

Comparative Ecological Studies on Blackbird (*Turdus merula*) and Song Thrush (*T. philomelos*) Populations. I. Nutritional Ecology

By

J. TÖRÖK*

Abstract. The food of nestlings of blackbirds and song thrushes was studied over a period of five years in various habitats. Food samples were obtained by placing neck-collars on the nestlings. Blackbirds consumed mainly lepidopterous larvae, dipterans and coleopterans. Besides great quantities of lepidopteran larvae and dipterans, song thrushes fed on more annelids and less beetles than the blackbirds. The blackbird proved to be a more generalist and mobile species than the song thrush. These properties have enabled the blackbird to easily penetrate into urbanized areas. Of the two studied niche dimensions (food composition and prey size) of the sympatric populations, there was greater degree of segregation between the species in food composition.

Introduction

The blackbird and the song thrush are the two most common species of the genus *Turdus* in Hungary. In Europe the blackbird is distributed mainly in the south-eastern parts. The range of the song thrush considerably overlaps with that of the previous species but penetrates much further north, and is absent from some parts of southern Europe (DYRCZ, 1969; NILSSON, 1979).

Besides similar geographical distribution, similar habitat preference is characteristic for the two species, though the blackbird is more common in certain habitats (reedbeds, orchards) than its congener. The penetration of the blackbird into urban habitats modified by man (synurbanization) was a clearly definable and rapid process (KROLL, 1975). In some parts of Europe the song thrush has also moved into towns, but the blackbird has been able to maintain its numerical predominance even in these habitats (SNOW, 1958).

In the breeding season both species feed in a clearly definable microhabitat, on the surface of the soil, and their prey searching tactics are similar (SMITH, 1973; TYE, 1981).

There are few comparative studies on the food composition of blackbirds and song thrushes (EBLE, 1963; DYRCZ, 1969), therefore the primary objective

* Dr. János Török, ELTE Állattrendszertani és Ökológiai Tanszék (Department of Systematic Zoology and Ecology of the Eötvös Loránd University), 1088 Budapest, Puskin-u. 3.

of the present work was to study the food segregation in sympatric populations of the two congeneric species. Detailed knowledge of the food resource utilization of the blackbird and the song thrush may help us understand the different adaptivities of the two species, and may provide further data to the phenomenon of resource segregation that has recently been widely studied in closely related species (CODY, 1974; DYRCZ, 1969; HARTLEY, 1953; JENNI, 1983; LACK, 1945, 1971; MacARTHUR, 1958).

Study areas

No. 1 (12 ha): A dry Turkey-oak woodland (*Quercetum petraeae cerris*) in the vicinity of Budapest, with dense shrub vegetation at the edges (*Ligustrum vulgare*, *Sambucus nigra*, *Cornus mas*, *Crataegus* sp. and *Rosa* spp.).

No. 2 (12 ha): An orchard contiguous with study area No. 1. bordered by a Turkey-oakwood in the north and north-east, by cultivated land in the south (wheat) and by a meadow in the west. The composition of the orchard is as follows: winter apple (4.5 ha), peach (2 ha), apricot (1.5 ha), pear (1.3 ha), plum (1.3 ha), cherry (0.7 ha) and sour cherry (0.7 ha).

No. 3 (4 ha): An old hornbeam-oakwood mixed with beech in a hilly suburb of Budapest (Normafa), with young oak saplings in the undergrowth.

No. 4 (4 ha): A Turkey-oak woodland with dense edge vegetation in the outskirts of Törökbalint. There is an extensive peach plantation under large-scale mechanized farming adjacent to the wood. The nests were located in the 200 m wide strip of the oakwood.

No. 5 (9 ha): A recreational park in the centre of Budapest. The varied vegetation is patchily distributed. *Quercus* spp., *Acer* spp., *Juniperus* spp., *Thuja plicata*, *Taxus baccata* and *Forsythia europaea* may be found in larger numbers.

No. 6 (2 ha): A resort area in the outskirts of Esztergom with varied cultivated vegetation, small plots with vegetable gardens and fruit orchards, with rows of bushes (*Ligustrum vulgare*, *Sambucus nigra*, *Rosa* spp.) and trees (*Robinia pseudoacacia*, *Juglans regia*, *Acer campestre*, *Aesculus hippocastanum*) along the roads and inbetween the plots. The nests were located in the rows of bushes along the road.

Study periods and methods

The study was carried out between 1978 and 1982. I collected food samples by placking neck-collars on the the nestlings throughout the five years in study area No. 1, in 1979, 1980 and 1982 in study area No. 2 and in 1980 in study areas Nos 3, 4, 5 and 6. A detailed description of the method is found in TÖRÖK (1981). The collected prey animals were measured to mm accuracy and preserved in isopropyl alcohol until identification. I separated 9 size intervals (each 5 mm) for the calculations. If only one individual could be ascertained in the sample, the length of earthworms was calculated as the total length of the pieces found in the sample. If several head or tail parts were found in the sample, then the sizes of the animals could only be estimated as based on the diameters of the pieces.

Nestlings were weighed on every second day to 0.1 g accuracy. No food samples were taken from these nestlings.

Following TINBERGEN (1960) and BALEN (1973), I estimated the abundance and dynamics of the leaf-consuming lepidopterous larvae by collecting the excrements of the caterpillars. Thirty carton sheets each 0.25 m² in size were laid out in study area No. 1 to collect the excrements for 48 hrs at 10-days intervals. The excrements collected over the two days were weighed after cleaning and air-drying.

Niche metrics

I calculated food niche width from the SHANNON formula (SHANNON & WEAVER, 1949),

$$H = - \sum_{i=1}^s \frac{n_i}{N} \log_2 \frac{n_i}{N}.$$

Evenness was computed using the formula $J = \frac{H}{H_{\max}}$

where $H_{\max} = \log_2 s$ (PIELOU, 1969).

