

Guild structure and seasonal changes in foraging behaviour of birds in a Central-European oak forest

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Foraging behaviour of 10 resident and 4 migratory species was studied throughout a year in an oak forest of the Bükk Mts., North-Hungary. The resident species could be grouped into two guilds by Principal Component Analysis. Tits (*Parus major*, *P. caeruleus*, *P. palustris*), Long-tailed Tit (*Aegithalos caudatus*) and Goldcrest (*Regulus regulus*) were included in the foliage-gleaning guild, while woodpeckers (*Dendrocopos major*, *D. medius*, *D. minor*), Nuthatch (*Sitta europaea*) and Treecreeper (*Certhia* sp.) formed the bark-foraging guild. Chiff-chaff (*Phylloscopus collybita*), Wood Warbler (*P. sibilatrix*) and both species of flycatchers (*Muscicapa striata* and *Ficedula albicollis*) were not separated from the resident species as flycatcher guild, instead they were included in the foliage-gleaning guild.

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1. Introduction

Foraging behaviour of tits, woodpeckers and associated species has been studied in several parts of Europe, e.g., in England (Hartley 1953, Gibb 1954, Morse 1978), in Scandinavia (Haftorn 1956, Ulfstrand & Nilson 1976, Hogstad 1978a, Alatalo 1981), in South Europe (Herrera 1978, Moreno 1981, Rolando 1983), in West Europe (Laurent 1986) and in the western part of Central-Europe (Winkler 1973, Jenni 1983). In the Eastern part of Central-Europe similar investigations are found in Jablonski (1967), Török (1986), and Székely (1986a, 1987).

Birds which feed on common resources can be called a guild (Root 1967). Although Root emphasized the ecological relation between species instead of taxonomical one, in practice the guilds are usually restricted to relatives e.g., to a genus or a family (Hairston 1981, Pöysä 1983). A strong desire for the explicit demonstration of guilds was urged by MacNally (1983) and Wiens (1983), but in fact only a few studies made efforts to a quantitative delimitation of guilds (Holmes et al. 1979, Landres & MacMahon 1983).

Multivariate statistics may be an appropriate method to delimitate the guilds, since the Hutchinsonian niche concept is basically a multivariate approach (Wiens 1983).

The field observations of foraging behaviour were usually interpreted by niche theory and competition (Gibb 1954, MacArthur 1958). The role of competition seems to be plausible at least in vertebrate communities (Cody 1974, Hairston 1981), but clear evidence is difficult to present. The need for experiments has been stressed in the last few years (Connel 1983, Schoener 1983), however recently the credibility of adequate observations was also demonstrated by Alatalo et al. (1986).

Foraging behaviour of birds was usually investigated either on small groups of species e.g., tits (Ulfstrand 1977, Hogstad 1978a), woodpeckers (Winkler 1973, Jenni 1983) or during certain part of the year, e.g., breeding season (Seather 1982) and winter (Morse 1978, Laurent 1986).

In our study foraging behaviour of the most common resident species and of some migrant ones were investigated

Tab. 6. Seasonal niche breadth of tits and bark-foragers in five niche dimensions. The mean niche breadths of species was standardized in each dimension separately. Then the mean standardized niche breadths was calculated for each species. Separate standardization were carried out on tits from bark-foragers. The standardization was performed only on species having more than 50 observations in each season.

	<i>P. major</i>	<i>P. caer.</i>	<i>P. palus.</i>	<i>D. major</i>	<i>D. med.</i>	<i>D. minor</i>	<i>S. europ.</i>	<i>Certh. sp.</i>
Height								
Winter	2.48	5.50	3.07	3.86	2.66	2.60	3.91	4.20
Breeding	4.38	4.13	3.79	2.44	2.56	2.15	2.90	3.44
Autumn	4.00	3.23	3.97	2.54	1.94	—	2.83	3.10
Mean	3.62	4.29	3.61	2.95	2.39	—	3.21	3.58
Substrate								
Winter	1.98	1.15	1.40	3.44	3.81	1.09	5.67	4.46
Breeding	1.50	1.57	1.30	4.23	4.03	1.04	4.44	5.93
Autumn	1.33	1.07	1.64	3.10	3.02	—	5.38	4.78
Mean	1.60	1.26	1.45	3.59	3.62	—	5.16	5.06
Posture								
Winter	2.07	2.04	1.89	2.07	3.21	2.67	6.40	2.27
Breeding	1.34	1.74	1.42	2.40	3.13	2.41	4.47	2.28
Autumn	1.23	1.85	1.41	1.97	2.84	—	3.75	2.16
Mean	1.55	1.88	1.57	2.15	3.06	—	4.87	2.24
Method								
Winter	1.52	2.02	1.77	2.71	2.39	2.07	1.70	1.25
Breeding	1.82	1.96	1.78	3.03	2.11	2.46	1.94	1.36
Autumn	1.45	1.99	1.78	2.32	2.25	—	2.28	1.24
Mean	1.60	1.99	1.78	2.69	2.25	—	1.97	1.28
Tree species								
Winter	2.36	1.67	2.04	1.19	1.55	1.01	1.31	1.35
Breeding	1.63	1.33	1.93	1.27	1.36	1.28	1.36	1.57
Autumn	1.62	1.48	1.60	1.14	1.46	—	1.26	1.97
Mean	1.87	1.49	1.86	1.20	1.46	—	1.31	1.63
Standardized	-0.17	0.19	-0.02	-0.32	-0.38	—	0.57	0.13

