

The Diet Niche Relationships of the Great Tit (*Parus major*) and Blue Tit (*Parus caeruleus*) Nestlings in an Oak Forest

By

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Abstract. The food composition of the nestlings of the great tit and blue tit was studied based upon 927 and 183 samples, respectively (one sample: food of one nestling per hour), in a mixed oak forest near Budapest. The main food type of both species was the Lepidoptera larva, followed by much smaller quantities of spiders. The greatest amount of spiders was consumed at the early stage of development of the nestlings. Niche breadth calculated for food composition and prey size distribution is wider in case of the great tit suggesting a more generalistic feeding habit of this species. Habitats of the prey animals of both species are very similar. Food niche segregation seems to be the greatest in the dimension of taxonomic composition of food.

The great tit (*Parus major*) and blue tit (*Parus caeruleus*) are characteristic breeding species of the bird communities of temperate deciduous forests. Due to their good adaptive ability and high abundance they can be found even in areas beyond their optimal habitats (pinewoods, parks). Especially the great tit settles in the human environment besides its natural habitats. Because of their wide distribution and high density both *Parus* species have been studied intensively. The researchers of the Edward Grey Institute of Oxford have continuously been investigating the feeding ecology (HARTLEY, 1953; GIBB, 1954; BETTS, 1955; GIBB & BETTS, 1963; ROYAMA, 1970), the population dynamics (LACK, 1958; KREBS, 1971) and behaviour (KREBS & al., 1977) of the tits. The works of the Dutch KLUJVER (1950), TINBERGEN (1960) and BALEN (1973), as well as that of the Belgian DHONDT (1977) are also closely connected with the tits.

This paper deals with the nutrition quality and quantity of the nestlings of great- and blue tits in a mixed oak forest which can be considered their optimal habitat. The aim of the study was a comparison between the two species considering their feeding habits first of all taxonomic composition and size distribution of their prey and foraging site preference of birds. Such studies may contribute to a better knowledge of the interspecific relationships of *Parus major* and *P. caeruleus*.

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Methods

The study area was a mixed oak forest near Budapest. Its dominant tree species is *Quercus cerris*, in a smaller quantity *Q. petraea*, *Carpinus betulus*, *Acer campestre* and *Cerasus avium* also occur. The most frequent shrubs are *Crataegus* spp., *Ligustrum vulgare*, *Rosa* spp., *Sambucus nigra*. The forest was bordered by an apple orchard from the south. In a 12 ha part of the forest chosen as examination area 40 artificial nesting holes were placed.

Food samples were collected from the great- and blue tit nestlings during the breeding periods 1978 and 1980 with the "neck collar" method. The mucous coating of the samples was washed off with water, then the food was stored in 70 per cent isopropyl alcohol until determination. If one hour's food of one nestling is considered 1 food sample, then in 3 years 927 samples were collected from the great tit and 183 ones from the blue tit. In the case of the blue tit the number of the samples was less because this species bred in the artificial holes in a much smaller number of individuals than the great tit.

When elaborating the data, the niche breadth and the niche overlap between the two species was calculated on the basis of taxonomic composition and prey size distribution as 2 special, hypothetical niche components. When calculating the value using the taxonomic composition of the food samples were pooled to families.

Niche breadth was calculated by SIMPSON's (1949) formula which was suggested by LEVINS (1968) for determining niche breadth:

$$B = 1 / \sum_{i=1}^s p_i^2$$

The niche overlap between the two species was calculated by RENKONEN's (1938) similarity index:

$$C_{hj} = 1 - 1/2 \sum_i p_{hi} - p_{ji}$$

In calculations of food taxonomic composition p_i is the frequency of food group i (mostly family) in the food (s : the number of food groups). In calculations of size distribution p_i is the proportion of the number of individuals belonging to the size class i in the food (s : the number of size classes). h and j specifies the great tit and blue tit, respectively.

Calculations on the foraging site of the great- and blue tits were drawn from the habitats of the prey animals. The habitats of some of the prey was difficult to determine exactly, therefore it was their most probable habitats that were taken as a basis. In this way 6 foraging sites were distinguished (Fig. 2). Since this method enables only rough and indirect determination of the prey habitats, this third possible niche component was not considered during the calculations of niche breadth and overlap.

