

## Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season

János Török

Török, J. 1990. Resource partitioning among three woodpecker species *Dendrocopos* spp. during the breeding season. – *Holarct. Ecol.* 13: 257–264.

Food composition, prey size utilization and foraging behaviour of three sympatric woodpecker species (*Dendrocopos major*, *D. medius*, *D. minor*) were studied in an oak forest near Budapest during the breeding season in 1983 and 1984. Considering these three aspects of feeding, the great spotted woodpecker is a generalist species. Food composition of this species resembled the arthropod supply on the bark of trees more than those of the other two species. The bark of the trees seems to be a relatively unproductive microhabitat in the breeding season, so woodpecker species use, to different degrees, the food supply of the foliage as well. The food and the foraging behaviour of the middle spotted woodpecker show that this species feeds on prey living both on barks and in the foliage; it occupies an intermediate position between the great and the lesser spotted woodpeckers. Prey size did not correlate with predator size suggesting that woodpeckers adapted not to the summer resources but rather the winter ones.

J. Török, Dept of Syst. Zoology and Ecology, Eötvös Univ., Budapest H-1088, Puskin u. 3., Hungary.

### Introduction

There are often great differences in food availability for forest birds between spring and winter seasons (Newton 1980). Regardless of whether or not food is the most important limiting factor, food resources undoubtedly affect the foraging of birds and cause interspecific segregation. Such segregation has been shown in several studies (MacArthur 1958, Morse 1968, Rabenold 1978, Alatalo 1982, Sabo and Holmes 1983, Recher et al. 1985, Holmes and Recher 1986, Conner 1979). Increased food supplies during the breeding period can relax pressure of competition and allow increased overlap among species (Rabenold 1978).

In temperate-forest bird communities some species, namely bark-foraging birds forage on prey located on or in the bark of trees. In Hungarian oak-dominated forests the bark-foraging bird assemblage consists of six species: the great spotted woodpecker, *Dendrocopos major*, GSW, the middle spotted woodpecker, *D. medius*, MSW, the lesser spotted woodpecker, *D. minor*,

LSW and three passerine species, *Certhia brachydactyla*, *C. familiaris*, *Sitta europaea*. Occasionally the black woodpecker, *Dryocopus martius* and Syrian woodpecker *Dendrocopos syriacus* are also present, but their numbers are low even in their preferred habitats. Of the woodpeckers the great spotted woodpecker is the most numerous.

Several studies have discussed the diet (Williams and Batzli 1979b) and foraging behaviour of woodpeckers during the nonbreeding season (Winkler 1973, Alatalo 1978, Hogstad 1978, Jenni 1983, Pettersson 1983), but there is a paucity of quantitative data (mainly on diet description) from the breeding season (Winkler 1973, Jenni 1983). The principal aim of this study is to describe the similarities in diet of nestlings and foraging behaviour of great, middle, and lesser spotted woodpeckers during the breeding season. In addition, some information on the availability of different prey types in the environment at the breeding season is given and its influence on the choice of food is discussed.

Accepted 25 September 1989

© HOLARCTIC ECOLOGY

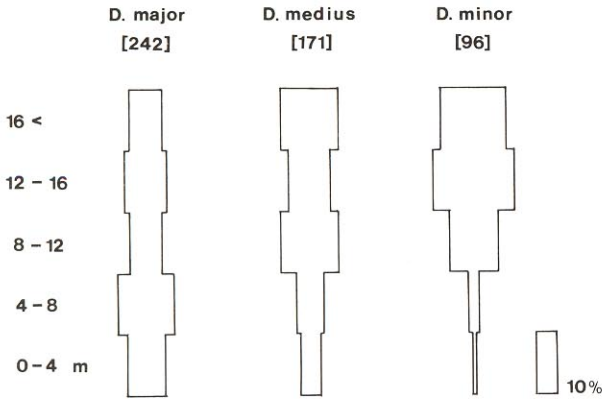


Fig. 1. Percentage distribution of foraging heights of woodpeckers in an oak forest during the breeding season. (Sample sizes in parentheses).

