

The predator-prey size hypothesis in three assemblages of forest birds

János Török

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

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Abstract. I investigated morphological pattern and prey-size preference of three bird assemblages (14 species altogether) in a Hungarian oak forest, during the breeding seasons of 1979–1986. To assess the occurrence of competition for food among forest birds I performed a 5-year removal experiment with two hole-nesting passerines, the great tit and the blue tit. Prey preference of both species was affected by the presence of the other species. The results of both the removal experiment and the estimation of available food supply indicated food limitation, at least for foliage-gleaning birds. However, I found neither a regular size ratio among species nor a strong relationship between predator size and prey size. Other phenomena such as foraging strategies may affect prey-size preference. Therefore, a competition model including only morphological ratios and predator-prey size relationships is too simplified.

Key words: Predator-prey size – Competition – Size ratio – Forest birds

One of the major hypotheses about structuring rules in ecological communities, the competition hypothesis, states that the close packing of predators based on their sizes along the prey-size spectrum is an important character of competition-determined communities. This relationship involves two components. One, the theory of limiting similarity, states that the ratios of larger to smaller predator species along a morphological size spectrum are “constants” (also termed Hutchinson’s rule; Hutchinson 1959). The other states that there is a pattern of ecological displacement along a resource spectrum (i.e. larger predators consume larger prey items (Schoener 1965; Schoener and Gorman 1968; Fenchel 1975; Hespenheide 1975). In the absence of these patterns, Wiens and his co-workers (Wiens 1974, 1983; Wiens and Rotenberry 1980, 1981, 1987) concluded that environmental stress is the main factor that determines the structure of

communities, at least in shrub-steppe birds during the breeding season, while not denying that competition may be important in “crunch” seasons and years or in stable environments. Based on the analyses of diet, morphology and other characteristics, Wiens and his colleagues suggested an “ecological-crunch” model for their grassland breeding bird communities.

Results of other studies (Dhondt 1977; Dhondt and Eyckerman 1980a, b; Minot 1981; Alatalo et al. 1985; Gustafsson 1987, 1988; Sasvári et al. 1987; Török 1986, 1987) conducted on forest passerine birds clearly demonstrated the importance of competition (for different resources) in woodland habitats. However, Noon et al. (1985) found no association between avifaunas and habitat types across North America, suggesting that habitat type alone could not explain the importance of competition (i.e. in a more complex habitat, like a forest, the biotic interactions may dominate over the physical-chemical environmental effects).

In this paper, I address the question of whether there are predator-prey size relationships in forest-bird assemblages (foliage-gleaning, bark-foraging and ground-foraging birds) during the breeding period and investigate the constancy of size divergence among species. I then demonstrate experimentally that competition for food may operate even in the absence of the predator-prey size relationships, in at least one of the three assemblages.

Methods

During the breeding seasons of 1979–1986 I collected samples of food consumed by 6 to 10-day-old nestlings of 14 dominant bird species in an oak forest near Budapest, Hungary by a modified neck-collar method (Török 1986). The species belonged to three assemblages of birds differentiated by foraging microhabitats (Table 1). The collared flycatcher (*Ficedula albicollis*) was classified with foliage-gleaning birds because caterpillars, spiders and hemipterans mainly collected from the foliage pre-

Table 1. The means in four morphological characters, and the mean prey sizes of bird species in three oak forest assemblages

