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Density dependent effects between three competitive bird species

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Summary. Density and breeding success of the great tit *Parus major*, blue tit *Parus caeruleus* and collared flycatcher *Ficedula albicollis* were studied in nest box colony in oak forest over a period of 19 years.

Intraspecific density dependent clutch size reduction was found with blue tit and great tit. In interspecific relation the high density of blue tits reduced the clutch size of great tits.

In the hatching period neither intraspecific nor interspecific density dependence were showed between the tits when the third competitive species, collared flycatcher was present. The collared flycatcher significantly reduced the hatching success of both tit species and the number of fledglings of great tit.

The effects of the great tits and combined density of the great and blue tits on the hatching failure and number of fledglings of collared flycatcher were found when the density of the tits was high. There were not significant relationships to the single density of blue tits.

The temporal variability of the competition of the three bird species is discussed.

Key words: Intraspecific competition – Interspecific competition – Birds

The theories of interspecific competition proposed by Volterra (1926), Lotka (1932), Gause (1934), Hutchinson (1959), MacArthur and Levins (1967) were confirmed by ecologists who gathered much data on species that coexist competitively or exclude one another (reviews in Schoener, 1983). However some critics questioned the interspecific competition in certain systems. Wiens (1977) suggested that the competition is seen as a temporally sporadic, often ineffective, interaction in a variable environment; Connell (1975) concluded that predation rather than competition, appears to be the predominant ecological interaction; Schroeder and Rosenzweig (1975) showed experimentally with two species of desert rodents, that they overlap in habitat without affecting the abundance each other.

Field experiments supporting the interspecific competition in birds were carried out in tits, (Dhondt and Eyckerman 1980a, 1980b; Minot 1981; Török and Tóth 1986) jackdaws and magpies (Högstedt 1980) sparrows (Davis 1973; Mewaldt 1964) breeding populations of spruce fir forest community (Stewart and Aldrich 1951) and bark-foraging populations (Williams and Batzli 1979). Density dependent interactions between birds were examined in most detail on two sympatric tit species, blue tit and great tit, by analysis of the population dynamics and breeding success (Löhrl 1977; Dhondt 1977, 1978) removal experiments (Minot 1978, 1981; Dhondt and Eyckerman 1980a; Török and Tóth 1986) and evidence emerged for intra- and interspecific competition. These studies measured the interactions between two species only where the abundance of the great tit and blue tit far higher than that of all other hole nesting bird species. Our aim was to analyse the interactions between three hole nesting species where the collared flycatcher, the third species was abundant, and therefore interactions between it and the two tit species were predicted.

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Methods

200 nest boxes with circular entrance 32 mm in diameter were sited in 27 ha of oak forest (Quercus petraea) on the west border of Budapest (18°55'E; 47°32'N) with a spacing of 6–9 nest boxes per hectare. The boxes were checked at weekly intervals starting from before nest building until the fledglings left the nest over a period of 19 years: 1965–1983. As the number of breeding pairs which bred a second time was low, the second broods were omitted from the calculations (i.e. no year when the number of second broods exceeded 20 percent of the number of first broods). The destroyed nest boxes were replaced continuously.

Studying intraspecific density dependence from annual average data we used *k factor* analysis (Southwood 1966; Varley and Gradwell 1960) applied by Krebs (1970) for calculation of density dependent great tit mortality. Considering interspecific relationships, clutch size reduction, hatching failure, nestling mortality and number of fledglings were related to the density of the species predicted as being competitors, where

$$\text{clutch size reduction} = 1 - \frac{\text{observed clutch size}}{\text{potential maximum clutch size}},$$

$$\text{hatching failure} = 1 - \frac{\text{number of eggs hatched}}{\text{observed clutch size}},$$

$$\text{nestling mortality} = 1 - \frac{\text{number of fledglings}}{\text{number of eggs hatched}},$$

potential maximum clutch size = the maximum observed annual average during 19 years.