### Methods

The study was conducted in 1983 and 1984 in an oak forest near Budapest. The dominant tree species are *Quercus cerris* and *Q. petraea*, with a lesser number of *Acer campestre*, *Fraxinus ornus*, *Sorbus torminalis*, *Carpinus betulus* and *Cerasus avium* trees. Food samples (6902 items in total) were collected from 4–15 d old nestlings of three woodpecker species using the neck-collar method (Kluijver 1933, Török 1981). Three nests of GSW and one nest each of MSW and LSW were studied in both yr. Data from the three GSW nests were pooled in both yr. The food samples were collected from 4 May to 20 May and from 11 May to 28 May in 1983 and 1984, respectively. It was assumed that in such a brief period the effect of seasonal changes in the food supply was negligible. The length of the prey items was measured to the nearest mm. Although each prey item was identified as far as possible, not all could be determined to the same taxonomic level, therefore for the comparisons I pooled those identified to species or to the genus, to a higher taxonomic level. Dry mass of prey items was computed using equations for length-weight relationships (Rogers et al. 1977). Dietary diversity was calculated based on the Shannon-formula (Shannon and Weaver 1949) and dietary similarity between any two species was calculated using Renkonen's (1938) proportional similarity index.

The caterpillar supply was estimated from frass production, using 20 frass collectors. The surface of each collector was 0.25 m<sup>2</sup>. Collectors operated during the whole breeding season but in the analysis I used the data gathered in the food sampling period. The composition and relative proportion of the arthropod fauna available to the bark-foraging species was determined by the use of traps placed around the tree trunks. The traps were similar to the arboreal photoelectors used by Funke (1971) and Nielsen (1974). The traps were 40 cm high inverted funnels made from thick aluminium

foil which formed a complete sleeve around tree trunks 3 m above the ground. The inner surface of funnels was painted and roughened with sand and their narrow necks ended in collecting jars containing preservative. Traps collected all the animals moving upward on the bark or flying near the trunk, however, immobile prey remained undetected. In 1984, 21 traps were used around 7 oak-trunks (three traps per trunk). They were checked every second wk during the breeding season and once a month outside the breeding season. The data for the period 1 to 31 May was an indication of spring food supply and that of the period between 30 November and 31 December as an indication of winter food supply.

The foraging behaviour of woodpeckers was observed between 7:00 and 11:00 from 1 May to 30 June in each breeding season. To minimize the effects of weather, observations were made only on fine days. Individuals were followed for up to 5 min and foraging variables were noted continuously at intervals of 20 s using a tape-recorder. Data for the two yr were pooled. The following foraging variables were recorded: (1) tree species used during foraging, (2) type of wood: dead or alive, (3) height of foraging above the ground, (4) part of tree used, and (5) foraging technique. Heights were estimated to the nearest meter but for illustration these have been grouped in 4-m intervals. Parts of the tree were divided into five categories: trunk, large branches ( $\varnothing > 5\text{cm}$ ), medium-sized branches (3–5 cm), small branches (1–3 cm) and twigs (<1cm). Five types of foraging technique were registered: (a) gleaning – picking arthropods from the surface, (b) probing – peering and poking for arthropods on the surface, (c) scaling – scaling the bark of dead branches or trunks for food, (d) excavating – subcambial excavation, (e) flycatching – the chasing of flying insects in the air.

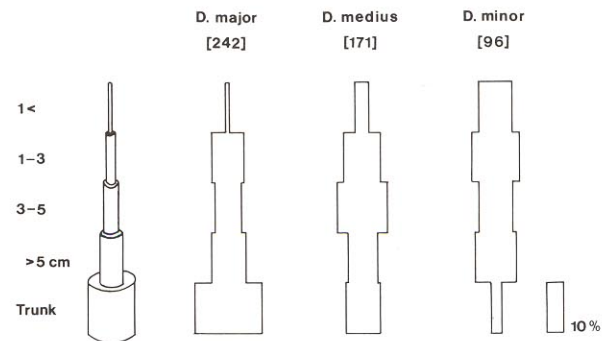


Fig. 2. Percentage distribution of parts of tree used by woodpeckers in an oak forest during the breeding season. (Sample sizes in parentheses).