	Bill length	Bill width	Tarsus length	Body mass	n	Mean prey size	
						AP	CA
Foliage-gleaning							
<i>Ficedula albicollis</i>	13.16	4.02	17.45	15.28	26	9.4 (378)	15.5 (98)
<i>Parus maior</i>	12.36	4.33	19.99	20.20	48	17.7 (486)	20.1 (86)
<i>P. caeruleus</i>	9.74	3.96	16.62	13.14	40	11.9 (389)	14.8 (257)
<i>P. palustris</i>	10.13	4.08	16.38	11.20	16	15.8 (102)	20.8 (66)
<i>Aegialos caudatus</i>	7.90	2.90	17.40	7.95	4	8.1 (306)	17.8 (53)
Bark-foraging							
<i>Dendrocopos maior</i>	29.58	8.66	24.07	83.34	22	5.4 (6305)	14.1 (777)
<i>D. medius</i>	25.17	6.14	21.01	60.08	10	9.2 (2955)	13.5 (1437)
<i>D. minor</i>	15.83	5.03	14.80	22.20	4	8.5 (1436)	14.4 (522)
<i>Sitta europaea</i>	20.20	4.47	20.55	24.19	51	10.7 (3692)	15.2 (1018)
<i>Certhia familiaris</i>	15.42	2.05	15.38	8.90	16	4.0 (997)	9.8 (92)
Ground-foraging							
<i>Garrulus glandarius</i>	32.42	8.02	39.12	161.52	6	18.6 (255)	19.4 (150)
<i>Sturnus vulgaris</i>	28.80	7.11	29.40	82.18	12	13.0 (249)	17.9 (47)
<i>Turdus merula</i>	25.98	5.82	32.47	89.64	34	13.0 (1821)	15.3 (619)
<i>T. philomelos</i>	20.70	5.54	29.21	74.00	8	15.0 (199)	16.4 (94)

Bill and tarsus measurements are in mm, body mass in g. Data of 5 years are combined

Explanations n: no. of measured specimens; AP: all prey; CA: caterpillars; the numbers of prey are in parentheses

dominated in its diet in the parental care period (Török 1986). The jay (*Garrulus glandarius*) was grouped with the ground-foraging birds because, although it forages on bushes and in the foliage, the prey collected from the ground formed a large proportion of its diet (J. Török, unpublished data). The sampling results were pooled for each species for every year. The body mass, bill length, bill width and tarsus length of adult birds were recorded. Measurements were made in both sampled and non-sampled nests. As caterpillars were the most important prey type for most bird species, I analysed the correlation between caterpillar size and the morphological characters separately from that between total prey size and morphology. I did not log-transform the data in the correlation analysis, as Spearman's method, which uses ranks, does not require it.

A removal experiment was carried out at a separate location, in an oak forest habitat 20 km east of the study plot. Here, allopatric and sympatric populations of great tit (*Parus maior*) and blue tit (*P. caeruleus*) were experimentally created by excluding one of the two species from nest-holes during the breeding period. A detailed description of the experiment is given in Török (1987).

Size distribution of caterpillars available in the environment was estimated by beating trees surrounding the nests. Samples from the nestlings and the environment were taken within 10 days to reduce the effect of temporal changes in the environment. Food supply of bark-foraging birds was monitored using funnel traps placed around the tree trunk (Török 1990).

Results and discussion

There was no relationship between predator size and preferred prey size in the three assemblages of forest birds during the breeding season (Table 2). Only one morphological feature, tarsus length, correlated slightly but significantly with preferred prey size when 14 species were pooled in one group. All ratios calculated in this study for linear size measurements (bill length, bill width and tarsus length; Table 3) were less than 1.3, which is the average value of the ratios calculated by Hutchinson (Hutchinson 1959; Roth 1981; Wiens and Rotenberry 1981).

The ratios of body mass between adjacent-sized spe-

Table 2. Spearman's rank correlations between morphological characters and prey sizes

Character	Foliage-gleaning		Bark-foraging		Ground-foraging		Community	
	AP	CA	AP	CA	AP	CA	AP	CA
Bill length	0.00	0.10	0.30	0.20	0.20	0.80	0.13	-0.15
Bill width	0.70	0.60	0.10	0.10	0.20	0.80	0.13	-0.15
Tarsus length	0.00	-0.10	0.10	-0.10	0.40	0.40	0.46*	0.24
Body mass	0.30	-0.10	0.30	0.20	0.40	0.60	0.36	0.02
	(5)		(5)		(4)		(14)	

