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Asymmetric competition between two tit species: a reciprocal removal experiment

JÁNOS TÖRÖK and LÁSZLÓ TÓTH

Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös University, H-1088, Budapest, Puskin u. 3, Hungary

Summary

1. In a 5-year field experiment, competition for food was tested between great tit (*Parus major* L.) and blue tit (*P. caeruleus* L.), two common hole-nesters in Central Europe. Experimental ('allopatric') populations of both species were created during the breeding seasons by preventing the nesting or egg laying of one of the competing species.

2. An asymmetric relationship was found between the two tits; blue tits were more successful in the competitive interaction. Detectable effects were found only in nestling condition. Great tits raised lighter nestlings when breeding sympatrically with blue tits.

3. A possible mechanism is suggested that could be responsible for the different competitive abilities of the two species; blue tits are more effective in utilizing the most abundant size categories of caterpillar food supply than great tits.

Key-words: blue tit, competition for food, diet segregation, great tit, removal experiment.

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Introduction

Seeking general rules, many biologists thought that interspecific competition is the major force in shaping community structure (Strong 1980; Brown 1981). In the past two decades the competitionist viewpoint has received strong criticism on both experimental (Wiens 1974; Wiens & Rotenberry 1981; Connell 1983) and theoretical (Schoener 1982; Simberloff 1982, 1983; Walter, Hulley & Craig 1984) grounds. However, nobody questions the importance of such interactions in specific cases. Recently, instead of its generality, the spatial and temporal variation of the intensity of competition and its relation to other factors such as predation and environmental variables have received much more attention from researchers (Thomson 1980; Ekman 1986, 1987; Anderson 1989; Hengeveld 1989; O'Neill 1989; Blondel *et al.* 1991; Niemelä 1993).

The purpose of this study was to show that interspecific competition for food between two small passerines during breeding seasons depends on the annually varying food supply. An experiment was conducted with the two commonest European tit species, the great tit and the blue tit.

Correspondence: J. Török, Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös University, H-1088, Budapest, Puskin u. 3, Hungary

Earlier studies have shown that interspecific competition for different resources in different seasons frequently occurs among the member of European tit assemblages (reviewed by Alatalo 1982). It is known that animal food is in short supply in winter and that competition between the blue tit and the great tit may exist during this period (Dhondt & Eyckerman 1980a). The situation is much more complicated in the breeding season, as British authors have suggested that food is then superabundant and therefore competition would not occur (see for references Dhondt 1977). However, correlative studies have given evidence for the possible occurrence of exploitative and/or diffuse competition for food among breeding tits (Dhondt 1977; Minot 1981; Dhondt & Eyckerman 1980b).

A field experiment was performed (*sensu* Schoener 1983) to test the hypothesis that interspecific competition for food between great tit and blue tit occurs in the breeding season in a Central European oak forest. The experiment was designed in such a way that both demographic (breeding) parameters and resource utilization could be studied. It was hypothesized that eliminating one of the competing species would result in increasing fitness (here, simply reproductive success) of the other species. The results indeed confirm that food can be a limited resource during the breeding season, and that the outcome of competitive interaction between the two tit species is disadvantageous for the great tit (decreased body mass of fledglings). Food resource utilization suggested that asymmetry may be caused by the different prey size preference of species.

Materials and methods

A removal experiment was carried out between 1982 and 1987. Three study plots (two experimental and one control) were chosen within a large, continuous oak woodland area near Budapest, Hungary. Plots were about 1·5–2·0 km apart, which ensured that there was no exchange of foraging birds between plots. Moreover there were no between-plot movements of adult birds in consecutive years. The vegetation structure and the age of trees (51 years old in 1981) were the same in each plot. The dominant oak species was *Quercus petreae* Lieb. High nest-box density (over 12 boxes ha^{-1}) was established to avoid possible interspecific competition for nest-holes (Minot & Perrins 1986). In 1985 the experiment was interrupted because of the small number of breeding great tits, presumably as a consequence of the harsh winter of 1984. To increase the sample size in 1986 and 1987, the size of the study plots was doubled but with the original box densities.