In the above formulae n_i is the number of prey items belonging to the i th prey or size category, N is the total number of prey specimens, and s is the number of prey categories.

The degree of niche overlap was calculated using RENKONEN's similarity formula (RENKONEN, 1938),

$$s_{1-2} = \sum_{i=1}^s \min(p_{1,i}, p_{2,i}),$$

where $p_{1,i}$ is the frequency of the i th prey or size category in sample 1 relative to the total number of prey items, $p_{2,i}$ is the same for sample 2.

During calculating food composition I considered the various semaphoront populations of most prey categories as separate entities because of their different habitats, feeding habits and mobilities. In the above calculations the term food category is usually equivalent to the taxonomical category of the family, but in certain cases when the prey could be identified only to the order, this taxon was considered a category.

Food composition

Based on 3833 collected prey items, it was found that the predominant food of the blackbird is lepidopterous larvae. Of the noctuids, *Orthosia* and *Agrochola* species, of the geometrids *Operophtera brumata*, *Colotois pennaria*, *Erannis* and *Boarmia* species occurred in considerable numbers. Although blackbirds feed on the surface of the soil, caterpillars living typically on herbs or in the soil were found only in low percentage in the food. The nestlings consumed approximately equal numbers of Diptera and Coleoptera. Among dipterans the most abundant were Tipulida and *Limonia* species which emerge in May. The order Coleoptera was primarily represented by members of the family Elateridae, Carabidae, Scarabaeidae and Silphidae. I often found among the food species like *Calosoma inquisitor* and *Dendroxena quadripunctata* which feed on carterpillars. Annelida, Hymenoptera, Heteroptera and Araneidae were found only in few numbers among the food samples collected from the blackbird nestlings. Among the annelids, species of the genera *Allolobophora* and *Lumbricus* were predominant. The species which inhabit the upper soil layers (*Lumbricus* spp., *Dendrobaena* spp.) outnumbered three to one those which live deeper in the soil (*Allolobophora* spp., *Octolasion* spp.). The same ratio was as high as four to one in the case of the song thrush. I found remains of any vertebrate species only on one occasion, the

Table 1. Food niche width (H) and evenness (J) of the blackbird and the song thrush (s - number of categories, N - number of prey items, 1-6 - study plots)

	1978		1979		1980						1981	1982
	1		1	2	1	2	3	4	5	6	1	2
<i>Turdus merula</i>												
prey taxon	H	4.64	4.10	3.53	4.53	4.82	4.15	4.07	1.85	1.69	3.29	3.16
	J	0.85	0.71	0.80	0.73	0.91	0.84	0.85	0.58	0.73		
prey size	s	44	56	21	77	40	31	28	9	5		
	N	247	770	67	768	121	104	98	53	15	1272	318
prey size	H	2.32	2.69		2.55	2.49	2.80	2.71	2.02	2.47	2.45	2.16
	J	0.77	0.85		0.80	0.83	0.88	0.85	0.64	0.88		
prey size	s	8	9		9	8	9	9	9	7		
	N	247	770	67	768	121	85	89	48	15		
<i>Turdus philomelos</i>												
prey taxon	H	3.51	3.03		3.49	3.42				3.10	2.32	3.15
	J	0.90	0.96		0.69	0.71				0.76		
prey taxon	s	15	9		34	28				17	167	91
	N	28	11		220	199				38		
prey size	H	2.15	2.18		2.23	2.68				2.79	2.31	1.88
	J	0.92	0.91		0.70	0.85				0.88		
prey size	s	5	5		9	9				9		
	N	20	11		220	199				32		

tail part of a young slow-worm. When feeding the young, the birds also consume plants as well (sour cherry), but the proportion of this food item is not significant.

In the urban environment artificial food (of human origin) were also found in the collected samples, but here the predominant prey categories were also earthworms and Diptera. In the samples from the oakwood in the outskirts of Budapest Lepidoptera and Diptera, in the samples from the Normafa Annelida and Coleoptera were the most significant prey categories. In the orchard, the samples from June of 1979 and 1982 contained mainly Coleoptera and Diptera, those from the end of May, 1982 contained Hymenoptera and Coleoptera in considerable numbers.

Similarly to the food of the blackbirds, that of the song thrush contained mainly lepidopterous larvae and Diptera. Of the caterpillars primarily species of the genera *Orthosia* and *Boarmia*, and *Operophtera brumata* and *Colotois pennaria* were fed to the nestlings, of the dipterans *Tipula* and *Limonia* species. Earth worms, molluscs and isopods were taken in greater proportion by song thrushes than blackbirds, and at the same time the former species took less Heteroptera and Diplopoda than the latter one. The proportion of plant material was also insignificant in this species, but about ten times that in the blackbird. The contents of the food samples from the orchard were characterized by Lepidoptera and Coleoptera, those from the woods by Lepidoptera and Diptera. In the study area at Esztergom mainly Coleoptera, Lepidoptera and Neuroptera were fed to the nestlings.

I found sand, gravel, earth and snail shells among the food of both species, but have not included them among the items. These are taken partly to help grind the food particles, partly to supplement the supply of inorganic elements (e. g. Ca).

Niche width of the blackbird was greater than that of the song thrush (Table 1). I did not include the samples from 1978 and 1979 in the results because of the small quantity of song thrush food collected in those years.

The similarity between the food composition of the two species was lower than that between the distributions of the size categories. The food samples collected from blackbirds in the oakwood resembled each other to a much greater degree than any other sample (Tables 2 and 3).

Temporal variation in food composition

I studied the variation in food composition of blackbirds by pooling the samples into 10-days intervals (Fig. 1). The diversity and evenness of the food composition was greater at the beginning and end of the breeding season than in the middle. In early spring Coleoptera, Annelida and Diptera predominated because of the paucity of caterpillars in that season, whereas in summer besides annelids and beetles caterpillars were also taken. These groups were taken in approximately equal proportions by the birds.