Number of bird species is in parentheses

Explanations: AP: all prey; CA: caterpillars

* $P < 0.05$

Table 3. The average ratios of four morphological characters of adjacent species (larger to smaller) in three bird assemblages, in an oak forest near Budapest

	Bill length	Bill width	Tarsus length	Body mass
Foliage-gleaning	1.14 (0.10,4)	1.11 (0.17,4)	1.05 (0.07,4)	1.27 (0.12,4)
Bark-foraging	1.18 (0.11,4)	1.48 (0.48,4)	1.14 (0.14,4)	1.86 (0.73,4)
Ground-foraging	1.16 (0.08,3)	1.14 (0.09,3)	1.11 (0.10,3)	1.34 (0.41,3)
Community	1.16 (0.09,13)	1.25 (0.34,13)	1.10 (0.10,13)	1.50 (0.53,13)

Standard deviation and the number of paired comparisons are in parentheses (SD, n)

cies varied from 1.09 to 2.49 ($\bar{x} = 1.50$), which differed substantially from the expected ratio of 2.1 (Whittaker 1975). It should be noted that I used only the 14 most common species in the calculations. If all species were taken into consideration, the average size ratios would probably change toward smaller values in foliage-gleaning and ground-foraging birds, as most birds excluded from the calculations fall within the size range of the species used for calculations. The ratios between the members of bark-foraging assemblage would not change as only one other species, the black woodpecker (*Dryocopus martius*) foraged, rarely, at the study plot. This species is much larger than the largest species of the assemblage, the great spotted woodpecker (*Dendrocopos maior*), and there is a large gap between black and great spotted woodpeckers (Oksanen et al. 1979).

The absence of both a constant size ratio among species and a close relationship between morphology and diet raise the question of whether the breeding season is the limiting one for these birds. Perhaps food is "superabundant" and interspecific competition for food does not play an important role in determining the structure of these assemblages during the breeding season. This concept is widely accepted by the British researchers (see citations in Dhondt 1977). Winter food scarcity could be more important than summer food limitation, and therefore more important as an evolutionary force in determining species morphology. The predator-prey size relationship may only exist in the winter, as Williams and Batzli (1979) found for bark-foraging birds in Central Illinois. Authors discussing this point agree that com-

petition may be important in the nonbreeding periods of the year (Smith et al. 1978; Dhondt and Eyckerman 1980a; Schoener 1982; Dunning 1986; Wiens and Rotenberry 1987), but few have demonstrated it. We need data on the prey-size preference of these woodland bird species in the winter period to test this idea.

Food superabundance is quite credible in the breeding season, but there are no appropriate methods to determine the total available food in a habitat as complex as a forest. This is possible, however, in some selected microhabitats. I gathered information on caterpillar supply available in the foliage during the breeding season (Török 1986, 1987; Török and Tóth 1988). The quantify of caterpillar frass, assumed to be proportional to the biomass of caterpillars (van Balen 1973), was between 0.031 and 0.219 g per 0.25 m² per day on average in the peak period, throughout the study years. Outside the peak period this value falls to a tenth or a hundredth of the peak value. Camouflage, degree of hairiness, activity, size distribution and the rate of parasitism and predation by organisms other than bird predators further decrease the quantity of food available for birds. It is difficult to decide whether the quantify of caterpillars in the peak period is or is not enough for birds, but it is possible that caterpillars are in short supply for birds foraging in the foliage before and after the peak period (Dhondt 1977; Minot 1981; Török 1986, 1987). Nevertheless, some forms of competition may exist even in the peak period when resources are abundant, if the resources are concentrated (the distribution is clumped) or unpredictable (Maurer 1984). It is likely that tits' food in the breeding season is concentrated (Tinbergen 1960).

I collected moving invertebrates from the bark surface (Török 1990), representing the available food supply for bark-foraging birds. The bark of trees is an unproductive microhabitat (Kuitunen and Törmälä 1983; Török 1990), and it is unlikely that food is superabundant for birds that primarily forage on the trunks of trees. This is supported by the fact that the bark-foraging birds usually have large territories and usually extend their foraging to the foliage as well. Moreover, they sometimes switch their foraging methods (Jenni 1983) and eat everything they can find on the bark, showing highly opportunistic foraging in the breeding season.