ones in each season. In substrate, the niche breadth of Lesser Spotted Woodpecker was smaller than that of the other bark-foragers due to the avoidance of thick branches (Tab. 4).

Standardizing all of the five niche dimensions of bark-foragers, the Nuthatch had the widest niche breadth (Tab. 6), and the Middle Spotted Woodpecker had small ones with the Great Spotted Woodpecker together, while that of the Treecreeper was a medium one. The average standardized niche breadths of bark-foragers were not significantly different (paired t-test, $p > 0.05$ for all possible combination of species).

3.3.3. Seasonal niche overlaps of foliage-gleaners

The overlap of foraging height between Marsh Tit and Long-tailed Tit was the highest in winter ($O=0.96$). The Marsh Tit foraged lower and the Spotted Flycatcher higher than the other foliage-

gleaners, therefore their pairwise overlaps with the other species were low in the breeding season. Between Chiff-Chaff and Wood Warbler was the highest overlap in the breeding season from the viewpoint of substrate ($O=0.98$). The foraging posture and method of Great Tit and Marsh Tit were the most similar (Tab. 7). The tree species of foraging Great Tit and Long-tailed Tit were extremely similar in winter ($O=0.99$), while in autumn the overlaps of three tits were high too (Tab. 7).

The pairwise overlaps varied in a definite way, from winter the overlaps increased to spring 11 cases out of 15, then decreased to autumn in 10 cases out of 15 (see Tab. 7). This tendency proved to be true for the Horn's index of overlap of guild as well. The value of Horn's index of overlap for the combined data of the foliage-gleaning guild were the highest in breeding season (except the substrate), while the overlaps were the lowest in

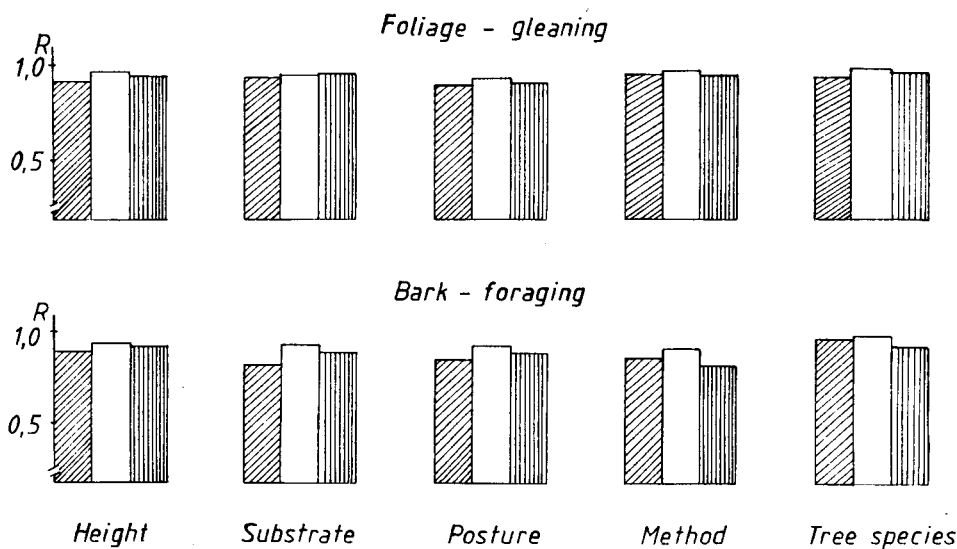


Fig. 6. Horn's indices of overlap of the two guilds for five niche dimensions. Symbols see in Fig. 1.

Tab. 7. Seasonal pairwise overlaps of tits for five dimensions.