Measurements of the differences in breeding success of collared flycatcher when density of tits was either extremely high or extremely low the t test was used.

Results

Intraspecific density dependent reductions

Table 1 presents the census data averaged over 19 years, and shows some years when the density of collared flycatchers is higher than that of the blue tits. This reinforces the importance of measuring the population dynamism of the flycatcher in the hole-nesting bird community of the oak forest. However in the key-factor analysis we did not find significantly density dependent k values in any of the breeding periods of collared flycatchers. Kluyver (1951) and Lack (1966) argued that clutch size end fledgling success of the great tit are weakly density dependent. Krebs (1970) pointed out, on the basis of data collected by Perrins (1965), near Oxford, that clutch size and hatching success are density dependent, but the mortality of young in the nest is not density dependent for great tits. We found density dependence only in clutch size {$Y = -0.216 + 0.120$, $r = 0.619$ $P < 0.01$, where

$$Y = \log\left[\frac{(\text{potential maximum clutch} + 2)\,N}{(\text{observed clutch size} + 2)\,N}\right],$$

$X = \log(\text{potential maximum clutch} + 2)\,N$, N = number of breeding pair per 10 ha}, and there were no significant correlations either with hatching failure or nestling mortality in relation to the density of great tits. Similarly in the key-factor analysis made for the blue tits there was significant density dependence exclusively in clutch size ($Y = 0.058 + 0.051\,X$, $r = 0.589$ $P < 0.01$, where Y and X = as seen for great tits).

Interspecific density dependent reductions

The clutch size reduction, hatching failure, nestling mortality and the number of fledglings of collared flycatcher, great tit and blue tit were related to the density of the two competitive species (Table 2). The combined density of the two competitive species was also counted.

It was determined by checking at weekly intervals, that the migratory collared flycatcher started nest building and laid eggs two weeks later than tit species. Presumably that is the reason why the number of eggs of the two tit species was not influenced by the density of flycatchers. Asymmetric interactions were found between the blue tit and great tit; the density of the blue tit reduced the clutch size of the great tit, but density of the great tit did not affect clutch size of blue tit.

In the hatching period there was no interaction between

Table 1. Breeding success data over 19 years

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Great tit																			
a	9.2	9.0	8.9	9.2	10.1	10.5	10.9	9.9	10.7	9.9	10.8	11.3	10.9	10.8	11.6⁺	11.6	10.1	9.5	11.0
b	8.3	8.4	8.1	8.3	9.3	8.6	8.9	9.2	9.8	9.0	9.3	9.1	9.1	9.8	10.5	10.0	9.1	8.2	10.5
c	8.3	8.3	7.8	8.0	9.1	8.0	8.3	8.9	9.2	8.1	9.1	8.3	9.0	9.8	9.4	9.6	8.9	7.9	10.4
d	17.0	16.5	14.3	17.3	11.9	10.5	8.6	15.9	11.2	12.9	10.0	7.6	7.1	5.0	11.6	10.8	18.3	23.3	15.8
Blue tit																			
a	11.0	11.3	11.0	11.7	11.2	12.2	12.4	11.9	12.8	12.0	12.3	12.2	12.2	13.0⁺	12.0	13.0	12.0	12.0	11.0
b	10.4	10.2	10.2	10.9	9.3	10.1	10.0	11.1	11.4	10.9	10.6	10.5	10.4	10.0	11.0	12.5	10.5	11.5	9.3
c	9.7	9.9	9.5	10.1	9.1	9.6	9.1	10.3	10.7	10.1	10.0	9.6	9.6	7.5	10.3	12.0	10.0	11.5	9.3
d	9.7	9.2	9.2	7.3	10.0	6.5	5.1	7.1	5.3	6.5	5.9	4.7	4.7	1.7	2.5	1.7	5.6	3.3	3.3
Collared flycatcher																			
a	5.1	5.2	5.6	5.6	6.1	6.4	6.3	5.8	5.4	5.6	6.2	5.9	6.2	–	5.5	6.4	5.6	5.6	6.5⁺
b	4.9	4.8	5.1	5.1	5.5	6.3	6.1	5.5	5.1	5.2	5.5	5.6	6.0	–	5.3	5.8	5.3	5.3	5.6
c	4.8	4.8	5.1	5.1	5.2	5.9	5.9	5.0	4.8	5.1	5.3	5.6	5.8	–	5.3	5.5	5.0	5.0	5.5
d	6.2	6.5	6.2	7.6	8.6	10.3	11.6	5.9	7.1	6.5	10.0	12.3	11.8	–	1.7	5.8	5.8	1.7	1.7