From the middle of May to the beginning of June foliage-consuming caterpillars were predominant in the food samples. This group reached its maximum in biomass around 20 May, as shown by the measurements of the quantity of caterpillar excrements in 1979 (Fig. 1). The exact timing of the "caterpillar peak" may vary from year to year because of differences in weather (BALEN, 1973), but it occurs usually at the end of May. With the sudden increase in the

abundance of the caterpillars the thrushes shifted to this prey category, and at the expense of other food items the larvae became the predominant food. Therefore the diversity and evenness of the food decreased during this period. The abundance of caterpillars decreased shortly after the peak, but their proportion was still considerable in the food of the nestlings.

Table 2. Similarities between food compositions

	1978	1979	1980	1981	1982
<i>T. merula</i> - <i>T. philomelos</i> 1. study plot 2. study plot	0.42	0.33	0.48 0.28	0.51	0.37
1. study plot - 2. study plot <i>T. merula</i> <i>T. philomelos</i>		0.26	0.31 0.38		
1. study plot - 4. study plot <i>T. merula</i>			0.39		
1. study plot - 3. study plot <i>T. merula</i>			0.24		
3. study plot - 4. study plot <i>T. merula</i>			0.17		

Table 3. Similarities between prey sizes

	1978	1979	1980	1981	1982
<i>T. merula</i> - <i>T. philomelos</i> 1. study plot 2. study plot	0.89	0.75	0.78 0.81	0.74	0.75
1. study plot - 2. study plot <i>T. merula</i> <i>T. philomelos</i>			0.78 0.76		

Prey size

Niche width of the blackbird, calculated from the pooled data as well as from the yearly data from the oakwood in the vicinity of Budapest, was greater than in the song thrush. In the orchard and the Esztergom study site, however, the niche width of the song thrush was the greater one in 1980. The differences were small in both cases.

There was considerable similarity between the preferred size categories as well. The interspecific prey size similarity was also high in various years and in the various habitats (Table 3). Within the species, the niche overlap of food size was also high between the various habitats.

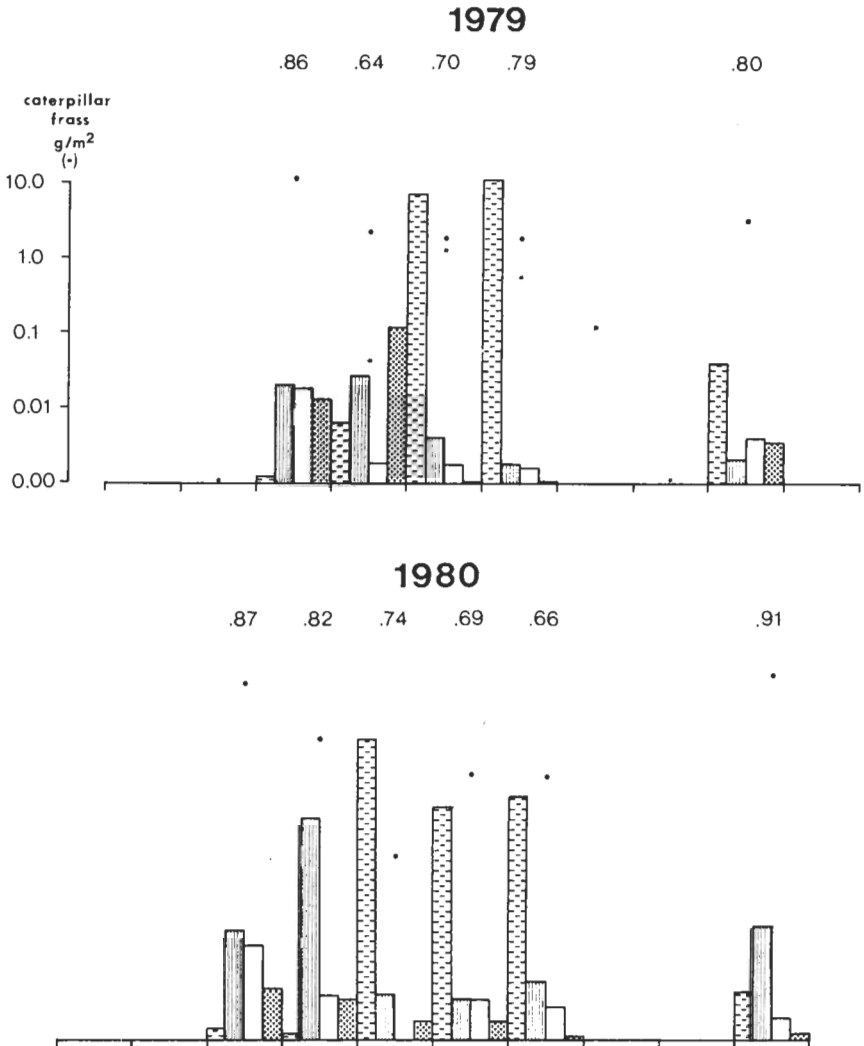
Changes in food composition with the growth of nestlings

The equations of logistic growth are widely used to describe the growth patterns of small passerines (RICKLEFS, 1967, 1968). I obtained the following equations for the growth curves (in body mass) of the blackbird (T_m) and song thrush (T_p) from the measurements of nestlings in study areas Nos 1 and 2:

$$wt_{T_m} = 54.5 / 1 + e^{-0.847(t-3.896)} \quad (N = 38)$$

$$wt_{T_p} = 43.1 / 1 + e^{-0.714(t-3.718)} \quad (N = 11)$$

where wt is the body mass (in g) at time t , which is the age of the nestling in days, N is the number of individuals.