	<i>P. major</i> & <i>P. caeruleus</i>	<i>P. major</i> & <i>P. palustris</i>	<i>P. caeruleus</i> & <i>P. palustris</i>	<i>P. major</i> & <i>R. regulus</i>	<i>P. caeruleus</i> & <i>R. regulus</i>	<i>P. palustris</i> & <i>R. regulus</i>	<i>P. major</i> & <i>A. caudatus</i>	<i>P. caeruleus</i> & <i>A. caudatus</i>	<i>P. palustris</i> & <i>A. caudatus</i>	<i>R. regulus</i> & <i>A. caudatus</i>
Height										
Winter	0.60	0.88	0.67	0.80	0.42	0.69	0.86	0.70	0.96	0.66
Breeding	0.89	0.72	0.63	-	-	-	-	-	-	-
Autumn	0.86	0.88	0.77	-	-	-	-	-	-	-
Substrate										
Winter	0.72	0.82	0.88	0.96	0.73	0.82	0.71	0.96	0.89	0.72
Breeding	0.94	0.93	0.89	-	-	-	-	-	-	-
Autumn	0.90	0.84	0.80	-	-	-	-	-	-	-
Posture										
Winter	0.72	0.88	0.77	0.83	0.59	0.74	0.79	0.72	0.86	0.64
Breeding	0.84	0.95	0.83	-	-	-	-	-	-	-
Autumn	0.72	0.88	0.80	-	-	-	-	-	-	-
Method										
Winter	0.71	0.89	0.81	0.92	0.63	0.81	0.88	0.60	0.78	0.97
Breeding	0.91	0.98	0.90	-	-	-	-	-	-	-
Autumn	0.74	0.88	0.85	-	-	-	-	-	-	-
Tree species										
Winter	0.69	0.85	0.80	0.70	0.40	0.60	0.99	0.71	0.87	0.69
Breeding	0.90	0.83	0.76	-	-	-	-	-	-	-
Autumn	0.95	0.97	0.96	-	-	-	-	-	-	-

winter, except the foraging method (Fig. 6). Due to the large data-set the differences seem to be small, so they were tested by the help of standardization. The overlaps of the three seasons were standardized in each dimension separately. The average of five standardized overlaps was calculated. The mean of standardized Horn's index of overlap increased from winter ($R=-0.81$) to breeding ($R=0.76$) (paired t-test, $t=5.03$, $p<0.01$) than decreased to autumn ($R=0.06$) (paired t-test, NS).

When both the winter and breeding season was divided into two subseasons, there were decreases of standardized overlaps from early winter ($R=0.10$) to late winter ($R=-1.24$) (pairwise t-test, $t=2.08$, $p<0.1$) and from early breeding ($R=0.84$) to late breeding ($R=-0.05$) ($t=2.42$, $p<0.05$). We obtained the highest overlap during the early breeding season.

3.3.4. Seasonal niche overlaps of bark foraging guild

The height of Nuthatch and Treecreeper overlapped markedly in the breeding season and autumn (Tab. 8). The substrate of Great Spotted Woodpecker and Middle Spotted Woodpecker were very similar in winter and in autumn (Tab. 8). The Treecreeper foraged on thicker branches and the Lesser Spotted Woodpecker on thinner ones than the other species, so these species were distinct from the others. The overlaps of foraging postures between Great Spotted Woodpecker and Middle Spotted Woodpecker were high throughout the year. The foraging methods of Great Spotted Woodpecker and Treecreeper were the less similar due to the frequent pecking of the first species and the almost exclusive searching of the latter one (Tab. 8). The overlaps of the tree species used for foraging were higher than 0.8 among the bark foragers, the only exception to the rule is the Treecreeper in autumn, since it foraged frequently on Turkey Oak (Tab. 8).

We think, it is particularly important, that the pairwise overlaps of bark-foragers increased from winter to spring (25 cases out of 30 and one remained the same), than they decreased to autumn in 28 cases out of 30. So we experienced the trend of niche overlaps

between bark-foragers similarly to foliage gleaners. This trend seem to be true for the Horn's index of overlap of the whole guild as well. The highest overlap of bark foragers in each dimension was in spring, while the lowest ones were in winter (3 cases out of 5) (Fig. 6). The standardized Horn's index of overlap increased from winter ($R=-0.53$) to breeding ($R=0.95$) (paired t-test, $t=5.79$, $p<0.001$). The values of Horn's index of bark-foragers were lower than that of the foliage-gleaners (paired t-test, $t=2.18$, $p<0.05$). Therefore in general the foraging behaviour of bark-foragers was more separated than that of the foliage-gleaners, that is while the foliage-gleaner can be a 'tightly packed guild', the guild of bark-foragers is less tight (see also Fig. 4).