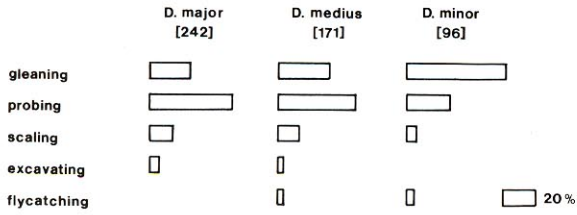


Fig. 3. Percentage distribution of foraging methods applied by woodpeckers in an oak forest during the breeding season. (Sample sizes in parentheses).

## Results

### Foraging behaviour

During the breeding season all three woodpecker species almost exclusively used *Q. cerris* and *Q. petraea* (94%, 96% and 95%, in GSW, MSW and LSW, respectively). This was expected as more than 85% of the forest consisted of these two oak species. During the period of parental care all three species fed mainly on live substrate (89%, 90% and 87% in GSW, MSW and LSW, respectively). The use of dead substrate by woodpeckers is known to vary seasonally (Jenni 1983, Pettersson 1983).

The range of foraging height in the trees was similar for GSW and MSW (Tab. 5), but MSW mainly used the

upper parts of the trees, GSW the lower ones (Fig. 1). LSW foraged as much as 94% on substrates above 8 m.

Observation on foraging showed that GSW mainly used trunks while the other two species foraged more on branches (Fig. 2). LSW generally spent more time on the twigs than the other species. This was expected from the foraging height observations. During the breeding season gleaning is the most prevalent foraging technique and scaling and excavating are used less frequently (Fig. 3). The greatest difference in foraging technique between species pairs was between GSW-LSW (Tab. 5). Although searching speed was not recorded, it is probably important and probably would clarify the differentiation between the foraging behaviour of woodpeckers (Robinson and Holmes 1982, Jenni 1983). Based on my impression, GSW is a slow searcher e.g. this species changes its position rarely as compared to the other species. LSW was a fast searcher while MSW was in an intermediate position between GSW and LSW. Jenni (1983) found a similar velocity pattern for GSW and MSW.

### General diet description and food supply

All three woodpecker species fed almost exclusively arthropods while feeding their young (Tabs 1, 2). Based on number, the most common prey types were aphids

Tab. 1. Prey distribution in the nestling diet of three *Dendrocopos* species in an oak forest in Hungary, 1983. Frequencies of major prey types of Lepidoptera and Diptera groups are in parentheses. (No = percent by number of individuals, DWT = percent by dry weight).

Prey type	GSW		MSW		LSW	
	No	DWT	No	DWT	No	DWT
Diplopoda	0.05	1.14	0.60	0.65	0.33	1.55
Heteroptera	0.37	0.47	3.36	0.86	1.09	0.74
Aphididae	78.50	5.10	41.03	0.65	49.40	1.63
Homoptera others	0.09	0.05	—	—	0.11	0.03
Coleoptera larva	—	—	0.09	0.07	0.11	0.08
Coleoptera adult	1.63	4.01	3.71	4.08	0.44	0.20
Neuropteroidea	0.05	0.96	—	—	—	—
Lepidoptera larva	6.01	44.41	36.98	68.86	30.71	69.11
(Tortricidae)	—	(1.33)	—	(0.70)	—	(7.32)
( <i>Operophtera brumata</i> )	—	(3.62)	—	(17.41)	—	(18.49)
( <i>Erannis</i> spp.)	—	—	—	(5.27)	—	(2.00)
(Geometridae others)	—	(17.12)	—	(29.57)	—	(17.17)
( <i>Orthosia stabilis</i> )	—	(15.53)	—	(9.30)	—	(10.62)
(Noctuidae others)	—	(6.81)	—	(3.51)	—	(5.01)
(Lepidoptera others)	—	—	—	(3.10)	—	(8.50)
Lepidoptera pupa	0.09	0.17	0.09	0.02	3.72	1.94
Lepidoptera adult	0.09	0.26	—	—	0.33	3.01
Diptera larva	—	—	—	—	0.11	0.01
Diptera adult	1.11	7.33	4.31	6.51	4.26	17.69
( <i>Limonia</i> spp.)	—	(1.36)	—	(3.95)	—	(3.50)
( <i>Tipula</i> spp.)	—	(5.97)	—	(2.56)	—	(4.05)
(Diptera others)	—	—	—	—	—	(0.14)
Hymenoptera	6.92	17.80	0.43	0.55	—	—
Phalangidea	3.92	16.62	7.67	9.66	1.97	4.38
Araneidea	1.17	1.65	1.47	5.17	7.43	9.63
Indet. arthropods	—	—	0.26	2.94	—	—
Total no. prey items	2168		1160		915	

Tab. 2. Prey distribution in the nestling diet of three *Dendrocopos* species and in the spring (May) arthropod supply on the bark of trees in an oak forest in Hungary, 1984. Frequencies of major prey types of Lepidoptera and Diptera are in parentheses. (No = percent by number of individuals, DWT = percent by dry weight).