a number of eggs laid per nest; *b* number of eggs hatched per nest; *c* number of fledglings per nest; *d* number of breeding pairs per 10 hectares; + potential maximum clutch size; – data were not available for evalution

Table 2. Significant correlations in the interspecific density dependent reductions

		a	*b*	*r*	
Great tit					
Clutch size reduction	Density of blue tit	0.014	0.022	0.756	$P<0.001$
Hatching failure	Density of collared flycatcher	0.049	0.009	0.680	$P<0.01$
Number of fledglings per 10 ha	Density of collared flycatcher	128.11	−4.44	−0.528	$P<0.05$
Blue tit					
Hatching failure	Density of collared flycatcher	0.044	0.008	0.618	$P<0.01$

Table 3. Significant differences in breeding success of collared flycatcher in various breeding periods when the density of great and blue tit is either extremely low or extremely high

Collared flycatcher		Combined density of great and blue tit		
		low	high	
Clutch size reduction	$\bar{x}$	0.066	0.154	t=3.994
	SD	0.055	0.053	$P<0.01$
Number of fledglings per 10 ha	$\bar{x}$	52.44	28.28	t=2.932
	SD	19.96	5.13	$P<0.05$
		Density of great tit		
		low	high	
Clutch size reduction	$\bar{x}$	0.046	0.154	t=4.157
	SD	0.030	0.053	$P<0.01$
Number of fledglings per 10 ha	$\bar{x}$	46.52	31.96	t=2.816
	SD	11.21	5.02	$P<0.05$

great tits and blue tits nevertheless the collared flycatcher significantly reduced the hatching success of both tit species. During the nestling period only one significant negative correlation was noted; the number of great tit fledglings on the density of collared flycatchers.

As it was seen from all annual average data throughout the 19 years, the breeding success of the collared flycatcher was not influenced in either phase of the breeding period by either blue tits or great tits. In order to find more evidence for the asymmetric interactions between the collared flycatcher and the two tit species, we measured die differences in breeding success of the collared flycatcher in years when the density if two tit spesies was either extremely high or extremely low.

Effects of tits at high densities

The five years of lowest density and five years of highest density of both great tits and blue tits were chosen and the differences in breeding success of the flycatchers between the years of lowest and highest density of tits, were measured at various phases of their breeding period. The lowest and highest combined densities of great tit and blue tit were also considered in the comparison.

The results are presented in Table 3. Breeding of the collared flycatcher was significantly affected in terms of the clutch size reduction and number of fledglings when the combined density of great tits and blue tits was extremely high. Nevertheless even the density of great tits without the blue tits influenced the clutch size reduction and the number of fledglings of collared flycatchers, such that it was significantly lower when the number of breeding pairs of great tits was high. There were no significant differences in relation to the single densities of blue tits. Neither the combined density nor the single density of the great and blue tit affected the hatching failure and nestling mortality of the collared flycatcher when the number of breeding pairs of two tit species was high.

Using the method described above we compared the breeding success of the great tit at high or low densities of blue tits and that of the blue tit at high or low densities of great tit. We did not find any significant effects.

