. In this paper we analysed only the data of the first clutches. Repeat clutches were registered 84 times out of the 514 clutches. We did not observe any breeding attempts in natural cavities within our study areas, probably because in the year prior to our experiment the dead trees were removed by the foresters.

Alatalo & Lundberg (1984) have pointed out that parental age and polygamy can confound the effect of density on breeding attempts. We found no significant differences between first-year ($n = 18$) and older birds ($n = 83$), either in breeding traits (except egg-laying date) or in morphological parameters. We think that even if our population differed in age structure this would not modify significantly the effect of density. Polygamy occurs in both the pied flycatcher (Haartman 1951) and the collared flycatcher (Löhrl 1951). Unfortunately, we do not have any data on polygyny frequency because most of the males could not be captured.

RESULTS

Effect of density on reproduction

Breeding densities of the collared flycatcher varied in different plots and years. The highest density was 9·3 nests ha^{-1} and the lowest 2·1 nests ha^{-1} (Table 1). Some other hole-nesting species, mainly blue tits (*Parus caeruleus*) and great tits (*P. major*), also bred in our plots and their density was between 0·8 and 1·8 nests ha^{-1}. The lowest tit density was found in 1982 at the start of the study and that was the year when the density of flycatchers was similarly low. Usually great tit density exceeded blue tit density, except in 1984 when the density of the two species was similar. We found no significant correlation between the breeding density of the tits and the reproductive output of the collared flycatcher (Table 2).

Mean clutch size was larger in the different plots and years when breeding started earlier ($r = -0{\cdot}757$, $P < 0{\cdot}02$, $n = 8$). Neither clutch size, nor the number of hatched eggs and fledged young was affected by the breeding density of the collared flycatcher and the tits. The hatching success was negatively affected by both the density of the collared flycatcher and the combined density of the flycatchers and tits. Both fledging success and breeding success depended only on the density of flycatchers. (Table 2).

Density effect on quality of the young

To test the effect of density on brood size we analysed three size categories. Small broods contained three or four, medium broods five or six and large broods seven or eight young. The weight of nestlings did not differ between low and high densities in any of the

TABLE 1. Reproductive data of collared flycatchers at different breeding densities and amount of precipitation. The average amount of precipitation was calculated from 47 days for the whole season (WS), from 18 days for the period before hatching (BH) and from 13 days for the period after hatching (AH). The number of nests are in parentheses. All the calculations were made by the sample sizes indicated under clutch size data except fledging success

Breeding density (nest ha^{-1})	Year, plot	Median laying date (in May)	Clutch size	Hatched eggs	Fledged young	Hatching success	Fledging success	Breeding success	Precipitation (mm day^{-1})		
									BH	AH	WS
2·1	1982, A	10	5·8 (19)	5·0	4·8	0·85	0·98 (18)	0·83	0·5	2·0	1·0
3·1	1982, B	13	5·5 (28)	4·9	3·9	0·87	0·80 (26)	0·70	1·4	0·0	1·0
5·3	1985, B	02	6·0 (24)	4·1	3·2	0·69	0·79 (19)	0·53	3·9	2·5	2·7
5·9	1984, B	05	6·5 (53)	4·9	3·9	0·74	0·77 (45)	0·57	7·8	5·1	3·9
5·9	1983, B	01	6·3 (53)	5·3	4·8	0·81	0·91 (47)	0·74	2·1	1·4	1·3
6·8	1983, A*	01	6·4 (61)	5·1	4·3	0·80	0·84 (52)	0·68	2·1	1·4	1·3
8·9	1984, A*	05	6·5 (80)	4·2	2·6	0·64	0·62 (62)	0·41	7·8	5·1	3·9
9·3	1985, A*	08	6·0 (84)	4·1	3·1	0·65	0·78 (66)	0·53	3·9	0·4	2·7

* The density of nest-holes was increased to a level of 22 boxes ha^{-1}.

TABLE 2. Correlations between the breeding density of the three dominant hole-nesting bird species and the reproductive traits of the collared flycatcher ($n = 8$). The data on reproductive success were arcsine transformed

Density	Clutch size	Hatched eggs	Fledged young	Hatching success	Fledging success	Breeding success
Collared flycatcher	0·639	−0·495	−0·645	−0·837***	−0·688*	−0·775**
Great tit	−0·126	0·459	0·503	0·565	0·455	0·544
Blue tit	0·037	−0·226	−0·113	−0·222	0·130	0·005
Two tits combined	−0·060	0·156	0·260	0·229	0·390	0·366
Tits and collared flycatcher combined	0·594	−0·422	−0·530	−0·725*	−0·527	−0·618

* $P < 0·05$, ** $P < 0·02$, *** $P < 0·01$.