Prey type	GSW		MSW		LSW		Supply No
	No	DWT	No	DWT	No	DWT	
Isopoda	—	—	0.86	0.91	—	—	—
Diplopoda	—	—	0.68	0.01	0.90	0.02	0.20
Heteroptera	1.20	0.33	4.74	0.72	1.35	0.15	46.43
Aphididae	32.30	0.79	6.74	0.15	20.02	0.50	5.32
Homoptera others	6.43	0.42	4.56	0.16	1.35	0.06	4.00
Coleoptera larva	0.09	0.01	—	—	—	—	0.20
Coleoptera adult	3.52	3.85	2.84	7.23	—	—	8.00
Neuropteroidea	—	—	0.19	0.04	—	—	0.20
Lepidoptera larva	25.02	46.94	69.01	75.40	54.00	85.12	3.77
(Tortricidae)	—	(3.47)	—	(0.63)	—	(10.34)	—
( <i>Operophtera brumata</i> )	—	(21.98)	—	(40.36)	—	(15.43)	—
( <i>Erannis</i> spp.)	—	(1.03)	—	(1.61)	—	(3.52)	—
(Geometridae others)	—	(9.84)	—	(29.12)	—	(32.67)	—
( <i>Orthosia stabilis</i> )	—	(4.16)	—	—	—	(21.11)	—
(Noctuidae others)	—	(6.46)	—	(2.23)	—	(2.05)	—
(Lepidoptera others)	—	—	—	(1.45)	—	—	—
Lepidoptera pupa	—	—	0.29	0.52	0.45	0.46	—
Diptera adult	6.69	41.26	7.70	12.31	11.01	10.30	1.77
( <i>Limonia</i> spp.)	—	(1.62)	—	(5.18)	—	(7.83)	—
( <i>Tipula</i> spp.)	—	(39.04)	—	(7.12)	—	(2.47)	—
(Diptera others)	—	(0.60)	—	—	—	—	—
Hymenoptera	19.86	1.63	1.72	0.37	6.87	0.22	6.43
Phalangidea	4.03	4.00	0.10	0.03	—	—	4.20
Araneidea	0.86	0.77	0.57	2.15	4.05	3.18	16.23
Indet. arthropods	—	—	—	—	—	—	0.20
Total no. prey items	1166		1048		445		225

and lepidopterous larvae, but by dry weight, lepidopterous larvae predominated. Diptera (mainly Tipulidae), ants and spiders were consistently found in high proportion on food samples while other prey groups were generally less frequent. There was a slight difference in the frequency distribution of prey groups between the two yr. In 1984 the proportions of lepidopterous larvae and Diptera were higher while the proportion of spiders was lower than in the previous yr, probably reflecting the relative abundance of these prey types in the environment.

Bark-living arthropods were captured only in 1984. In May the traps collected 518 arthropods, of which 293 individuals (Collembola, Physopoda, Acarina) were omitted from the analysis because their small size (<2 mm) it is unlikely that woodpeckers eat them. Prey belonging to these three groups were never found in the woodpecker diet (Jenni 1983, Pettersson 1983, Török unpubl. data). In the spring supply the predominant prey were heteropterans, spiders, beetles and ants (Tab. 2). Caterpillars and aphids were very rare in May, however, birds probably obtained them in foliage. In December 1984, the number of trapped arthropods was 870 after omitting 2223 extremely small-sized arthropods (Collembola, Physopoda, Acarina). The number of potential prey items was surprisingly large in this

period even though I omitted 646 small (4 mm) adult dipterans in addition, the rest was about as many as in May. I omitted these small sized dipterans as they were present for a short period only in the traps and were absent in the next two yr (Török unpubl. data).