Results

In the diet of the great tit nestlings a total of 63 species, from that of the blue tit nestlings 24 species were found (Appendix 1 and 2). Numerous individuals could only be determined as genera or families. The dominant food type of both

species was the Lepidoptera larvae, which, on an average of 3 years, amounted to 63,3% of the total food of the great tit and to 74,0% of that of the blue tit, both measured in dry weight. The largest amount of caterpillar food consumed by the great tit consisted of *Colotois pennaria*, *Amphipyra pyramidea*, *Orthosia* spp. and *Drymonia chaonia*. Among this prey type of the blue tit *Orthosia* spp., *Colotois pennaria* and the small-sized *Tortrix viridana* were significant. Lepidoptera adults were found in the diets of both species, Lepidoptera pupae only in that of the great tit. In the other important food group, the spiders, the majority of *Xysticus lanio* and *Philodromus aureolus* were observed in case of both tit species. *Araneus cucurbitinus* and *Xysticus ulmi* were found in the food of the blue tit, while the soil inhabiting *Pisaura mirabilis* and *Alopecosa* spp. were found in the food of the great tit. Diptera were significant only in the diet of the great tit nestlings.

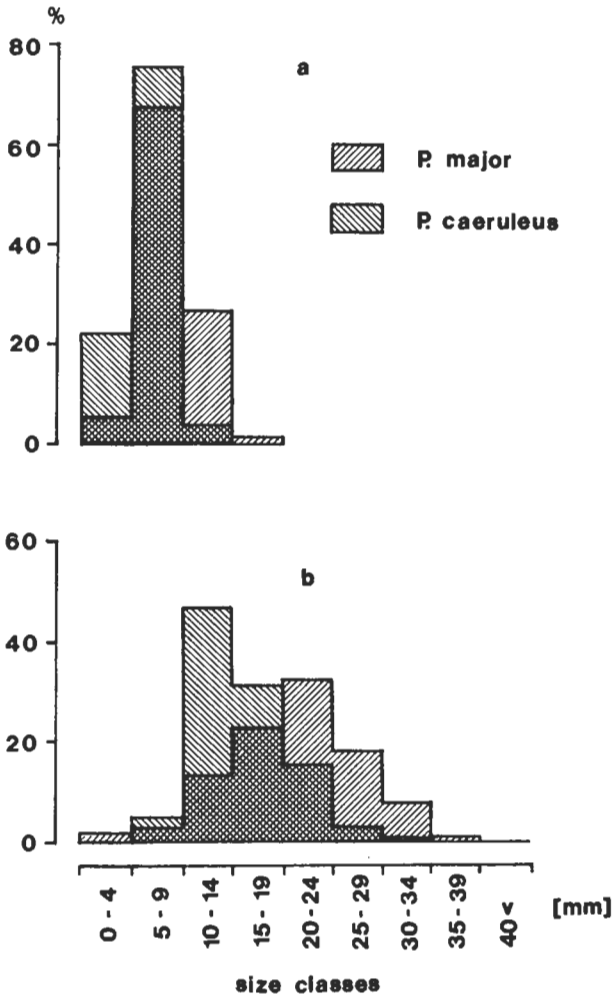


Fig. 1. Size distribution of spiders (a) and caterpillars (b)

Especially *Tipula* species (mainly females carrying eggs and therefore moving slowly) were consumed in large amounts in certain periods. The other food groups (see Appendix 1 and 2) were found only in small quantities and in certain years, in case of both bird species. In numerous food samples snail shells and grit occurred as grinding material.