The likelihood of food limitation can be demonstrated by the result of removal experiments if the presence or absence of a species affects the prey-size preference of a competing species. I performed this experiment with the great tit and blue tit, which are abundant hole-nesters in

Table 4. The mean caterpillar size (mm) taken to the nestlings of the great tit and the blue tit in experimentally created allopatric and sympatric populations and the differences (mm) between the average prey size in the nestling diet and the supply for 4 years

	Mean prey size		Differences from the supply	
	Allopatric	Sympatric	Allopatric	Sympatric
Blue tit				
1984	18.3 (19.36)	15.8 (10.50)	+2.1	+0.8
1985	17.3 (11.11)	17.9 (24.78)	+2.5	+1.2
1986	19.9 (11.77)	19.4 (8.70)	+0.6	+0.8
1987	18.1 (41.60)	16.7 (24.60)	+3.3	+1.6
Great tit				
1984*	-	19.9 (21.90)	-	+4.9
1985	21.9 (30.92)	20.2 (3.99)	+4.1	+3.5
1986	25.3 (15.68)	22.7 (14.59)	+4.5	+4.1
1987	26.8 (12.25)	20.5 (13.73)	+12.4	+5.4

Coefficients of variation in parentheses

* Data are absent because of the low number of great tits that bred in that year

European oak forests and belong to the foliage-gleaning assemblage. It was clear that, when allopatric, both species ate larger caterpillars on average, with larger coefficients of variation than when sympatric (except one case; Table 4). Species released from the effect of the other species foraged for larger prey and extended their prey size resource spectrum as well. Although the vegetation structure of "sympatric" and "allopatric" plots was similar, the difference in the prey size distribution of the supply might have caused a complication. Therefore, I compared not only the mean size of the prey, but also the mean prey size in the supply and in the prey utilized, in the two plot types. The average prey size taken by birds is closer to the average of the available supply in sympatric populations than in allopatric ones (except one case, Table 4). This shows that birds utilize the smaller but more numerous prey to a greater extent when the more profitable, larger prey are less available. This shift toward smaller prey size caused reduced nestling weight of great tits when sympatric with blue tits (Török 1987). These results indicate that caterpillars are limiting for these birds in the breeding season or at least during the parental care period. Reduced breeding success of the most numerous foliage-gleaning birds (tits and flycatchers) in sympatric populations is also supported by the results of Dhondt (1977), Minot (1981), Gustafsson (1987), Sasvári et al. (1987) and Török (1987).

Other hypotheses can also explain the absence of the morphological size patterns. For example, the "ecological-crunch" model originated by Wiens and others (see citations in Dunning 1986) emphasizes the importance of stochastic environmental (e.g. climatic) effects in the structuring of some bird communities. This idea does not