TABLE 3. Weight and tarsus length (mean, ±S.D., number of broods) of nestlings at 13 days of age at low (5·6 nests ha^{-1}) and high (9·1 nests ha^{-1}) breeding densities. Data for 1984 and 1985 were combined

	Brood size categories								
	3–4 young			5–6 young			7–8 young		
	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n	$\bar{x}$	S.D.	n
Weight (g)									
Low density	14·3	1·29	11	14·2	0·94	19	14·4	0·67	6
High density	13·7	1·31	21	14·2	0·85	25	14·0	0·79	9
	$t = 1·475$		N.S.	$t = 0·000$		N.S.	$t = 1·016$		N.S.
Tarsus (mm)									
Low density	17·3	0·82	11	17·5	0·49	19	17·7	0·23	6
High density	17·1	0·49	21	17·4	0·53	25	17·4	0·34	9
	$t = 0·776$		N.S.	$t = 0·830$		N.S.	$t = 1·922$		$P < 0·05$*

* We expected smaller nestlings at high density so we used one tailed Student's *t*-test.

three size categories. We found no density effect on tarsus length in small and medium broods, but in large broods tarsus length of the young was shorter at high density (Table 3). This does not prove unambiguously that the condition of nestlings is density-dependent, though tarsus length is a better indication of the condition of the young than weight, which is quite variable even within short periods while tarsus length is dependent on the food supply of nestlings during the first 10 days (Alatalo & Lundberg 1984).

Weather effect

In the spring of 1984 the weather was extremely bad with heavy rainfall, and we found a lot of abandoned nests with wet nest materials, eggs and sometimes with dead nestlings. Since precipitation often causes low temperatures, at least these two weather factors were correlated. Clutch size and number of hatched eggs were independent of the amount of precipitation during the whole season but fledged young and reproductive successes were negatively affected (Table 4). To analyse in detail the effect of rainfall on reproductive traits, we distinguished two periods. The first period started with the average date of the first egg-laying in a plot and ended with the average hatching date of the first nestling (18 days). The second period lasted 13 days from the date of hatching of the first nestling to

TABLE 4. Correlations between the amount of precipitation and the reproductive traits of the collared flycatcher ($n = 8$). The average amount of precipitation was calculated from 47 days for the whole season, from 18 days for the period before hatching and from 13 days for the period after hatching. The data on reproductive success were arcsine transformed

Precipitation	Clutch size	Hatched eggs	Fledged young	Hatching success	Fledging success	Breeding success
Before hatching	0·670*	−0·432	−0·676*	−0·750**	−0·782**	−0·838***
After hatching	0·685*	−0·163	−0·341	−0·476	−0·426	−0·514
Whole season	0·589	−0·584	−0·747*	−0·840***	−0·752**	−0·871***

* $P < 0.05$, ** $P < 0.02$, *** $P < 0.01$.

the time of fledging. Clutch size showed a slight positive correlation with amount of rainfall in both periods (Table 4). The precipitation in the first period affected negatively all three measures of reproductive success and the number of fledged young but later precipitation had no significant effect on them (Table 4).

Effect of food availability

The diet of collared flycatcher nestlings consisted of three main food types: caterpillars, flying insects and spiders (Török 1986). To analyse the effect of food availability on the flycatcher, one has to collect information on at least these three food types in the environment. The most difficult problem is to estimate the number of spiders, because flycatchers eat a large variety of spider species (Török 1986) which live at different microhabitats from the ground to the high canopy of the foliage. There is no appropriate method to measure the spider supply exactly. Lundberg *et al.* (1981) assessed the relative abundance of flying insects. The number of these insects increased continuously from mid-May to the end of June. The huge number of flying prey in June suggests that the second half of the breeding period (roughly the parental care period) is more rewarding for flycatchers. We measured only the supply of the third food type, the caterpillars, based on the frass production between 1983 and 1985. The highest frass production was in 1984 (0·42 g/0·25 m^2) and the lowest value was in 1985 (0·19 g/0·25 m^2). In 1984, when the caterpillar supply was high flycatchers fed their young mainly on this prey type. The weights of fledged young, however, were lower in this year than in 1985 ($t = 3.72$, $P < 0.0005$; based on sixty-six and twenty-five broods in 1984 and 1985, respectively). The rainy spring in 1984 presumably limited the availability of both caterpillars and flying insects. The bad foraging conditions might have caused lighter young in this year. Although the caterpillar supply was smaller in 1985 than in the previous year, foraging conditions were better so flycatcher young were heavier than in 1984. The frass production showed a strong positive correlation with the average clutch size of the flycatchers (Spearman's $r_s = 0.995$, $P < 0.01$, $n = 6$), but other reproductive parameters (hatched eggs, fledged young, hatching success, fledging success, breeding success) were independent of the caterpillar availability.