Discussion

Dhondt (1977) provided evidence that the great tit and blue tit complete interspecifically during the breeding season and found a significant inverse correlation between great tit reproductive rate and blue tit breeding density, but not significant inverse correlation between blue tit reproductive rate and great tit density was found. Minot (1981) confirmed that great tit breeding success was negatively correlated with the density of blue tits and that the annual fluctuations in the great tit population were intra- and interspecifically density-dependent, but that the blue tit populations was only intraspecifically density dependent. Török and Tóth (1986) confirmed these findings by removal experiments carried out through three years and concluded that blue tit had advantage in competition for food during parental care. It was hypothesized that the specialist blue tit could exploit more efficiently the caterpillar supply then the more generalist feeder great tit did (Török 1986). Dhondt and Eyckerman (1980a) suggested from field experiments that blue tit breeding population size is limited by interspecific competition with the great tit during the winter.

We found density dependent, intraspecific competition both in blue tit and great tit and significant effects of blue tit density on great tits, but at that time of the breeding period when collared flycatcher had not yet arrived at the nesting area. No intraspecific or interspecific interactions were observed with the blue tit and great tit populations when collared flycatchers were present. Presumably neither intraspecific nor interspecific competition could occur in either of the tit populations because of the effects of the collared flycatchers. Except the high density of the tits extremely throughout the 19 years we found asymmetric competition between the collared flycatcher and both blue tits and great tits, with respect to the hatching failure and the number of fledglings of the tits, and the negative effects of the collared flycatcher were greater for the great tits.

Nevertheless there were no intraspecific interactions found within the collared flycatcher population. Alatalo and Lundberg (1984), Virolainen (1984) for pied flycatcher and Gustafsson (1985) for collared flycatcher argued that flycatchers produce smaller and fewer youngs in dense populations than in rare populations. Probably the density dependence acts throughout the diminishing food supply. The reproduction is influenced by climatic factors (temperature, precipitation) and the structure of population (polygamy, age structure) as well. The lack of intraspecific density dependent effects of collared flycatcher in breeding success may be attributed to the low breeding density and/or the superabundant food environment.

Nevertheless we also considered the effects of the tits on collared flycatchers and we have provided evidence that they exist by showing the differences in the breeding success of the collared flycatcher in years of highest and lowest density of blue tits and great tits. As the effects of the tit species on the collared flycatcher could only be found with high tit population density, the asymmetric competition between the tits and flycatchers was confirmed. However Slagsvold (1978) showed that flycatchers are suffered by the overcompetition of the tits, and Gustafsson (1985) found that the reproduction of a Baltic flycatcher population was reduced in term of number and weight of young at high breeding density of tits.

It could be seen the asymmetric competition between the collared flycatcher and tits was greatest during the hatching period. There are two possible reasons for this phenomenon. It was observed that the collared flycatchers arriving and seeking a nesting hole for egg-laying disturbed the nests of the tits despite there being numerous empty nest boxes tits did not disturb the collared flycatchers during their egg laying and incubation because the tits had already nested; they were incubating or feeding young. (Tits disturbed the hatching of the collared flycatcher only when the populations of tits were high.) The second reason may be that the diets overlap. There is evidence (Gibb and Betts 1963; Tinbergen 1960; Minot 1981; Török 1986) which shows high overlap in the diets of nestling blue tits and great tits in pine woods and oak forest. Provided that there is high overlap of the diet between collared flycatchers and the tits, direct competition for food may exist during the time prior to hatching and may influence the egg formation and egg-laying by the females.

Interferences were not found in the nestling period. Thus breeding failure caused by the competition cannot be occuring in the parental care. This may be explained in two ways. The first of them is that the disturbance of the nest hole ceases, and the second reason is that the peak availability of food coincides with the time of the parental care, as was pointed out by Balen (1973) for great tits and there is no competition because of a rich food supply.

We found data on the temporal variability of the competition and provided evidence that two species with high abundance can compete with each other in their preferred habitat. However, their competitive relationship is transformed by a third species in another habitat where they maintain their high populations.