In 1984, when woodpeckers took a large proportion of caterpillars, the number of caterpillars was twice as estimated from frass production (0.42 g 0.25 m<sup>-2</sup>) that in the previous yr when the birds gathered much less of these prey (0.22 g 0.25 m<sup>-2</sup>). LSW and MSW delivered proportionally more lepidopterous larvae to their nestlings than GSW did, whilst the latter fed their nestlings more dipterans and phalangids based on dry weight. Two caterpillar species, *Operophtera brumata* and *Orthosia stabilis* were the most common in the diet of the nestlings of each woodpecker species.

#### Dietary diversity and mean prey length

In 1983 food composition diversity of LSW was the greatest ( $H = 2.51$ ) and the values for the other two species were the same ( $H = 2.28$  for GSW and for MSW). In the following yr the diversities of LSW ( $H = 1.90$ ) and GSW ( $H = 1.94$ ) were very similar while MSW ( $H = 1.74$ ) showed a less variable diet ( $p < 0.001$ ).



Tab. 3. Prey size diversity (H) of three *Dendrocopos* species. Calculations were made separately for caterpillars and all prey. (n = number of prey categories).

	Caterpillars		All prey	
	H	n	H	n
1983				
GSW	2.91	25	1.63	30
MSW	2.82	25	2.50	28
LSW	2.77	25	2.36	28
1984				
GSW	2.81	24	2.68	30
MSW	2.63	24	2.93	30
LSW	2.85	25	3.00	29

Probabilities of Hutcheson's (1970) statistic for differences between diversity values

		Caterpillars	All prey
GSW-MSW	1983	NS	***
	1984	***	***
GSW-LSW	1983	NS	***
	1984	NS	***
MSW-LSW	1983	NS	**
	1984	***	NS

\*\* p<0.02, \*\*\* p<0.001, NS not significant

GSW had the lowest prey size diversity in both yr (Tab. 3). However, if we consider the diversity of caterpillar sizes only, then it was high in both yr. Pooled data (based on three nests of GSW in each yr) was used for these comparisons. However, if we consider the diversity values calculated separately for each nest (1983: 1.44, 1.31, 1.29; 1984: 2.25, 2.19, 1.47) they are slightly smaller than the value computed from pooled data. This small discrepancy did not influence the comparison as GSW had the smallest diversity values at least by all prey in each yr. Although in case of caterpillar size GSW had the greatest diversity value but it did not differ significantly from the other species except MSW in 1983.

The mean prey size differed significantly among the three woodpecker species, except between MSW and LSW in 1984 (Tab. 4). In both yr GSW usually took smaller prey (aphids, heteropterous larvae) than MSW and LSW. There were no differences in the mean caterpillar sizes taken by GSW and MSW while LSW fed on smaller caterpillars in 1983 and larger ones in 1984.

#### Similarities in the diet

The greatest similarity in food composition of the nestlings was found between MSW and LSW, while GSW and LSW differed most (Tab. 5). Unfortunately, within-species similarity patterns was impossible to test because of the small sample size, except GSW, of which

Tab. 4. Morphological characters and mean length of prey taken by three *Dendrocopos* species. Prey size calculations were made separately for caterpillars and all prey. Six individuals of GSW and two individuals of MSW and LSW were measured in both yr.

	Character				Prey size						
	Bill length	Bill width	Tarsus length	Body mass	Caterpillars			All prey			
					$\bar{x}$	SD	n	$\bar{x}$	SD	n	
1983											
GSW	29.7	8.4	24.3	84.0	14.9	5.02	130	3.9	4.02	2168	
MSW	25.4	6.1	20.9	61.5	14.4	4.62	430	7.7	6.34	1160	
LSW	17.4	5.1	14.9	24.5	12.8	4.42	281	6.3	5.47	912	
1984											
GSW	29.3	8.7	23.5	86.4	12.9	4.54	293	6.7	6.08	1166	
MSW	26.1	5.9	20.8	63.5	12.7	3.83	725	10.7	5.07	1048	
LSW	16.7	5.0	15.3	23.5	15.5	4.64	243	10.7	6.63	445	

Probabilities of Student's t-test

		Caterpillars	All prey
GSW-MSW	1983	NS	***
	1984	NS	***
GSW-LSW	1983	***	***
	1984	***	***
MSW-LSW	1983	***	***
	1984	***	NS

\*\*\* p<0.001, NS not significant.