Experimental plots were created by preventing one of the two tit species from breeding. Using nest-boxes with a 26 mm entrance hole diameter only blue tits were allowed to breed in one of the experimental plots ('allopatric' for blue tit). To prevent the blue tits breeding in the other experimental plot ('allopatric' for great tit), the entrance of those boxes occupied by a blue tit pair during the nest-building period was closed. Not all blue tits left the experimental plot immediately after disturbance. If a new box occupation was noticed, the entrance of that box was also closed. Natural holes in study plots were also checked but there was no breeding attempt in either species. Although excluded blue tits used the food supply of the experimental plot for a while, it was assumed that their feeding did not reduce the amount of supply significantly as they did not raise nestlings. In the control plot both tit species could breed (sympatric populations) as the entrance hole diameter was 32 mm. Beside the two tit species the most numerous breeding species was the Collared Flycatcher (*Ficedula albicollis* Temm.) in the boxes with the larger entrance hole diameter.

Female tits were captured mainly during the incubation period, and bill, wing and tarsus length as well as body weight were measured. Body weight and tarsus length of nestlings were recorded on day 15. All nestlings and about 80% of the adult females were ringed in each year.

Analysis of variance (ANOVA/ANCOVA) was used to determine the differences between reproductive success of experimental and control tit populations. Five variables (clutch size, number of hatchlings and fledglings, body mass and tarsi of nestlings on day 15) were included in the analysis. Each of them is a component of fitness as they affect it in a slightly different way; for example, early clutches are usually larger and produce more fledlgings (Klomp 1970) and there is evidence for a causal relationship between hatching date and offspring survival in tits (Verhults & Tinbergen 1991; Norris 1993).

Two groups of reproductive variables were established. The first three variables are called 'reproductive output variables', while the last two are known as 'condition variables'. Although both condition variables are controlled partly by genetic and environmental factors, the body mass is affected much more by the food availability than tarsus length (Alatalo & Lundberg 1984). A separate analysis was performed for each of the five variables in both species to examine the effects of experimental treatment. Treatment and year were considered as independent variables in computation of two-way ANOVA for each variables. ANCOVA models were applied for condition variables, including two covariates, the brood size (number of hatched young) and hatching date, as both can affect the final body mass and tarsus length of fledglings (Perrins 1965; Nur 1984; Martin 1987). The data were analysed by the ANOVA/MANOVA program of STATISTICA (1994) statistical package. Reciprocal transformation was applied for the first three variables, while logarithmic transformation of body mass and tarsi was performed to stabilize the variances and to give an approximately normal distribution of the variables.

In addition, food resource utilization of both tit species was recorded. Food samples were collected from 8- to 12-day-old nestlings by the neck-collar method (Kluijver 1933). In 1984 one blue tit and one great tit nest were sampled at the control plot, while two blue tit nests were sampled at the experimental plot. Because of the small number of breeding great tits, it was not possible to collect food from nestlings at the experimental plot in that year. In 1986 one great tit and two blue tit nests were sampled in the control plot and also in the experimental plots. In 1987 one great tit and two blue tit nests were selected for food collection in the control plot, while two great tit and one blue tit nests were sampled in the experimental plots. Previous work has shown that prey size is an important factor in food niche differentiation of tits (Török 1986). In the study reported here, about 70% of the total prey items taken from nestlings was lepidopterous larvae, so attention was focused on the size distribution of this abundant food type. To estimate the size distribution of available caterpillars a total of 3353 specimens were collected by beating the surrounding trees adjacent to the nests that were sampled. The amount of available caterpillars living in the foliage was measured by the frass production during the breeding season of each year (four collectors per plot with surface of $0{\cdot}25\,m^2$). Usually, the collectors were emptied every 2–3 days between 15 April and 30 May. To make a comparison of food supply on the different plots, the quantity of frass collected in the peak period (lasting from 4 to 12 days, depending on plots and years) when the biomass of caterpillars reached the maximum was used.