According to the 5 subseasons the standardized Horn index of overlaps of bark-foragers were the highest in late breeding ($R=0.87$), while the lowest ones were in early winter ($R=0.66$) and in autumn ($R=-0.58$). In contrast to the foliage-gleaners, the overlap of bark-foragers was higher in late winter ($R=-0.42$) than early winter (paired t-test, NS) and it increased from early breeding ($R=0.79$) to late breeding (paired t-test, NS).

3.4. Foraging behaviour of male and female Great Spotted Woodpecker

The foraging height of sexes were not significantly different in either of the three periods (Tab. 4). During the year the male foraged on thinner branches than the female. In autumn the mean branch diameter for male was 9.01 cm, and that of the female was 9.48 cm (t-test, NS). However the differences between the two sexes tend to be greatest in the breeding season, that is the overlaps should be less during breeding (Tab. 8). The female pecked less frequently on shrubs than the male. Furthermore, the female foraged more frequently on Turkey Oak than the male in the breeding season (χ^2 -test, $p<0.001$).

In contrast to both foliage-gleaning and bark foraging guilds, the standardized Schoener overlap between the two sexes was the lowest in the breeding season ($O=-0.68$). The intraspecific overlaps were higher both in winter ($O=0.50$) and autumn ($O=0.18$) than in the breeding season

(paired t-test, $t=2.83$, $p<0.05$ and $t=1.47$, NS).

4. Discussion

4.1. Foraging behaviour

Foraging behaviour of birds is basically determined by food-resources (Lack 1971). However, other factors could modify the foraging behaviour too, e.g., the structure of habitat (Bilcke et al. 1986), the composition of trees via crop mass (Gibb 1954) and weather (Grubb 1975). Recently the role of predation and of dominance relationships were shown by Ekman (1987). Moreover, the composition of foraging flocks (Alatalo 1981), and the absence of competing species could affect foraging too (Alerstam et al. 1974, Alatalo et al. 1985a). Since these factors are varied among different deciduous forests, both the foraging behaviour of birds in Sífókút and the guild structure should be quite different from other deciduous forests.

However, there are a number of similarities between foraging behaviour of our populations and other deciduous ones. For example in Wytham Wood (England) the Great Tit foraged more often on the ground in late winter than in middle winter (Gibb 1954), while in April it suddenly modified its foraging substrate not only in our study site, but in England too (Hartley 1953). The Blue Tit foraged frequently in foliage than the Great Tit (Colquhoun & Morley 1943). The typical foraging substrates of Marsh Tit are slightly thicker branches than that of the Blue Tits, and they were more often on shrubs than on oaks (Morse 1978). In England each tits foraged frequently on leaves in spring (Gibb 1954) similarly to our findings. Jenni (1983) stated that the Great Spotted Woodpecker stays more frequently and longer at the same place in a Swiss oak forest, while it searched more rarely than the Middle Spotted Woodpecker. This agrees with our results in Sífókút Forest.

4.2. Guild structure

Based on the PCA the resident birds could be divided into two guilds. The foliage-gleaning guild and the bark-foraging guild were separated, since they exploited very different food resources. While in our analysis the Nuthatch and Treecreeper belonged to the bark-forager guild, Ulfstrand (1977) considered these two species as members of pariform guild. We suggest for these two species be included in the bark-foraging guild, because they forage chiefly on trunks and thick branches.

Generally the food of woodpeckers and Nuthatch is chiefly in or under the bark, so it is less superficial than that of the tits. It could be expected, that the food supply of woodpeckers is less exposed to weather, so it can be more stable than that of the tits. Due to the stable food of woodpeckers, their seasonal foraging behaviour can be expected to be less variable throughout the year than that of tits (Székely 1986b). Indeed, the bark-foragers showed weaker seasonal variation, than that of tits. So the foraging behaviour of bark-foragers could have evolved to species specific. For the foliage-gleaners the specialization to a variable food supply should not be advantageous, rather they could feed on each other's foods with almost the same efficiency (Alatalo and Lundberg 1983).

There are a lot of mechanisms which could cause different foraging behaviour (see above). In our case it seems to be feasible that the so often cited resource partitioning of tits should be the result of actual processes in ecological time, e.g., interspecific competition, which have been demonstrated by field observations (Herrera 1978, Alatalo 1981, Alatalo et al. 1985a) and laboratory ones (Alatalo & Lundberg 1983). In contrast to the foliage-gleaners, the foraging behaviour of bark-foragers seems to us as a result of a long-term adaptation to the stable food supply, which may have involved competition in the past during evolutionary time (R. Alatalo pers. comm.). Therefore, we conclude that the effect of present-day interspecific competition could be different within guilds of the same bird community.