Tab. 5. Renkonen's similarities between woodpecker species in different diet and foraging parameters. Categories indicated in Tabs 1, 2 were used for diet composition similarities.

	Food composition		Prey size		Foraging height	Branch diameter	Foraging technique
	1983	1984	1983	1984			
GSW-MSW	0.56	0.50	0.73	0.68	0.79	0.75	0.91
GSW-LSW	0.55	0.42	0.72	0.77	0.61	0.66	0.59
MSW-LSW	0.64	0.60	0.79	0.75	0.80	0.76	0.68

three nests were sampled in both yr. The individuals' resource utilization was compared to that of the three combined GSW nests sampled as a whole. These were high in both yr (0.86, 0.79, 0.92, and 0.79, 0.95, 0.77 for the three GSW nests in 1983 and 1984, respectively). Similarities in prey-size spectrum were higher than those in food composition and there was no apparent difference among the three species in any of the two yr.

The diet of GSW nestling resembled the food supply of tree trunks more closely (0.31) than that of the other two species (0.25 for MSW, 0.24 for LSW). This was expected as GSW foraged exclusively on trunks while other two species frequently used other substrates as well.

## Discussion

The crucial point in studying the structure of a temperate bird assemblage are the limiting factors and their timing. Most of the authors agree that food is limiting during the winter and resulting in a competitive situation (Lack 1954, 1966, Schoener 1971, Conner 1979, Williams and Batzli 1979a, b). It has been demonstrated especially for North-American bark-foraging birds (see references in Dickson et al. 1979), but there is some evidence that this limitation occurs in the European bark-foraging assemblage as well (Winkler 1973, Alatalo 1978, Hogstad 1978, Jenni 1983, Pettersson 1983). During the winter period by excavating for food, woodpeckers are able to use a relatively little used microhabitat, the tree trunk (Grubb 1975, Hogstad 1978, Conner

1979). The morphological features (bill size, tongue length, structure of feet and tail) of the woodpeckers are adapted to this foraging method (Jenni 1981). Because of methodological problems, unfortunately, there are no meaningful data on the seasonal changes in potential food supply in a specific habitat (including ground, bark, tree canopy and in the air). The animal prey are probably much more abundant in most of the microhabitats (i.e. canopy, air and perhaps ground) during the breeding season than in winter. However, my one-year study indicates that there is little difference in bark surface food stock between the spring and winter seasons. Comparing the food stock of different microhabitats in the breeding season, we can assume that the number of prey living on the trunks is probably much less than that in the foliage, simply because of the difference in the surface areas. (Although I have no data on the abundance of arthropods inhabiting the bark and wood, one may assume that this resource is probably unimportant compared with other microhabitats.) Nestling demands force the adult woodpeckers to search for suitable abundant prey types such as caterpillars. This results in the frequent use of foliage where gleaning and probing techniques predominate, as reflected in the high proportion of caterpillars taken and that the "typical" woodpecker foraging method is relatively infrequently used. Seasonal changes in foraging appear in different ways in the three woodpecker species. The foraging microhabitats and techniques of the large-sized GSW were more similar to those of the MSW than to those of the small-sized LSW. GSW foraged more on the trunks than did the other two species.

Tab. 6. Spearman's rank correlations for prey size vs. character size for five woodpecker nests in 1983 and 1984. As the sexes of MSW could not be identified, I used the average values of the male and the female in each nest. Total length refers to average length of all prey items in the nestling diet. (\*  $p < 0.05$ )

Character	Spearman's rank correlation							
	aphid length		spider length		caterpillar length		total length	
	1983	1984	1983	1984	1983	1984	1983	1984
Bill length	-.10	-.70	-.30	-.50	.60	-.70	-.60	-.90*
Bill width	.00	.05	.20	-.50	.10	-.20	-.50	-.85
Tarsus length	-.20	-.40	.00	-.50	.30	-.60	-.70	-1.00*
Body mass	.00	-.60	.20	-.50	.10	-.50	-.50	-.70