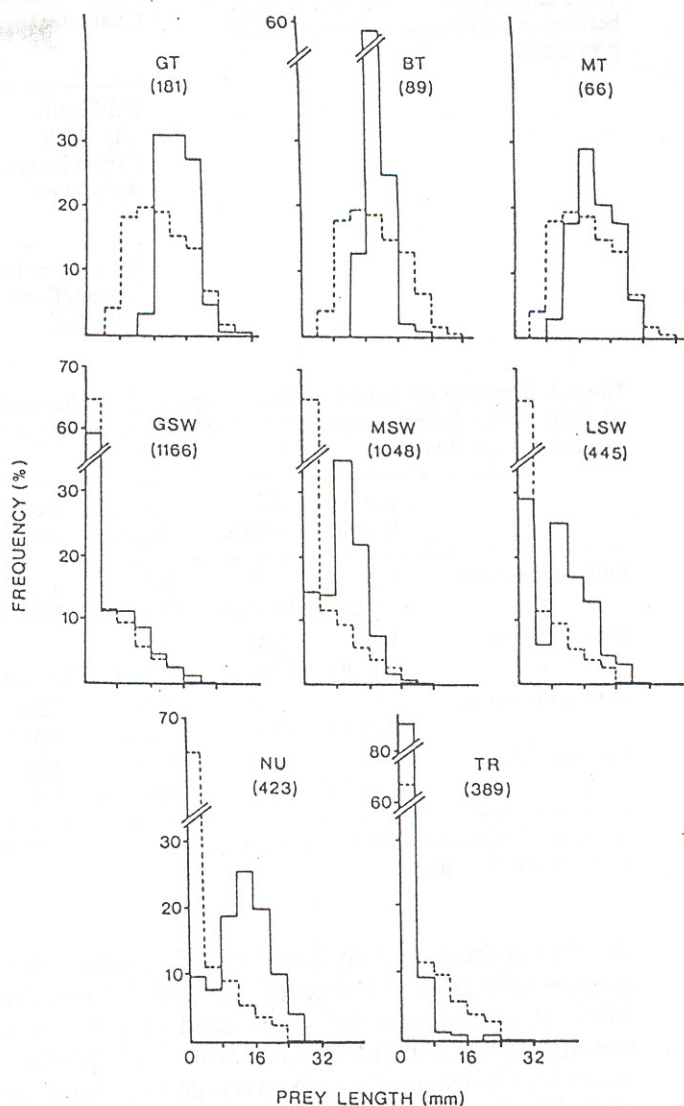


Fig. 1. The size distribution of prey of eight bird species (solid line) belonging to two forest assemblages, and that of the available food supply (broken line) during two years. The supply is represented by caterpillars (935 specimens in total) for foliage-gleaning birds (great tit, *GT*; blue tit, *BT*; marsh tit, *MT*) in 1986 and all prey moving on bark (982 specimens in total) collected with funnel traps in May of 1984 for bark-foraging birds (great spotted woodpecker, *GSW*; middle spotted woodpecker, *MSW*; lesser spotted woodpecker, *LSW*; nuthatch, *NU*; treecreeper, *TR*). Total numbers of prey items gathered by birds are in parentheses

require the existence of morphological size patterns in the communities. But woodland habitats are deterministic rather than stochastic. To test this model we should gather precise data on how resources vary in time and how birds response to these variations in both breeding and nonbreeding periods, but it is almost impossible in woodland habitats.

It is likely that central place foraging (Orlans and Pearson 1979) can affect the relationship between morphology of a species and its preferred prey size. This theory predicts that predators forage for larger prey when feeding their nestlings because of the travelling cost. Birds usually eat larger prey than characteristic of the available supply during the parental care period (Fig. 1). Different nestling demands (depending on the

number of nestlings and their growth rates) may lead to different prey-size preferences in bird species. Moreover, differences in territory size would change preferred prey sizes because the round-trip length would be different. This might cause the predator-prey size relationship to be eroded during this period.

The role of foraging modes may also be an important determinant of morphological size patterns of bird species inhabiting complex habitats like forests. For example, in the bark-foraging assemblage the bill, wing and tarsus morphology and the body mass of species are affected by different foraging modes. Treecreepers utilize the trunks, climbing from the lower to the upper parts of trees and moving in a zigzag path or spirally, and quite quickly. They pick the prey from the surface with their long, curved, thin bill. This foraging mode could shape the bill morphology of this species. In this example, I focus on the importance of foraging behaviour, but more attention should be devoted toward testing the hypothesis of predator size displacement due to different foraging techniques in complex habitats.

Summing up, even though some forms of competition probably exist in the breeding season (Dhondt 1977; Minot 1981; Gustafsson 1987; Sasvári et al. 1987; Török 1987; this study), there is no apparent size-structure in these three forest bird assemblages. This study strengthens the view that the connection between a size-structured community and competition is too complex to be described by a simple model including only morphological ratios and predator-prey size relationships.

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