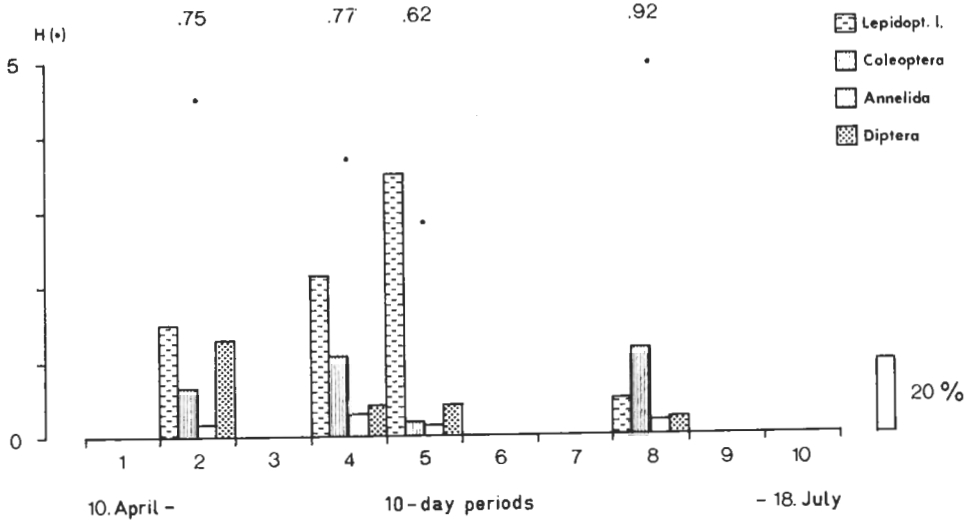


Fig. 1. Temporal variation of food composition and niche width of the blackbird in three years

The growth of the blackbirds and song thrushes is rapid, similarly to other altricial bird species which construct their nests in uncovered situations. They fledge on day 11 or 12 after hatching, though their ability to fly is still poor. Of the two species studied, the smaller song thrush has a greater growth rate (0.714). The hatching and fledging weights of the larger blackbird are greater than in the song thrush. The weight at hatching expressed as percentage of the asymptotic weight is about equal in the two species ($T_m = 12.4\%$, $T_p = 11.0\%$).

Food composition changed with the growth of the nestlings (Fig. 2.) In the samples from study area No. 1 collected in 1978, the younger nestlings of both species were fed mainly soft invertebrates (e. g. earthworms). With the growth of the nestlings the proportion of Coleoptera, lepidopteran larvae and diplopods increased and at the same time the proportion of Annelida and Hymenoptera decreased.

Discussion

The literature on avian ecology is rich in studies on sympatric populations of closely related species. The primary objectives of these studies had been elucidation of the interspecific similarities, mechanisms of segregation, competitive interrelationships, and clarification of the causes of different adaptivities, all of which lead to a better understanding of the regulatory mechanisms responsible for the structuring of avian communities. The present paper deals with the food of two species of the genus *Turdus*, the blackbird and the song thrush, which are abundant over much of Europe.

The results of the present work suggest that, similarly to other temperate birds, these two species are generalists. The difference between the species is manifested in the narrower food niche of the song thrush as compared with that

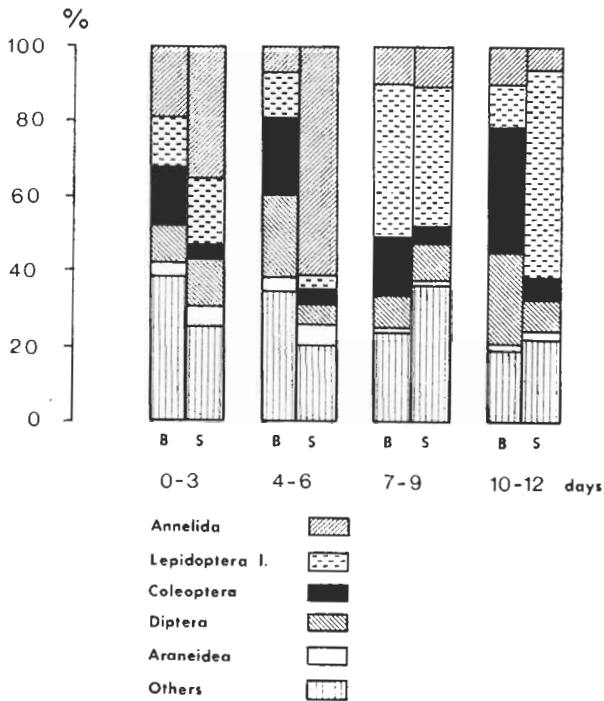


Fig. 2. Changes in food composition and the growth of nestlings (B = blackbird, S = song tursh)

Table 4. Average precipitation and dry weight of earthworms collected by blackbirds over 10-day periods (L - *Lumbricus* spp., D - *Dendrobaena* spp., A - *Allolobophora* spp., O - *Octolasion* spp., r - correlation coefficient, ns - nonsignificant correlation, x - the relative proportion of earthworms to total number of prey)

	10-day periods							r
	1	2	3	4	5	7	8	
	30.04 -			-18.07.				
1979								
Precipitation (mm)	0.8	0.0	2.4	0.6	-	2.5	-	
L + D	.17*	.05	.03	.03	-	.12	-	0.548 ns
A + O	.08	.005	.004	-	-	-	-	-0.200 ns
Total	.25	.05	.05	.04	-	.12	-	0.003 ns
1980								
Precipitation (mm)	1.7	2.1	-	1.9	2.8	-	0.7	
L + D	.17	.12	-	.07	.03	-	.05	-0.090 ns
A + O	.07	-	-	.03	.05	-	-	-0.170 ns
Total	.25	.12	-	.11	.09	-	.06	0.093 ns

Table 6. Principle food items of blackbirds and song thrushes from literature data (Only categories exceeding 10% of total prey indicated). Methods of food collection: + — analysis of stomach contents * — neck-collared nestlings □ — observation

	Blackbird						Song thrush					
	Annelida	Coleoptera	Lepidoptera	Gastropoda	Hymenoptera	Plant food	Annelida	Coleoptera	Lepidoptera	Gastropoda	Hymenoptera	Plant food
Csiki (1908) +		×						×		×		×
Siivonen (1939) +						×						
Eble (1963) +		×										
Mustafaeva (1964)											×	×
Davies and Snow (1965) □							×					
Korodi (1967)*	×	×	×				×		×			
Dyrcz (1969)*	×	×	×			×	×		×	×		
Vauk and Witting (1971) +		×			×	×						
Havlin (1977) +		×				×						
This study*		×	×				×					

of the blackbird. As regards actual food composition, the song thrush takes softer prey in greater quantities than the blackbird which shows preference for harder prey.