Results

REPRODUCTIVE SUCCESS

Comparing the control and experimental plots there was no clear trend in the five breeding parameters of blue tits (Table 1). In 1983 and 1986 reproduction of blue tit was slightly better on the control plot, while in the other three years reproductive success was greater on the experimental plot for one variable but greater on the control plot for another variable in the same year. In great tit, condition variables were usually greater in the experimental plot, while, with regard only to reproductive output variables, clutch size showed a similar trend (Table 2).

Using the three reproductive output variables of five years, ANOVA did not show differences between control and experimental populations in either species (Table 3). To analyse the effects of treatment and year on the two condition variables, ANCOVA was applied with brood size and hatching date as covariates. The body mass of great tit nestlings was found to be significantly reduced when they bred sympatrically with blue tit. On the other hand, the presence of great tit did not affect the condition of blue tit nestlings (Table 4). Tarsus length was measured in the last three experimental years only. There was no significant difference in tarsus length between control and experimental nests in either species, while year significantly affected the tarsus length of nestlings in both species (Table 5).

All the five fitness variables showed a significant variation among years, however no indication was found for interaction between year and treatment in any of the five dependent variables in either species. In short, these results show that the presence of blue tit affected the fledging weight only of chicks of great tit but not the other reproductive success variables.

Table 1. Means and standard deviations (SD) of breeding parameters of blue tit on control (Cont) and experimental (Exp) populations during the 5 years. Number of nests are in parentheses

		1982		1983		1984		1986		1987	
		Cont (10)	Exp (11)	Cont (9)	Exp (7)	Cont (5)	Exp (9)	Cont (14)	Exp (12)	Cont (17)	Exp (18)
Clutch	Mean	12·0	11·9	12·8	12·4	12·2	12·8	11·6	11·3	12·7	12·8
size	SD	2·16	1·14	1·56	0·54	1·48	1·20	1·56	2·61	1·69	1·72
Hatched	Mean	11·2	10·7	11·8	11·4	11·4	11·8	10·5	9·8	12·0	11·6
young	SD	2·90	1·95	1·64	0·98	0·90	1·20	1·95	2·92	1·28	2·45
Fledged	Mean	9·9	10·7	11·7	11·3	9·2	11·1	10·4	9·7	11·5	9·9
young	SD	3·76	1·95	1·66	1·25	5·22	2·26	1·95	2·74	0·94	4·06
Body	Mean	12·0	12·0	11·8	11·5	11·7	11·5	11·8	11·6	11·2	11·2
mass	SD	0·58	0·48	0·56	0·59	0·94	0·58	0·41	0·63	1·02	0·64
Tarsus	Mean	–	–	–	–	16·6	17·1	17·2	17·1	16·8	16·7
length	SD	–	–	–	–	0·38	0·25	0·20	0·38	0·46	0·67

Table 2. Means and standard deviations (SD) of breeding parameters of great tit on control (Cont) and experimental (Exp) populations during the 5 years. Number of nests are in parentheses

		1982		1983		1984		1986		1987	
		Cont (12)	Exp (7)	Cont (10)	Exp (3)	Cont (5)	Exp (4)	Cont (15)	Exp (7)	Cont (11)	Exp (7)
Clutch	Mean	9·7	10·4	11·6	10·3	10·2	10·3	11·2	12·1	11·1	12·4
size	SD	1·37	1·62	1·51	0·58	0·84	2·36	1·32	1·07	1·58	0·54
Hatched	Mean	9·1	9·4	10·1	8·7	9·8	10·3	9·6	10·1	10·6	10·4
young	SD	1·62	2·15	1·37	0·58	0·84	2·36	1·81	1·22	1·70	2·51
Fledged	Mean	9·0	9·4	10·0	8·7	8·6	7·0	9·4	10·1	10·1	10·0
young	SD	1·76	2·15	1·25	0·58	2·71	4·97	1·77	1·22	2·02	2·38
Body	Mean	18·4	18·3	16·7	18·4	16·3	17·3	17·8	18·2	17·8	18·1
mass	SD	0·77	0·93	2·59	1·13	0·74	1·05	0·52	0·56	0·71	0·77
Tarsus	Mean	–	–	–	–	14·5	19·7	20·0	20·2	20·1	20·2
length	SD	–	–	–	–	0·39	0·37	0·27	0·24	0·38	0·07