Table 1. Niche breadth of the great- (*Pm*) and blue (*Pc*) tit (B^* -samples of the three years are pooled; + sample size)

	1978		1979		1980		B^*	
	<i>Pm</i> (15)+	<i>Pc</i> (32)	<i>Pm</i> (578)	<i>Pc</i> (42)	<i>Pm</i> (334)	<i>Pc</i> (119)	<i>Pm</i> (927)	<i>Pc</i> (193)
Prey taxon	3.52	4.95	6.05	2.87	4.84	3.97	5.90	5.68
Prey size								
spider	1.80	1.47	2.23	1.20	1.53	1.71	1.90	1.63
caterpillar	2.08	2.86	4.66	3.93	4.62	2.31	4.77	2.98
total prey	3.81	3.41	7.37	4.67	5.55	3.91	5.52	4.29

Table 2. Niche overlap of the great- and blue tit (C_{hj}^* -samples of the three years are pooled)

	1978	1979	1980	C_{hj}^*
Prey taxon	0.38	0.61	0.70	0.59
Prey size				
spider	0.53	0.69	0.71	0.75
caterpillar	0.55	0.88	0.42	0.57
total prey	0.83	0.69	0.60	0.72

The total niche breadth values (B^*) were similar but sharp yearly differences were obtained between the two species (Tab. 1). Neither breadths nor similarity indices were evaluated in the case of 1978 data because of the low sample size. Food composition niche breadth values of the great tit were higher than those of the blue tit in both 1979 and 1980.

The analysis of measurements performed in the two dominant food groups, in caterpillars and spiders, led to the following results (Fig. 1). In its majority, the great tit consumed the caterpillars of 20–24 mm, the blue tit the ones of 10–14 mm. In the case of spiders, specimens of 5–9 mm size dominated the food of both bird species.

Niche breadth calculated from the size distribution of the caterpillars and the total prey amount was greater in case of *P. major* than of *P. caeruleus* in both years (Tab. 1). Food composition niche overlap was lower than the value obtained on the basis of prey size. Size distribution of spiders (C_{hj}^*) in the food of the two tit species was more similar than that of the caterpillars (Tab. 2, Fig. 1).

In the breeding period the most important foraging site of both tit species was the tree foliage (Fig. 2). From this prey habitat type the blue tit's food proportion was higher than the one of the great tit. On the other hand, with the quantity of food picked up from the soil and from the grass, the great tit surpassed the blue tit.

In the development of the nestlings the stages presented in Fig. 3 were distinguished. The greater part of the food of the 1–3 days old great tit nestlings was caterpillars (29,8%), Diptera (25,5%) and spiders (24,0%). The proportion

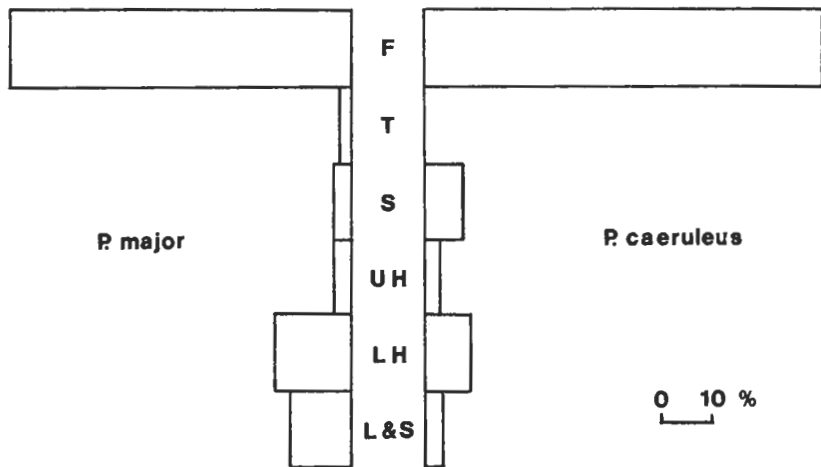


Fig. 2. Foraging sites of the great- and blue tit (L & S – leaf litter and soil, LH – lower herb, UH – upper herb, S – shrub, T – trunk, F – foliage)

of caterpillars gradually increased during development, and reached 83,7% by the time of leaving the nest. The proportion of spiders decreased to 8,3% from the initial 24,0% while that Diptera fell from 25,5% to 1,1%. The other animals groups (Lepidoptera adults and pupae, Coleoptera, Hymenoptera, Homoptera, etc.) were found only a small quantities. Among grinding materials insignificant proportions of grit and snail shells occurred in each stage of development.