In both species lepidopterous larvae predominated in the food of the nestlings, the majority of which was made up by foliage-consuming caterpillars. Since these larvae live in the foliage and the thrushes feed on the surface of the soil, only in the period subsequent to the larval peak did the proportion of caterpillars increase in the food taken to the nestlings, when the larvae moved down to the soil to pupate.

Within the other prey category of importance, Diptera, the *Tipula* and *Limonia* species of poor flying ability which emerge in May predominated (mainly females full with eggs). The majority of other dipteran species were immediately after they had emerged from population and were yet unable to fly. Fully developed dipterans of powerful flying ability were found only rarely among the food items.

Both blackbirds and song thrushes consumed considerable quantities of earthworms. Presumably both the species living in deeper soil layers (*Allolobophora* spp., *Octolasion* spp.) and the ones near to the surface (*Lumbricus* spp., *Dendrobaena* spp.) are brought to the surface by sufficient rainfall and thus become susceptible to depredation by birds. To substantiate this presumption, I calculated for each 10-day period of 1979 and 1980 the dry weight of earthworms consumed by the nestlings (because of the uncertainty in estimation of the number of individuals), its relative proportion to total food and compared with the average precipitation of the periods (Table 4). I found no significant correlation between the amount of earthworms consumed and the amount of rainfall. Therefore it is probably not because of rainfall that earthworms are present in the food, though in spring, when there is more rainfall, they are taken in greater numbers to the nestlings than in the dryer period of the summer (SNOW, 1958).

Table 5. The common spider species of the litter layer of Turkey oakwoods (Loksa, unpublished data)
A - abundance, * - spring, early summer period, + - for juveniles only, B - total number consumed by blackbird nestlings

Species	A/m ²	size of cephalothorax (mm)	Activity	B
<i>Pardosa lugubris</i> *	8.0 - 10.4	2.5 - 3.0	diurnal quickly moving	1
Micryphantidae spp.	1.6 - 10.2	1.0 - 2.0	nocturnal	-
Linyphiidae spp.	3.2 - 9.6	1.9 - 2.4	nocturnal	9
<i>Leptyphantes flavipes</i>	3.2 - 6.4	1.0 - 1.5	nocturnal	-
<i>Trochosa terricola</i>	1.6 - 6.4 (9.6) +	3.7 - 5.0	nocturnal	3
<i>Harpactes rubicundus</i>	1.6 - 4.8	3.5 - 4.5	nocturnal	19
<i>Dysdera erythrina</i>	1.6 - 4.8 (9.6) +	3.0 - 4.0	nocturnal	1
<i>Xysticus cambridgei</i>	1.6 - 3.2	3.5	nocturnal	6
<i>Oxyptila</i> spp.	1.6 - 3.2	2.0 - 2.5	nocturnal	3

Because of the seaching tactics of the thrushes, spider species which do not occur on the surface of the soil were found only rarely in the food, though large numbers were taken of some species, e. g. *Xysticus lanio*. Of the species commonly occurring in the litter layer of the Turkey oakwood, principally the ones of greater dimensions and slow locomotion were captured (Table 5). JANSOON and BRÖMSSÉN (1981) found in their studies in coniferous forests that the birds' predation on the larger spiders was greater than on the smaller ones.

A number of authors have found molluscs to be important (DAVIES & SNOW, 1965; DYRCZ, 1969; SNOW, 1958), but except study area No. 3, where slugs were important prey, snails occurred only in small quantities in the food of the nestlings. The cause of this discrepancy may be that the forests in Hungary are drier and hence poorer in molluscs than the habitats in England and Poland, where the above observations have been reported from. CSIKI (1908) and HAVLIN (1977) also reported high proportion of molluscs, though these findings may reflect the inadequacy of the stomach analyses, in which the proportion of animals with highly chitinized integumen or calcified shell is greater than the proportion taken (Table 6).

RICKLEFS' generalization (1968), that of the closely related species the larger ones have lower growth rates, proved to be valid for the two *Turdus* species. The younger animals feed on softer food, the older ones take harder prey categories. KORODI (1967) also found that during the growth of blackbird nestlings the proportion of Coleoptera increased and that of the spiders and Lepidoptera decreased.

The food compositions of the generalist thrush species are closely related to the food resources of their environment (Table 7.). At the beginning of the breeding season, when the thrushes took even proportions of the various prey categories, the food composition niche width of the thrushes was great. Caterpillars, which play a central role in the food of most passerines, become the predominant food of the birds when they are available and thus the food niche width of the thrushes decreases. Even when a prey category becomes superabundant, the thrushes take other prey as well because besides the energy requirements of the nestlings, other circumstances also influence the search for prey (ROYAMA, 1970;

Table 7. Temporal variation in food composition of the two thrush species from literature data. (Only categories exceeding 10% of total prey indicated, in decreasing order of percentile proportion. Abbreviations: Co - Coleoptera, An - Annelida, Di - Diptera, Ga - Gastropoda, He - Heteroptera, Hy - Hymenoptera, Le - Lepidoptera)

	April	May	June	July
<i>Turdus merula</i> KORODI (1967)	Co, He, Hy, An	Le, Co	Le, Co	Le, Co, An
This study	-	Co, Di, An	Le, Co	Le, Co, An
<i>Turdus philomelos</i> DAVIES and SNOW (1965)	An, Ga	An, Le	Le, An	Ga, An
DYRCZ (1969)	-	An, Di, Ga	Co, Ga, Di, An	Co, Le, Ga
This study	-	An, Di, Le	Le, An	-

TINBERGEN, 1982). With the decrease in availability of the caterpillars, other items are also taken and thus the food spectrum and the food niche width decreases.