Table 3. Two-way ANOVA on effects of treatment and year on reproductive output variables of great and blue tit for 5 years

		Clutch size			Brood size			Number fledged		
Source	d.f.	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
Great tit										
Treatment	1	0·0001	0·66	0·42	0·0001	0·17	0·71	0·0013	1·36	0·25
Year	4	0·0009	4·91	0·002	0·0004	0·70	0·63	0·0002	0·22	0·89
Year × treatment	4	0·0002	1·27	0·29	0·0003	0·52	0·74	0·0014	1·56	0·20
Blue tit										
Treatment	1	0·0001	0·07	0·79	0·0005	0·76	0·39	0·0005	0·16	0·69
Year	4	0·0008	2·18	0·08	0·0017	2·96	0·02	0·0035	1·21	0·31
Year × treatment	4	0·0002	0·44	0·78	0·0003	0·47	0·76	0·0041	1·40	0·24

Table 4. Result of ANCOVA on effect of treatment and year on body mass of great and blue tit nestlings for 5 years. Brood size and date of hatching were included as covariate

	Great tit				Blue tit			
Source	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
Treatment	1	0·0040	8·85	0·004	1	0·0010	2·71	0·10
Year	4	0·0119	26·30	0·0001	4	0·1404	370·48	0·0001
Year × treatment	4	0·0009	1·98	0·11	4	0·0002	0·39	0·82
Brood size	1	0·0004	0·85	0·36	1	0·0008	2·04	0·16
Error	70	0·0005			101	0·0004		
Treatment	1	0·0037	8·29	0·0053	1	0·0009	2·25	0·14
Year	4	0·0120	26·50	0·0001	4	0·1108	286·64	0·0001
Year × treatment	4	0·0010	2·21	0·08	4	0·0002	0·37	0·83
Hatching date	1	0·0005	1·03	0·31	1	0·0001	0·007	0·93
Error	70	0·0005			101	0·0004		

Table 5. Result of ANCOVA on effect of treatment and year on tarsus length of great and blue tit nestlings for 3 years (1984, 1986, 1987). Brood size and date of hatching were included as covariate

	Great tit				Blue tit			
Source	d.f.	MS	*F*	*P*	d.f.	MS	*F*	*P*
Treatment	1	0·0002	1·43	0·24	1	0·0002	0·38	0·54
Year	2	0·0113	80·28	0·0001	2	0·2827	494·43	0·0001
Year × treatment	2	0·0001	0·04	0·96	2	0·0002	0·42	0·66
Brood size	1	0·0001	0·18	0·67	1	0·0001	0·20	0·66
Error	42	0·0001			68	0·0006		
Treatment	1	0·0002	1·40	0·24	1	0·0003	0·54	0·46
Year	2	0·0117	82·94	0·0001	2	0·2661	466·68	0·0001
Year × treatment	2	0·0001	0·02	0·98	2	0·0003	0·47	0·63
Hatching date	1	0·0001	0·05	0·83	1	0·0002	0·39	0·54
Error	42	0·0001			68	0·0006		

NESTLING DIET AND CATERPILLAR SUPPLY

Published data on the diets of the two tit species show that diet compositions are broadly similar (Betts 1955; Tinbergen 1960; van Balen 1973; Minot 1981; Török 1986). The results of the present study strengthen these findings, however, it must be noted that the prey size utilization of these species is quite different. It was found that blue tits fed mainly on smaller caterpillars (which is the commonest food type), while great tits