The smaller proportion of caterpillars and the higher proportion of phalangids in the diet of the nestlings also show that this species uses foliage less extensively (phalangid numbers decrease upwards along a trunk, Jackson 1979). The movement of the GSW appeared to be slower than that of the other two species which allowed this species to utilize the clumped prey (aphids, ants) more efficiently. This slow searching speed remains the same or becomes even slower in winter as the excavation and scaling methods – which characterize GSW in this season – are time-consuming (Jenni 1983). Both with respect to morphological characters, food composition and foraging methods, MSW occupies an intermediate position between GSW and LSW. Among these three species LSW is the one that forages most in the foliage. Food composition of nestlings of LSW is similar not only to that of the other woodpeckers but also to that of other foliage-gleaning birds for which caterpillars are an essential food (Török 1986).

Hespenheide (1971) stated that prey size is an increasing function of body size among birds applying similar foraging techniques. Williams and Batzli (1979b) have shown a clear relationship between the morphological characters (bill length and body weight) and mean prey size in a bark-foraging bird assemblage (consisting of five species) in the winter period. I tested whether this relationship can exist during the breeding season between the three woodpecker species. I used the size of prey taken to the nestlings by parents for computation. Out of the 32 correlations only two were significant (Tab. 6). These showed negative relationships between morphology and prey size, indicating a trend opposite to that found by Williams and Batzli (1979b). Probably it is not prey size but rather foraging behaviour which is the main segregating factor during the breeding season. Woodpeckers usually prefer the trunk microhabitat during their foraging and eat all types of prey found, independently of their sizes (except extremely small prey such as Collembola, Physopoda and Acarina). As the trunk is a relatively unproductive microhabitat (32 prey per trunk in May), they extended their foraging to the foliage to collect caterpillars (and probably aphids). The proportions of foliage foraging, and of caterpillars in the nestling diet, increased with decreasing body size of the species. Due to its morphology LSW uses the abundant resource, caterpillars, more efficiently than the two larger woodpeckers. Owing to the lack of the predator size prey size relationship, I assume that woodpeckers' morphology is probably adapted not to the breeding season but rather to the nonbreeding one. Similar results were obtained by Wiens (1974) and his coworkers in shrubsteppe ground-foraging birds. He hypothesized that the morphological divergences might well be adaptive during other times of resource limitation than in the breeding season.

In summary, foraging behaviour showed a clear segregation between woodpeckers, however, the lack of consistent trends between prey size and morphology did

not support the idea of food limitation in the breeding season. The proportion of foliage-consuming caterpillars in the diet depended on the caterpillar supply in the environment, also indicated an opportunistic feeding strategy in these species. However, more detailed studies are needed on the food supply of all microhabitats of a certain habitat to clarify the effects of food in the organization of bird communities.

*Acknowledgements* – I thank G. Csorba for his assistance in the field and A. Demeter and N. Nur for improving the English of the paper. H. Källander, I. Nilsson and L. Otvos made valuable suggestions on an earlier draft of this paper.