DISCUSSION

The collared flycatcher is a common hole-nesting passerine species throughout Central and South-Eastern Europe, but it is absent from the northern and western parts of the continent except some Baltic islands (Alerstam *et al.* 1978). In the northern and western parts of Europe the pied flycatcher replaces the collared flycatcher in the hole-nesting bird assemblage. The collared flycatcher is closely similar to the pied flycatcher in all aspects of its breeding and feeding ecology (Löhrl 1957; Lack 1966; Alerstam *et al.* 1978). However, there are two marked differences in reproduction between Central and North European flycatcher populations. First, in the northern regions the intensity of interspecific density dependence is more important in shaping the population dynamics of flycatchers (Slagsvold 1975, 1978; Gustafsson 1985, 1987). Resident hole-nesters such as the great and the blue tit reduce the reproductive success of flycatchers in higher latitudes while in Central Europe tits do not significantly affect the reproductive output of flycatchers (Sasvári, Török & Tóth, 1987; this study). Secondly, intraspecific density dependence may exist in relatively sparse populations (0·5–1·8 pair ha^{-1}, Alatalo & Lundberg 1984) in northern regions. It seems that in Central Europe intraspecific density dependence operates only at high population levels (2·1–9·3 pair ha^{-1}, this study) but not at low levels (0·2–1·2 pair ha^{-1}, Sasvári, Török & Tóth 1987). We can provide two possible explanations for the differences in the effect of tit density on breeding success between Hungarian and northern populations of flycatchers. First, the density of flycatchers was so high in our study area that intraspecific effects could mask the interspecific effects. The density of northern populations was much lower so the effect of tits might have been more important. Second, in the northern regions the breeding season is shorter owing to the high latitude, so the overlap in breeding between tits and flycatchers was larger than in our plots. This may lead to stronger interspecific conflicts between tits and flycatchers.

Caterpillars are an essential food for both tits and flycatchers (Löhrl 1957; Dornbusch 1981; Török 1986), but our data showed that the caterpillar availability did not affect the reproductive traits of the collared flycatcher except the clutch size. When flycatchers arrive at their breeding sites they assess the caterpillar supply. The rich food supply allows females to spend more energy on forming eggs and they lay larger clutches. At that time flycatchers cannot predict the final breeding density (Alatalo, Lundberg & Ulfstrand 1985) so clutch size is uneffected by the final breeding density as we found. Only one paper, based on experimental data, gives evidence of the effect of density upon the clutch size of the pied flycatcher (Virolainen 1984). On the other hand, there are at least six studies which argue that density does not affect clutch size (Tompa 1967; Campbell 1968; Slagsvold 1975; Alatalo & Lundberg 1984; Harvey, Greenwood & Campbell 1984; Sasvári, Török & Tóth 1987).

Our study area was in an immature forest, where the number of natural nest cavities must be limiting. When we erected a large number of artificial nest-boxes the breeding density of hole-nesters increased quickly in the subsequent years. There was a difference between species. The number of tits did not rise over 1–1·8 pairs ha^{-1} because of their territoriality, while the density of flycatchers could increase to 8–10 pairs ha^{-1}, since they do not maintain a 'tit-like' territory but only a small area around the nest (Haartman 1956). In this dense population food became scarce for flycatchers, and the density-dependent limitation is reflected in the reproductive success of the flycatchers. Moreover, bad weather (high precipitation) may also reduce food availability. Precipitation acts either directly—by breaking down the insulation of nestlings and adults or reducing the foraging capacity of parents, resulting in higher reproductive losses—or indirectly, by reducing the availability of both the caterpillars and flying insects, which may also lead to lower reproductive success. We showed that the high precipitation before hatching affected both hatching success and fledging success but precipitation during the nestling period was ineffective on both types of reproductive successes. These two types of reproductive successes depend on the number of breeding flycatchers as well. So bad weather together with high density may reduce the food supply substantially. Diffuse competitors can also contribute to this effect so we can assume a high intraspecific competition for food in this collared flycatcher population during the parental care period. In some years when the spring is too rainy, as in 1984, foraging conditions are even worse and competition is strong so the reproductive success of the flycatchers is low.

Alatalo & Lundberg (1984) also showed that in a dense population flycatchers produce lighter offspring than in a sparse population. We could not provide strong evidence that the quality of young is also affected negatively by breeding density but our data show a tendency in this direction. Although our plots were similar in vegetative structure in May, foraging conditions may change in plots later in the season but flycatchers cannot predict these changes because of the unpredictable factors (final breeding density, precipitation and number of flying insects in the parental care period). So the condition of young reared from large broods may become poorer in high densities.

In summary, our results indicate that intraspecific competition for food exists in dense flycatcher populations mainly during the nestling period. Weather factors like precipitation can influence the intensity of competition.

We raised the density of breeding flycatchers artificially and by maintaining a high number of nesting holes (10–20 boxes ha^{-1}) we could reduce the competition for holes. Most of the European forests are under intensive management and the availability of nest cavities for hole-nesters is lower than in nest-box colonies. In these forests the competition for holes must be more important than for food. Balen *et al.* (1982), however, found a high density (6·2–30 cavities ha^{-1}) of natural cavities in areas without artificial boxes. Although the properties of natural nest sites may be quite different (Balen *et al.* 1982) because of their high availability they are not limiting so we can assume that intraspecific competition for food may become more frequent than competition for nest sites in unmanaged forests as well.

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