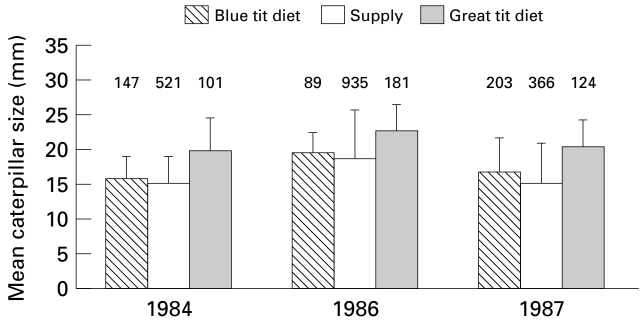

Fig. 1. Mean caterpillar size in the supply and in the diet of nestling great and blue tits on the control plot during 3 years. (Lines denote ± SD, number of caterpillars is above the bars.)

(the larger species) took larger ones in the control plot ($F = 2{\cdot}08$, $P = 0{\cdot}001$; $F = 1{\cdot}58$, $P = 0{\cdot}001$; $F = 1{\cdot}82$, $P = 0{\cdot}001$; in 1984, 1986, 1987, respectively; see sample sizes in Fig. 1), just as the predator–prey size hypothesis predicts (Hespenheide 1971). Either in control or in experimental plots the mean prey size of both species was larger than the mean caterpillar size in the supply. All these comparisons were statistically significant in each year ($F > 1{\cdot}36$, $P < 0{\cdot}05$ in all cases). As the mean size of available prey differed significantly between plots in each year ($F > 1{\cdot}15$, $P < 0{\cdot}01$ in all cases, except 1987, when means were the same in the control and blue tit experimental plots) the differences between mean prey sizes taken by tits and the mean prey sizes in the supply should be considered. Prey size eaten by blue tits differed more from those available in the experimental plot than those in the control plot, except in 1986, when the differences were rather similar (Fig. 2). Similar results were found for great tits, however, the absolute differences were far larger in both plots (Fig. 3).

Using the Renkonen's percentage similarity index to compare the size distribution of available prey and nestling diet (Table 6), a greater similarity was found in the control plot than in the experimental one for both species (except for the blue tit in 1986). However, similarity of blue tit between diet and supply was larger than that of the great tit in both sympatric and allopatric populations (except sympatric population in 1986). The main conclusion that can be drawn from these findings is that both tit species specialize when breeding without the other species, while in a sympatric population the blue tit becomes a more generalist feeder than the great tit.

Data on diet composition showed that blue tit brought significantly more spiders than great tit (Table 6; Wilcoxon test: $z = -2{\cdot}023$, $P = 0{\cdot}043$, $n = 10$). An opposite but not significant trend was observed for caterpillars ($z = -1{\cdot}483$, NS). Moreover spider consumption rates were higher in experimental populations than control ones for both species, however, blue tits brought 2–6 times more spiders than great tits in control populations (Table 6).

The basic assumption was that food was in limited supply in study plots, however, the amount of food can vary between plots. If the available food is scarce in experimental plots, this could result in such a low reproduction as that in interspecific competition. Tinbergen (1960) showed that the population size of caterpillars, which are the main food of tits, in forests could be predicted from the frass production. This sampling technique suffers from large errors, however, it can be used for relative estimates (Zandt 1994). Thus the data obtained in the present study were used to