The food composition of the blue tit nestlings showed similar trends (Fig. 3). By the time of leaving the nest, the proportion of the caterpillars increased to 90,1% from the initial 54,7%. In every stage of development – except the third one – the nestlings of the blue tit consumed more caterpillars than those of the great tit. Similarly, the proportion of the spiders was high (23,6%) in the early stage of development, later it decreased (9,9%). Diptera were found in blue tit nestlings in the first three stages of development, however then their proportion was not significant. The other animal groups and the grinding material occurred irregularly.

The analysis of the monthly changes in food composition was carried out in 1979 and 1980 only for the great tit (Appendix 2). The diet of the nestlings showed the widest variety in May. Species of 28 and 12 food groups were found in the food samples in 1979 and 1980, respectively. In June the food consisted of species of 20 and 10 groups, respectively, and in July 1980 species of only 9

groups. The proportion of Lepidoptera larvae was high in all the three months the highest value was obtained in July. Out of the caterpillars, the proportion of Noctuidae gradually increased in the breeding period, on the other hand the one of Geometridae decreased. Lepidoptera adults were present in the food of the nestlings mainly in May, and their pupae in all three months. *Tipula* species (Diptera) were found only in May samples but their proportion was high in this month. The proportion of other groups of Diptera was low both in May and in June; by July they vanished from the diet entirely. The frequency of the spiders was even during the whole breeding period, although their species composition varied in the different months. Thus e.g. *Alopecosa* spp. were present only in May food samples, *Philodromus aureolus* only in June and *Xysticus lanio* in all three months.

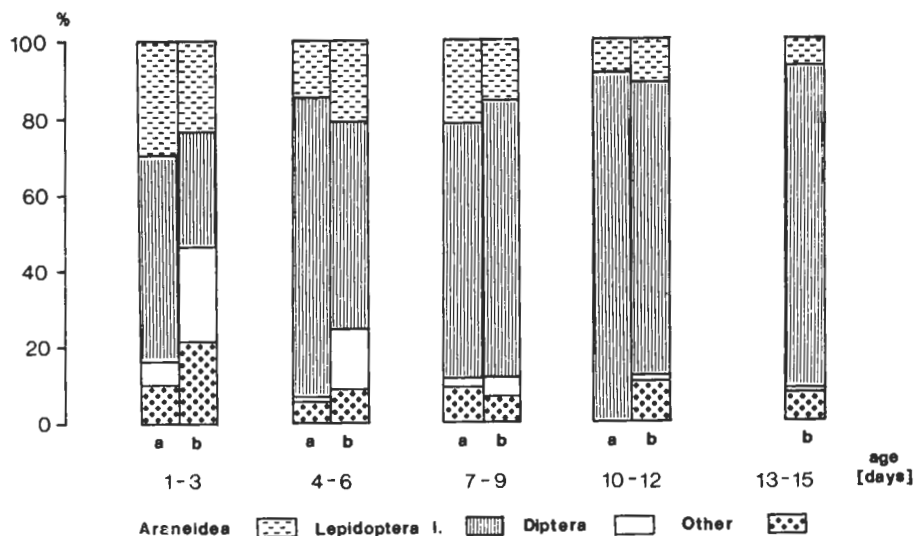


Fig. 3. Food composition of the nestlings of great- (a) and blue tit (b) in five developmental stages

Discussion

According to feeding studies conducted in various habitats, the most important food of the great- and blue tit was the Lepidoptera larva (BETTS, 1955; GIBB, 1954; GIBB & BETTS, 1963; ROYAMA, 1970; TINBERGEN, 1960). My own results also show that in a mixed oak forest both species mainly consume caterpillars. The proportion of caterpillars increased with the advance of the breeding period and with the progress of the nestlings' development even if there is a second brood. The species richness of caterpillar food of the great tit was higher than the one of the blue tit. ROYAMA (1970) found similar proportion and species composition of Lepidoptera larvae in the food of the great tit in a mixed oak forest. In pure oak forests and in pine forests, the caterpillar diet of the tits is much less rich in species, generally it is composed of only a few superabundant species (e.g. *Operophtera brumata* and *Tortrix viridana* in oak forests and *Panolis flammea* in pine forests — BETTS, 1955; GIBB & BETTS, 1963; BALEN, 1973).