Of the two studied niche dimensions, the similarity between prey sizes of the two species was greater than that between food composition. The similarities between food compositions of the species and habitats show that the food resources of the given habitat determine the food composition of the two species. In an altered habitat, the orchard, considerably changed as compared with the natural habitat of the oakwood, the food of the song thrush changed to a lesser extent than that of the blackbird, indicating that this species does not readily follow the changes in its food resources. This fact, coupled with a smaller food niche width, indicates the specialized food regime of the song thrush that is accompanied by a less mobile dietary shift than that characteristic for the blackbird.

Appendix I. Food of blackbirds (B) and song thrushes (S) in the study areas (1-6)

	1978		1979						1980						1981		1982		Total		
	B ₁	S ₁	B ₁	B ₂	S ₁	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	S ₁	S ₂	S ₆	B ₁	S ₁	B ₂	S ₂	B	S	
Annelida																					
Lumbricidae																					
<i>Lumbricus rubellus</i>																				8	3
<i>L. spp.</i>																				119	22
<i>Allolobophora caliginosa</i>																				2	
<i>A. rosea</i>																				12	1
<i>A. spp.</i>																				25	8
<i>Dendrobaena octaedra</i>																				1	
<i>D. spp.</i>																				3	13
<i>Octolasion</i> spp.																				5	
Lumbricidae indet.																				82	32
Enchytraeidae																					
<i>Fridaeriza</i> sp.																				5	
Enchytraeidae indet.																				1	
Mollusca																					
Enidae																					
<i>Zebrina detrita</i>																					
Arionidae																				10	11
Helicidae																				15	1
Gastropoda indet.																				4	8
																				2	8
Arthropoda																					
Isopoda																					
Porcellionidae																					
<i>Porcellio scaber</i>																				1	1
<i>P. collicola</i>																				9	2
<i>P. spp.</i>																				2	2
<i>Protracheoniscus amoenus</i>																				18	2
<i>Ortometaxon planum</i>																				1	1
Armadillidiidae																					
<i>Armadillidium vulgare</i>																				3	1
<i>A. sp.</i>																				1	1
Oniscoidae indet.																				15	3

	1978		1979				1980						1981			1982			Total		
	B ₁	S ₁	B ₁	B ₂	S ₁	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	S ₁	S ₂	S ₆	B ₁	S ₁	B ₂	S ₂	B	S	
Scarabaeidae																					
<i>Ondophagus coenobita</i>			5			7	5													10	
<i>O. verticicornis</i>			3				1													11	
<i>Aphodius aequestris</i>							1													1	
Scarabaeidae indet.							1								7					7	
Melolonthidae																					
<i>Melolontha melolontha</i>	7	1	1			1		2											11	1	
<i>Melotrogus aequinoctialis</i>	4	1	2			2					1								8	2	
<i>Rhizotrogus aestivus</i>						4		1											12		
<i>Amphimallon solstitialis</i>	2				1														4	1	
Melolonthidae indet.	1		1												5		1		8		
Cetoniidae																					
<i>Cetonia a. aurata</i> Lavrø						1													1		
Cantharidae																					
<i>Cantharis fusca</i>			3			1													4		
<i>C. obscura</i>			3														1		4		1
<i>C. rustica</i>																	1		1		
<i>Metacantharis haemorrhoidalis</i>			1																1		3
<i>Malachius</i> spp.																					
Cantharidae indet.															11				2		
Cantharidae larvae																					
<i>Isomys noctiluca</i>						7													7		1
<i>Cantharis</i> sp.																					
Elateridae																					
<i>Prosternon tessellatum</i>						6													9		1
<i>Selatosomus latus</i>						2						1							2		
<i>Athous rufus</i>			41																41		2
<i>A. haemorrhoidalis</i>						1					2								2		
<i>Pseudathous hirtus</i>						1													1		
<i>Melanotus castanipes</i>						4													4		
<i>M.</i> sp.			1																1		

	1978		1979				1980						1981			1982			Total			
	B ₁	S ₁	B ₁	B ₂	S ₁	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	S ₁	S ₂	S ₆	B ₁	S ₁	B ₂	B ₂	S ₂	B	S	
<i>A. tragopoginis</i>															1						1	1
<i>Apamea monoglypha</i>															1						1	1
<i>Tholera cespitis</i>															3						3	3
<i>Cerastis rubricosa</i>															1						1	1
<i>Agrotis</i> spp.															20						20	20
<i>Hoplodrina</i> spp.															2						2	2
<i>Diloba coeruleocephala</i>																		1			1	1
Noctuidae indet.	5		15			9							5		115	12	9			7	153	24
Tetheidae p.				1																	1	1
Geometridae																						
<i>Alsophila aescularia</i>						1																1
<i>Theria ruficaparia</i>						1																1
Geometridae indet.															1						2	2
Geometridae larvae																						
<i>Colotois pennaria</i>			3	1		32			5			6	13		13	6					54	25
<i>Phygadeuon pilosaria</i>						2						4	1								2	5
<i>Operophtera brumata</i>			1			54						16	14		37	21					92	51
<i>Erannis defoliaria</i>	1					6							2		8	5					15	7
<i>E. marginalis</i>																					1	1
<i>E. leucophaea</i>																					1	1
<i>E. spp.</i>						10			1				3		5						25	4
<i>Pseudopanthera macularia</i>																					1	1
<i>Boarmia roburaria</i>																					1	1
<i>B. spp.</i>																					39	25
<i>Rhodostrophia vibicaria</i>	1		16			19	1		1			16	9		1						1	1
<i>Lycia hirtaria</i>																					12	2
<i>Ascutis selenaria</i>																					3	3
<i>Angerona prunaria</i>																					3	3
<i>Tephritia arenacearia</i>																					1	1
<i>Ectropis biatorata</i>																					1	1
<i>Selenia lunaria</i>																					2	2
<i>Biston betularia</i>																					1	1
Geometridae indet.	6		34			32			1			9	11		94	14	1		4		168	40