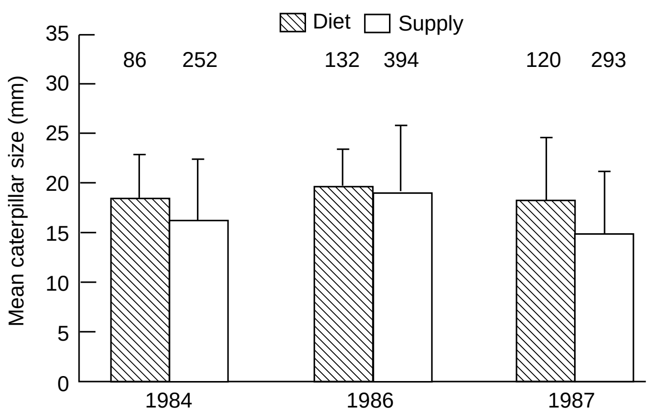

Fig. 2. Mean caterpillar size in the supply and in the diet of nestling blue tits on the experimental plot during 3 years. (Lines denote ± SD, number of caterpillars is above the bars.)

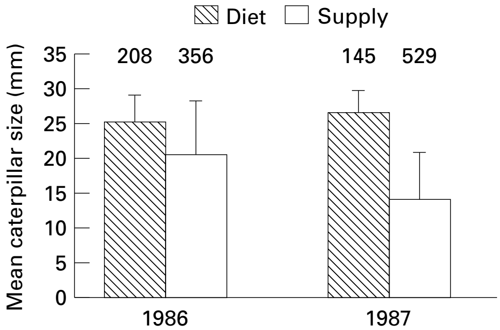

Fig. 3. Mean caterpillar size in the supply and in the diet of nestling great tits on the experimental plot during 2 years. (Lines denote ± SD, number of caterpillars is above the bars.)

compare caterpillar food supply among plots in a certain year only. Significant differences were not found in amount of frass fall between plots in either years. However, in 1984 and 1986 frass production in the control plot was about twice as large as in the great tit experimental plot during the peak period (Table 7). In spite of this, the body mass of great tit nestlings was worse in the control plot in these years, which supports the existence of interspecific competition between the two tit species.

Discussion

Great and blue tits coexist continuously in the same preferred habitats. Large overlap in resource utilization (breeding and roosting holes, food types, foraging sites) implies competition between the two species if resources are limiting. Based on nonexperimental data, an asymmetric competition between blue tit and great tit was proposed by Dhondt (1977). He hypothesized that the good exploitative competitor, blue tit, is superior to the great tit in the utilization of the food supply during the breeding season, resulting in reduced fitness (fewer young produced) in the great tit. Unfortunately, the methods used by Dhondt (i.e. combined density affected the relative competitive ability of the tits) did not separate intra- from interspecific effects (Minot 1978), as well as effects existing outside the breeding season. Using demographic changes it is possible to predict the outcome of competition but hardly anything can be said about how it happened. In another study Dhondt & Eyckerman (1980a) found a reversed dominance during the winter

Table 6. Frequency of spiders and caterpillars in the diet of the two tit species and the caterpillar size similarity between nestling diet and supply. See number of sampled nests in Materials and methods

Year	Plot	Species	Spider (%)	Caterpillar (%)	Caterpillar size similarity
1984	Exp	BT	36·4	45·8	0·64
	Cont	BT	11·9	83·4	0·77
	Cont	GT	1·9	95·3	0·44
1986	Exp	BT	35·3	57·6	0·64
	Cont	BT	33·7	59·3	0·50
	Cont	GT	13·0	81·2	0·54
	Exp	GT	19·3	64·6	0·51
1987	Exp	BT	32·3	64·5	0·46
	Cont	BT	15·0	66·1	0·68
	Cont	GT	8·8	84·4	0·45
	Exp	GT	25·5	45·6	0·15

Cont, control; Exp, experimental; BT, blue tit; GT, great tit.