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References

Alatalo RV, Lundberg A (1984) Density-dependence in breeding success of the pied flycatcher (Ficedula hypoleuca). J Anim Ecol 53:969–977

Balen JH van (1973) A comparative study of the breeding ecology of the great tit. Ardea 61:1–93

Connell JH (1975) Producing structure in natural communities. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities, Belknap, Cambridge, Mass, pp 460–490

Davis J (1973) Habitat preferences and competition of wintering juncos and golden-crowned sparrows. Ecology 54:174–180

Dhondt AA (1977) Interspecific competition between great and blue tits. Nature 268:521–523

Dhondt AA (1978) Interspecific competition in tits (reply). Nature 275:463–464

Dhondt AA, Eyckerman R (1980a) Competition between the great tit and the blue tit outside the breeding season in field experiments. Ecology 61:1291–1292

Dhondt AA, Eyckerman R (1980b) Competition and the regulation of numbers in great and blue tit. Ardea 68:121–132

Gause GF (1934) The struggle for existence. Hafner, New York

Gibb JA, Betts MM (1963) Food and food supply of nestling tits (Paridae) in Breckland pine. J Anim Ecol 32:489–533

Gustafsson L (1985) Life history traits as fitness components in collared flycatcher (Ficedula albicollis). PhD thesis, Uppsala University

Högstedt G (1980) Prediction and test of the effects of interspecific competition. Nature 283:64–66

Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals. Am Nat 93:145–159

Kluyver HN (1951) The population ecology of the great tit, Parus m. major L. Ardea 39:1–135

Krebs JR (1970) Regulation of numbers in the Great tit (Aves: Passeriformes). J Zool, London 162:317–333

Lack D (1966) Population studies of birds. Oxford University Press, London

Löhrl H (1977) Nistökologische und ethologische Anpassungserscheinungen bei Höhlenbrütern. Vogelwarte, Sonderheft, 92–101

Lotka AH (1932) The growth of mixed populations: two species competing for a common food supply. J Wash Acad Sci 22:461–468

MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. Am Nat 101:377–385

Mewaldt LR (1964) Effects of bird removal on a wintering population of sparrows. Bird-Banding 35:184–185

Minot EO (1978) Interspecific competition in tits. Nature 275:463

Minot EO (1981) Effects of interspecific competition for food in breeding blue and great tits. J Anim Ecol 50:375–385

Perrins CM (1965) Population fluctuation and clutch size in the great tit (Parus major). J Anim Ecol 34:601–647

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Schroeder GD, Rosenzweig ML (1975) Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. Oecologia (Berlin) 19:9–28

Slagsvold T (1978) Competition between the great tit Parus major and the pied flycatcher Ficedula hypoleuca: an experiment. Ornis Scandinavica 9:46–50

Southwood TRE (1966) Ecological methods. Methuen, London

Stewart RE, Aldrich JW (1951) Removal and repopulation of breeding birds in a spruce fir forest community. Auk 68:471–482

Tinbergen L (1960) The natural control of insects in pine woods. Factors influencing the intensity of predation by song birds. Arch Néerlandaises Zool 13:265–343

Török J (1986) Food segregation in three hole-nesting bird species during the breding season. Ardea 74:129–136

Török J, Tóth L (1986) Competition for food between two tit species: a removal experiment. Proc. 20th Intern. Ornithol Cong, Abstracts 178

Varley CC, Gradwell GR (1960) Key factors in population studies. J Anim Ecol 29:399–401

Virolainen M (1984) Breeding biology of the pied flycatcher Ficedula hypoleuca in relation to population density. Ann Zool Fenn 21:187–197

Volterra V (1926) Variatzioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem R Accad Lincei Ser 6, II

Wiens J (1977) On competition and variable environments. Am Sci 65:590–597

Williams JB, Batzli GO (1979) Competition among bark-foraging birds in central Illinois: experimental evidence. Condor 81:122–132

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