Lycaenidae																			1
<i>Thecla quercus</i>																			
Nymphalidae larvae																			
<i>Nymphalis polychloros</i>																			1
Nymphalidae indet.																			1
Nymphalidae p.																			1
Lepidoptera indet.																			17
Lepidoptera larvae indet.																			126
Lepidoptera p. indet.	8	1	38	1	3	4	4	1	17	1	1	3	1	2	1	2	1	1	16
			13																1
Diptera																			
Bibionidae																			
<i>Biblio marci</i>																			1
<i>B. hortulanus</i>																			17
<i>Biblio</i> spp.																			2
Bibionidae indet.	7		11		1	2													21
																			12
Tipulidae																			
Tipulidae larvae	12	1	167		1	15	1												303
Tipulidae p.	2																		21
Limoniidae	1		2			6													41
Limoniidae p.	15		87			28													199
Sciariidae																			1
																			3
Tabanidae																			
<i>Tabanus bromius</i>																			1
Stratiomyidae																			4
Asilidae																			
<i>Dialria flavipes</i>																			2
Asilidae indet.	2				2														7
Bombyliidae																			
Empididae																			2
																			8
Syrphidae																			
<i>Episyrphus balteatus</i>																			23
<i>Ferdinandea cuprea</i>																			1
<i>Metasyrphus corollae</i>																			1

	1978		1979				1980						1981		1982		Total			
	B ₁	S ₁	B ₁	B ₂	S ₁	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	S ₁	S ₂	S ₆	B ₁	S ₁	B ₂	S ₂	B	S
<i>Cheilosia</i> sp.	1													1	1		1		1	
Syrphidae indet.				2										1			1	1	4	2
Syrphidae larvae															1				1	
Muscidae																		3		3
Calliphoridae																				
<i>Sarcophaga carnaria</i>													1							
Calliphoridae indet.															2				2	
Tachinidae	1														2				6	1
Diptera indet.			12	4						31		3		1	7	1	4	1	72	6
Diptera larvae indet.	38	2	1				1					1		1	6	1	2		48	5
Diptera p. indet.		1																	1	1
Hymenoptera																				
Tenthredinidae																				
<i>Dolerus gonager</i>			1																1	
<i>Allanthus masculus</i>			1																1	
Tenthredinidae indet.	6														1			1	9	1
Tenthredinidae larvae																				
Cynipidae																				
Ichneumonidae																				
Formicidae																				
<i>Camponotus</i> spp.	3		1		1							2			6		1		12	
Formicidae indet.			2												12		33	4	63	7
Formicidae p.																	65		65	
Vespidae																				
<i>Vespa crabro</i>			1					1							3				3	
Vespidae indet.																				3

♀*	2	1	1	6	1	1	2	1	1	5	4
Apidae	4	1	1	1	1	1	3	1	1	16	4
Hymenoptera indet.		1								3	
Hymenoptera p. indet.										1	
Pseudoscorpioidea										1	
Phalangid ea											
Opilionidae										7	
<i>Zacheus crista</i>		1	1	1	3		4			3	1
<i>Opilio saxatile</i>				5	1		1			6	1
<i>Platybunus bucephalus</i>										6	
P. spp.		5								2	
<i>Lophopilio palpinalis</i>	2										4
<i>Egeanus convexus</i>											4
Opilionidae indet.										30	
Araneida											
Atypidae											
<i>Atypus affinis</i>		1		11						16	1
Dysderidae											
<i>Harpactes rubicundus</i>		9		3						19	3
<i>Dysdera erythrina</i>		1								1	
Dysderidae indet.										1	
Drassida											
<i>Drassodes silvestris</i>		1								1	
Clubionidae											
<i>Clubiona terrestris</i>				1						1	
Thomisidae											
<i>Philodromus aureolus</i>	1									1	
<i>Xysticus latio</i>	1	3		3						7	3
<i>X. kochi</i>				3						3	1
<i>X. erraticus</i>					1					1	
<i>X. cambridgei</i>		2		2						6	1
X. spp.		1								1	4
<i>Oxyptila praticola</i>										2	1
<i>O. atomaria</i>		1		2						1	
<i>Heriacus hirtus</i>										2	
<i>Thanaos formicinus</i>		2								2	
Thomisidae indet.										6	3

	1978		1979				1980						1981			1982			Total				
	B ₁	S ₁	B ₁	B ₂	S ₁	B ₁	B ₂	B ₃	B ₄	B ₅	B ₆	S ₁	S ₂	S ₆	B ₁	S ₁	B ₂	S ₂	B	S			
Theridiidae															2						2		
Linyphiidae																							
<i>Linyphia clathrata</i>			1			5		1													7		
<i>L. hortensis</i>			1																		1		
Linyphiidae indet.																					1		
Agelenidae																							
<i>Tegenaria torpida</i>			1			1															1		
<i>Coelotes</i> sp.																					1		
Pisauridae																							
<i>Pisaura mirabilis</i>	1																				1		
Lycosidae																							
<i>Alopecosa trabalis</i>	1		2			1															3		
<i>A. schulzeri</i>			2			1															3		
<i>A. sp.</i>												1									1	1	
<i>Trochosa terricola</i>			1		1	1		1													3	1	
<i>Pardosa lugubris</i>												1									1	2	
<i>P. agrestis</i>			1			1															1		
Lycosidae indet.										1										4	1	1	
Dictynidae																							
<i>Titanoea schineri</i>			1																		1		
Araneidea indet.																							
Araneidea cocoon			2					1	1										9	1	21	2	
Acaridea																							
Insecta indet.																							
Vertebrata																							
Squamata																							
Anguillidae																							
<i>Anguis fragilis</i>																				12	2	16	3