Table 7. Frass production (air dry weight g per 0·25 square m per day) by caterpillars during the peak period (mean, SD, $n = 4$ for each year and plot)

	Experimental plot					
	Blue tit		Great tit		Control plot	
Year	Mean	SD	Mean	SD	Mean	SD
1983	0·26	0·049	0·23	0·001	0·32	0·215
1984	0·24	0·080	0·26	0·076	0·58	0·227
1986	0·38	0·220	0·18	0·046	0·34	0·078
1987	0·14	0·047	0·21	0·097	0·21	0·570

period. In addition to his descriptive study, Minot (1981) performed an asymmetric experiment by manipulating the density of only one of the competing species, the blue tit, during the breeding season. Where all blue tits were removed on hatching, the nestling weights of great tit increased.

The reciprocal experiment in the present study included removal of each species. The results demonstrate that the fitness (in terms of nestling condition) of great tits was affected by the presence of blue tits. Lighter offspring produced by great tits in control populations were probably the consequence of competition for a limited food resource.

HOW ARE NESTLING WEIGHT AND SUBSEQUENT NESTLING SURVIVAL RELATED?

In the great tit, several studies have found evidence that nestling survival increases with increasing nestling weight (Perrins 1965; Dhondt 1971; Garnett 1981). Larger body mass of a nestling means less energy is required for existence (Kendeigh 1970) and there is a larger energy reserve for dominating over other individuals in assessing resources (Garnett 1981). Perrins (1965) showed that heavier fledglings have a better chance of surviving the immediate post-fledging period than lighter fledglings. Later, Garnett (1981) extended this hypothesis, suggesting that the dominance status, which is determined by the body size of fledglings, is related directly to survival. With more precisely designed experiments (to filter out the effect of other 'brood traits', like parental quality, brood size and/or environmental factors), Tinbergen & Boerlijst (1990), in the great tit, and Nur (1984), in the blue tit, could show that nestling weight does play a causal role in the nestling weight–local survival relationship. Considering this causality it can be concluded that weight differences between nestlings can be taken as fitness differences between them.

One can say that the other bird species, e.g. the collared flycatcher breeding in large number in plots, can influence the outcome of this experiment. This is not the case, as migrating flycatchers arrived in April at study plots and started to breed 13 days (in average of years and plots) later than did tits. By that time tits have usually incubated their eggs. Nestlings of flycatchers hatched 10 days later than those of tits on average, thus the overlap in nestling care period was small. Although caterpillars, which are the most important prey type for tits (Royama 1970; Balen 1973; Minot 1981), form about one-third of the diet of collared flycatcher (Löhrl 1976; Török 1986), the food demand of flycatcher nestlings is small (simply because they are young) during the short overlapping parental care period. This implies that competition for food between flycatchers and tits was probably insignificant in the present study plots.

The most likely mechanism responsible for the competitive dominance of blue tit lies in the different food resource utilization of tit species. Although caterpillars were the most frequent prey type taken by birds in all situations, they gathered more from this prey in the control plot in each year. However, the proportion of spiders in the nestling diet was higher in experimental plots in both species. Spiders, usually, are more profitable food types in terms of their energy (Török 1981) and specific nutrient (i.e. Ca) content (Royama 1970), than caterpillars. One limitation of the present study is that it was not possible to estimate spider density in the environment. Presumably birds can forage for not so abundant but profitable prey (spiders) in a relaxed competitive situation ('allopatric' populations). In competition, because of increasing efforts to gather enough food for nestlings, probably both tit species drop spiders from the nestling diet and increase the proportion of caterpillars, which are the more readily available prey. In this way birds can cover the food demand of nestlings in crowded (sympatric) populations as well. Similar results were obtained by Cowie & Hinsley (1988) studying tits' food in urban areas where tits take more artificial food (bread) to older nestlings. Young nestlings received proportionally more spiders. Lower demand of young nestlings allowed parents to spend more time foraging, so profitable and/or nutrient-rich prey were included in the nestling diet (see also Tinbergen 1981).

In conclusion, the results presented here provide evidence for interspecific competition for food between great and blue tits during the breeding season. The difference in prey size preference and the exploitation of the food supply caused an asymmetry in the competition; blue tits were competitively superior to great tits.

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