The blue tit consumed the greatest amount of caterpillars of 10–14 mm, the great tit those of 20–24 mm in length. Other studies (BETTS, 1966; GIBB & BETTS, 1963; BALEN, 1973) reported preference of smaller animals in the diet of both species. The difference is caused presumably by the fact that these authors conducted their examinations in pure stands, where the above mentioned caterpillars (all are of small size) were characteristic.

Due to their low chitin content and easy digestibility, the spiders are important in the earlier stage of the nestling development (BETTS, 1955; ROYAMA, 1970), yet they can continuously be found in the diet even later. In the diet of the great tit ROYAMA (1970) found a smaller proportion of spiders in an oak forest, TINBERGEN (1960) a higher in a pine forest than did the present study. The size of the spiders in the diet of the two tit species was very similar.

The other animal groups were present in the food samples temporarily, probably according to the changes in their abundance in the environment.

The results show that the great tit, because of its higher niche breadth values, is less specialised in terms of feeding than the blue tit. This is probably one of the reasons why the great tit settles more often in less advantageous habitats.

Referring to the examinations of GIBB (1954) and BETTS (1955), DHONDT (1977) supposes that in the breeding period the diet niche of the blue tit is wider than the one of the great tit. According to his explanation, the blue tit can search for food on both the thinner and thicker branches while the great tit only on the thicker ones. On the other hand, 41% of the blue tit's food cannot be found in the food of the great tit while only 7% of the great tit's food is not contained in the food of the blue tit. In the present study these values are 29% and 60%, respectively, which also seems to prove a wider diet spectrum of the great tit.

Foraging sites as well as prey size distribution of the two species showed high overlap. Comparing the size distribution of only the caterpillars and the spiders, the overlap is smaller in the latter group. Therefore prey taxon seems to be the most important factor in the food segregation of the great tit and blue tit.

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REFERENCES

1. BALEN, J. H. van (1973): Comparative study of the breeding ecology of the great tit (*Parus major*) in different habitats. — *Ardea*, 61: 1–93.
2. BETTS, M. M. (1955): The food of titmice in oak woodland. — *J. Anim. Ecol.*, 24: 282–323.
3. DHONDT, A. (1977): Interspecific competition between great and blue tit. — *Nature*, 268: 521–523.
4. GIBB, J. (1964): Feeding ecology of tits, with notes on treecreeper and goldcrest. — *Ibis*, 96: 513–542.

5. GIBB, J. & BETTS, M. M. (1963): Food and food supply of nestling tits (Paridae) in Breckland pine. — *J. Anim. Ecol.*, 32: 489–533.
6. HARTLEY, P. H. T. (1953): An ecological study of the feeding habits of the English titmice. — *J. Anim. Ecol.*, 22: 261–288.
7. KLUYVER, H. N. (1950): Daily routines of the great tit, *Parus m. major* L. — *Ardea*, 38: 99–135.
8. KLUYVER, H. N. (1951): The population ecology of the great tit, *Parus m. major* L. — *Ardea*, 39: 1–135.
9. KREBS, J. R. (1971): Territory and breeding density in the great tit, *Parus major* L. — *Ecology*, 52: 2–22.
10. KREBS, J. R., ERICHSEN, J. T., WEBBER, M. J. & CHARNOV, E. L. (1977): Optimal prey selection in the great tit (*Parus major*). — *Anim. Behav.*, 25: 30–38.
11. LACK, D. (1958): A quantitative breeding study of British tits. — *Ardea*, 46: 91–124.
12. LEVINS, R. (1968): *Evolution in changing environments*. — Princeton University Press, Princeton, New Jersey, 120 pp.
13. RENKONEN, O. (1938): Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. — *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo*, 6: 1–231.
14. ROYAMA, T. (1970): Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). — *J. Anim. Ecol.*, 39: 619–668.
15. SIMPSON, E. H. (1949): Measurement of diversity. — *Nature*, 163: 688.
16. TINBERGEN, T. (1960): The natural control of insects in pinewood. I. Factors influencing the intensity of predation by songbirds. — *Archs. Néerj. Zool.*, 13: 265–343.