Acknowledgements

I wish to thank the staff of the Department of Zoosystematics and Animal Ecology of the Eötvös University, Budapest, the Department of Zoology of the Jozsef Attila University of Szeged, the Plant Protection Research Institute of the Hungarian Academy of Sciences, and the Zoological Department of the Hungarian Natural History Museum, for identifying the various food categories. My sincere thanks are especially due to DR. IMRE LOKSA, who identified the spiders, and DR. ANDRÁS ZICHI, who supplied me with invaluable advice on the annelids. I am most grateful to the directors and staff of the Plant Protection Research Institute and the Törökbalint State Farm for their support throughout my work.

REFERENCES

1. BALEN, J. H. VAN (1973): A comparative study of the breeding ecology of the Great Tit, *Parus major* in different habitats. — *Ardea*, 61: 1–93.
2. CODY, M. L. (1974): Competition and structure of bird communities. — Princeton, 318 pp.
3. CSIKI, E. (1908): Biztos adatok madaraink táplálkozásáról. — *Aquila*, 15: 183–206.
4. DAVIES, P. W. & SNOW, D. W. (1965): Territory and food of the Song Thrush. — *Br. Birds*, 58: 161–175.
5. DYRCZ, A. (1969): The ecology of the song-thrush (*Turdus philomelos* Br.) and blackbird (*Turdus merula* L.) during the breeding season in an area of their joint occurrence. — *Ekol. Pol.*, 39: 735–793.
6. EBLE, H. (1963): Ernährungsbiologische Untersuchungen an *Turdus philomelos* Brehm, *Turdus merula* L. und *Sturnus vulgaris* L. — *Wiss. Z. Martin-Luther-Univ. Halle-Wittenb.*, 12: 211–234.
7. HARTLEY, P. H. T. (1953): An ecological study of the feeding habits of the English titmice. — *J. Anim. Ecol.*, 22: 261–288.
8. HAYLIN, J. (1977): Ein Vergleich der Nahrung des Stars und der Amsel. — *Folia Zool.*, 26: 45–56.
9. JANSSON, C. & VON BRÖMSEN, A. (1981): Winter decline of spiders and insects in spruce *Picea adies* and its relation to predation by birds. — *Holarct. Ecol.*, 4: 82–93.
10. KORODI, G. J. (1967): Beiträge zur Kenntnis der Brutbiologie der Amsel (*Turdus merula* L.) und zur Ernährungsdynamik ihrer Jungen. — *Zool. Abh. Mus. Dresden*, 29: 25–53.
11. KROLL, F. (1975): 180 Jahre Gartenamsel (*Turdus merula*). — *J. Ornith.*, 116: 215–216.
12. LACK, D. (1945): The ecology of closely related species with special reference to Cormorant (*Phalacrocorax carbo*) and Shag (*P. aristotelis*). — *J. Anim. Ecol.*, 14: 12–16.
13. LACK, D. (1971): Ecological isolation in birds. — Oxford and Edinburgh, 404 pp.
14. MACARTHUR, R. H. (1958): Population ecology of some warblers of northeastern coniferous forests. — *Ecology*, 39: 599–619.
15. MUSTAFAEVA, R. G. (1964): K ekologii chernovo drozda (*Turdus merula* L.) v Azerbaidzhane. — *Izv. Akad. Nauk Azerbaidzhanskoj SSR. S. Biol.*, 5: 47–51.
16. NILSSON, S. G. (1979): Density and species richness of some forest bird communities in South Sweden. — *Oikos*, 33: 392–401.
17. PIELOU, E. C. (1969): An introduction to mathematical ecology. — New York, 286 pp.
18. RENKONEN, O. (1938): Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. — *Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo*, 6: 1–231.
19. RICKLEFS, R. E. (1967): A graphical method of fitting equations to growth curves. — *Ecology*, 48: 978–983.
20. RICKLEFS, R. E. (1968): Patterns of growth in birds. — *Ibis*, 110: 419–451.
21. 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.

22. SHANNON, C. E. & WEAVER, W. (1949): The mathematical theory of communication. — Urbana, Univ. of Illinois Press.
23. SIVONEN, L. (1939): Zur Ökologie und Verbreitung der Singdrossel (*Turdus ericetorum philomelos* Brehm). — Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo, 7: 1–285.
24. SMITH, J. N. M. (1973): The food searching behaviour of two european thrushes. II. The adaptiveness of the search patterns. — Behaviour, 49: 1–61.
25. SNOW, D. W. (1958): A study of blackbirds. — London, 192 pp.
26. TINBERGEN, J. M. (1981): Foraging decisions in starlings (*Sturnus vulgaris* L.). — Ardea, 69: 1–67.
27. TINBERGEN, L. (1960): The natural control of insects in pine woods. I. Factors influencing the intensity of predation by song birds. — Arch. Néer. Zool., 13: 265–343.
28. TÖRÖK, J. (1981): Food composition of nestling blackbirds in an oak forest bordering on an orchard. — Opusc. Zool., 17–18: 145–156.
29. TYE, A. (1981): Ground-feeding methods and niche separation in thrushes. — Wilson Bull., 93: 112–114.
30. VAUK, G. & WITTING, E. (1971): Nahrungsökologische Untersuchungen an Frühjahrsdurchzüglerin der Amsel (*Turdus merula*) auf der Insel Helgoland. — Vogelwarte, 26: 238–245.