## References

- Alatalo, R. H. 1978. Resource partitioning in Finnish woodpeckers. – *Ornis Fenn.* 55: 49–59.
- Alatalo, R. V. 1982. Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. – *Ornis Scan.* 13: 56–71.
- Conner, R. N. 1979. Seasonal changes in woodpecker foraging methods: strategies for winter survival. – In: Dickson, J. G., Conner, R. N., Fleet, R. R., Kroll, J. C. and Jackson, J. A. (eds), *The role of insectivorous birds in forest ecosystems.* Academic Press, New York, pp. 95–105.
- Dickson, J. G., Conner, R. N., Fleet, R. R., Kroll, J. C. and Jackson, J. A. (eds) 1979. *The role of insectivorous birds in forest ecosystems.* – Academic Press, New York.
- Funke, W. 1971. Food and energy turnover of leaf-eating insects and their influence on primary production. – In: Ellenberg, H. (ed.), *Integrated experimental ecology.* Springer, Berlin, pp. 101–120.
- Grubb, T. C. Jr. 1975. Weather dependent foraging behaviour of some birds wintering in a deciduous woodland. – *Condor* 77: 175–182.
- Hespenheide, H. A. 1971. Food preferences and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. – *Ibis* 113: 59–72.
- Hogstad, O. 1978. Sexual dimorphism in relation to winter foraging and territorial behaviour in the three-toed woodpecker and three *Dendrocopos* species. – *Ibis* 120: 198–203.
- Holmes, R. T. and Recher, H. F. 1986. Determinants of guild structure in forest bird communities: an intercontinental comparison. – *Condor* 88: 427–439.
- Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. – *J. theor. Biol.* 29: 151–154.
- Jackson, J. A. 1979. Tree surface as foraging substrates for insectivorous birds. – In: Dickson, J. G., Conner, R. N., Fleet, R. R., Kroll, J. C. and Jackson, J. A. (eds), *The role of insectivorous birds in forest ecosystems.* Academic Press, New York, pp. 69–93.
- Jenni, L. 1981. Das Skelettmuskelsystem des Holsen von Buntspecht und Mittelspecht *Dendrocopos major* und *medius*. – *J. Orn.* 12: 37–63.
- 1983. Habitatnutzung, Nahrungserwerb und Nahrung von Mittel- und Buntspecht (*Dendrocopos medius* und *D. major*) sowie Bemerkungen zur Verbreitungsgeschichte des Mittelspechts. – *Orn. Beob.* 80: 29–57.
- Kluijver, H. N. 1933. *Bidrage tot de biologie en de ecologie van den spreeuw, *Sturnus vulgaris*, gerunde zijn voortplantingstijd* – *Verl. Med. Plant. Deints. Wageningen.* 69: 1–145.
- Lack, D. *The natural regulation of animal numbers.* – Oxford Univ. Press, Oxford.

- 1966. Population studies of birds. – Oxford Univ. Press, Oxford.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. – *Ecology* 39: 599–619.
- Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. – *Ecology* 49: 779–784.
- Newton, I. 1980. The role of food in limiting bird numbers. – *Ardea* 68: 11–30.
- Nielsen, B. O. 1974. Registrering af insektaktivitet pa bogestammer ved hjælp af fangtrage. – *Entomol. Medd.* 42: 1–18.
- Pettersson, B. 1983. Foraging behaviour of the middle spotted woodpecker *Dendrocopos medius* in Sweden. – *Holarct. Ecol.* 6: 263–269.
- Rabenold, K. N. 1978. Foraging strategies, diversity, and seasonality in bird communities of Appalachian spruce-fir forests. – *Ecol. Monogr.* 48: 397–424.
- Recher, H. F., Holmes, R. T., Schultz, M., Shields, J. and Kavanagh, R. 1985. Foraging patterns of birds in eucalypt forest and woodland in the tablelands of southeastern Australia. – *Aust. J. Ecol.* 10: 399–421.
- Renkonen, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. – *Ann. Zool. Soc. Bot. Fenn. Vanamo.* 6: 1–231.
- Robinson, S. K. and Holmes, R. T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet and habitat structure. – *Ecology* 63: 1918–1931.
- Rogers, L., Buschbom, R. L. and Watson, C. R. 1977. Length-weight relationships of shrub-steppe invertebrates. – *Ann. Entomol. Soc. Am.* 7: 51–53.
- Sabo, S. R. and Holmes, R. T. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. – *Condor* 85: 121–138.
- Schoener, T. W. 1971. Theory of feeding strategies. – *Ann. Rev. Ecol. Syst.* 2: 369–404.
- Shannon, C. E. and Weaver, W. 1949. The mathematical theory of communication. – Univ. Illinois Press, Urbana.
- Török, J. 1981. Food composition of nestling blackbirds in an oak forest bordering on an orchard. – *Opusc. Zool. (Budapest)* 17–18: 145–156.
- 1986. Food segregation in three hole-nesting bird species during the breeding season. – *Ardea* 74: 129–136.
- Wiens, J. A. 1974. Climatic instability and the “ecological saturation” of bird communities in North American grasslands. – *Condor* 76: 385–400.
- Williams, J. B. and Batzli, G. O. 1979a. Competition among bark-foraging birds in Central Illinois: Experimental evidence. – *Condor* 81: 122–132.
- 1979b. Winter diet of bark-foraging guild of birds. – *Wilson Bull.* 91: 126–131.
- Winkler, H. 1973. Nahrungserwerb und Konkurrenz des Blutspechts, *Picoides (Dendrocopos) syriacus*. – *Oecologia (Berl.)* 12: 193–208.