Appendix 1. Food composition of the blue tit nestlings (percentage values given in dry weight)

Taxa	1978		1979		1980		Total (three years)		
	n	%	n	%	n	%	^g dry wt	n	%
Heteroptera									
Miridae larva indet.					17	0.84	0.0105	17	0.31
Coleoptera									
Cerambycidae									
<i>Cortodera humeralis</i>	1	0.31			4	1.52	0.0300	5	0.72
Chrysomelidae									
<i>Pyrrholla viburni</i>					1	0.59	0.0089	1	0.22
Melolonthidae									
<i>Miltotrogus aequinoctialis</i>	3	0.67					0.0150	3	0.36
Coleoptera indet.	3	1.33					0.0294	3	0.71
Lepidoptera									
Tortricidae indet.					2	1.32	0.0200	2	0.48
Lepidoptera larvae									
Tortricidae									
<i>Tortrix viridana</i>	16	22.64					0.4600	16	13.08
Tortricidae indet.	2				3	2.64	0.0830	5	

Appendix 1 (Cont.)

Taxa	1978		1979		1980		Total (three years)		
	n	%	n	%	n	%	g dry wt	n	%
Noctuidae									
<i>Orthosia stabilis</i>			1		8		0.1006	9	
<i>Orthosia schmidtii</i>			17	52.61	5	14.58	0.0550	5	15.80
<i>Orthosia</i> spp.	1	9.99	17		4		0.2567	22	
Noctuidae indet.	7		1				0.1990	8	
Geometridae									
<i>Colotois pennaria</i>			2		31		0.3977	33	
<i>Operophtera brumata</i>					16		0.1025	16	
<i>Erannis defoliaria</i>	2	25.69		22.57	11	42.73	0.0350	2	31.52
<i>Erannis</i> spp.	1				1		0.1670	12	
<i>Boarmia</i> sp.					1		0.0270	1	
Geometridae indet.	18		4		5		0.5898	27	
Tettheidae indet.	1	0.16					0.0035	1	0.09
Lepidoptera larva indet.	13	26.67	1	0.73			0.5996	14	14.44
Diptera									
Limoniidae indet.	1	0.27					0.0060	1	0.18
Bibionidae indet.	1	0.09			1	0.59	0.0110	2	0.27
Tachinidae indet.					2	1.32	0.0200	2	0.45
Diptera indet.	1	0.27			1	0.73	0.0170	2	0.40
Hymenoptera									
Tenthredinidae indet.	1	0.07					0.0015	1	0.04
Phalangiidea									
Phalangiidae									
<i>Zacheus crista</i>	1	2.70					0.0600	1	1.08
Araneidea									
Argiopidae									
<i>Araneus strumii</i>					2		0.0085	2	
<i>Araneus cucurbitinus</i>			1		11		0.0605	12	
<i>Araneus angulatus</i>				2.47	3	5.87	0.0120	3	2.92
<i>Araneus gibbosus</i>	2	1.01					0.0113	2	
<i>Araneus triguttatus</i>	1						0.0111	1	
<i>Zillodia</i> sp.					1		0.0090	1	
Thomisidae									
<i>Xysticus lanio</i>	1		3		12		0.2208	16	
<i>Xysticus ulmi</i>	1						0.0650	1	
<i>Xysticus</i> spp.					2	20.16	0.0460	2	10.83
<i>Philodromus aureolus</i>	2	4.09	2	13.10	4		0.0646	8	
<i>Misumena vatia</i>			2				0.0172	2	
<i>Misumenops tricuspoidatus</i>					5		0.0360	5	
Linyphiidae									
<i>Linyphia</i> sp.	1	2.03					0.0450	1	1.08

Appendix 1. (Cont.)

Taxa	1978		1979		1980		Total (three years)		
	n	%	n	%	n	%	^g dry wt	n	%
Clubionidae									
<i>Clubiona coerulescens</i>					2	} 3.20	0.0030	2	} 1.16
<i>Clubiona</i> spp.					2		0.0215	2	
<i>Chiracanthium</i> sp.					1		0.0090	1	
Salticidae									
<i>Carrhotus bicolor</i>			1	1.06			0.0043	1	0.10
Araneidea cocon indet.	1	1.62	2	4.49			0.0542	3	1.31
Others (plant debris, grit, snail shell, indet.)		0.27		1.97		3.91	0.0733		1.76
Total	82		37		162		4.0680	281	