The Wood Warbler and Chiff-Chaff are obviously foliage-gleaners. However, for the flycatchers a separate guild has been

suggested (Alatalo & Alatalo 1979). The food of flycatchers was very similar to the food of tits in another Hungarian oak forest during the breeding season (Török 1986). Therefore, the foraging behaviour of tits and flycatchers should be similar up to certain degree.

4.3. Niche measures

The standardized breadth of Blue Tit was the widest, and that of the Great Tit the narrowest. The same trend was reported by Morse (1978) and Alatalo (1982a). The opposite trend was demonstrated by Hartley (1953), Gibb (1954), Rolando (1982) and Seather (1982). The niche breadth of Great Tit was wider than that of the Blue Tit based on food composition during the breeding season in another Hungarian oak forest (Török 1986). This contradiction may not reflect real biological facts, rather they could be artificial, since the niche breadth is very sensitive to the number of categories (Colwell & Futuyma 1971). Therefore, we suggest the niche breadth is not directly related to generalised or specialised foraging behaviour unless one find a relevant type of categorization for a bird community (Cody 1974). Although it may be suitable to reveal broad differences in resource exploitation.

Within both guilds the overlaps are the highest in the breeding season, and the smallest in winter. Similar observations were reported by Betts (1955), Haftorn (1956), Stallcup (1968), Lister (1980) and Alatalo (1982a). The opposite tendency was reported by Ulfstrand (1977), who found the smallest overlaps in summer. He interpreted his findings by the help of diffuse competition (Pianka 1974). Due to the migratory visitors more species exploited the same food supply in summer, therefore the diffuse competition should be strong.

Based on the 5 subseasons in late winter and in the second part of breeding season the overlaps of foliage-gleaners were the smallest. We suppose, both decreases of niche overlaps were caused by the difficult periods of the birds (Perrins 1979), when interspecific competition for food become intensive. The tits are usually non-terri-

torial during winter in Hungary, in contrast to the British populations (Székely 1987). The bark-foragers are territorial during winter, so their food is spatially divided. Due to the territories, the exploitation of bark-forager's food could be slower than those of tits. The second decrease of overlap in summer agrees with the findings of Minot (1981). He suggested, the insects are superabundant only for a short period during the breeding season. The peak density of caterpillars was between April-May in Siskókút Forest (Szabó et al. 1983), then it sharply decreased. This is one of the main food of tits during their breeding cycle (Török 1986). Therefore, our results are consistent with the view, that the interspecific competition is an important mechanism of tits, at least in some periods (Alatalo 1982b, Alatalo et al. 1986).

Great Spotted Woodpeckers have individual territories throughout the year, only in the breeding season do the female and male share joint territories (Hogstad 1978b, Rychlik 1979). The foraging behaviour of the two sexes was the most different in the breeding season, so the enhanced foraging separation could be the result of interspecific competition. Therefore our result support the views of Selander (1966) and Ligon (1968), that the different niche utilization of sexes is one possible way of avoiding competition.

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Összefoglalás

Egy közép-európai tölgyerdő madarainak táplálékkereső viselkedése és guild szerveződése

Tíz állandó és 4 vonuló fajt vizsgáltunk egy éven keresztül a siskókúti cseres-tölgyes erdőben. A madarak táplálékkereső viselkedését a keresési

magasság, ágvastagság, keresési irány és mód, továbbá fajfaj alapján jellemeztük. Az állandó fajokat főkomponensanalízissel (PCA) két csoportba soroltuk. A cinegék (*Parus major*, *P. caeruleus*, *P. palustris*), az őszap (*Aegithalos caudatus*) és sárgafejű királyka (*Regulus regulus*) a cinegeguildet képezték, míg a harkályguild a harkályokat (*Dendrocopos major*, *D. medius* és *D. minor*), a csuszkát (*Sitta europaea*) és a fakuszt (*Certhia* sp.) foglalta magában. A csilp-csalp füzike (*Phylloscopus collybita*), sisegő füzike (*P. sibilatrix*) és két légykapó (*Muscicapa striata* és *Ficedula albicollis*) nem különült el az állandó fajoktól mint légykapó guild, hanem a főkomponensanalízis a cinegeguildbe sorolta őket.

A táplálékkereső viselkedés niche-szélessége fajonként változott, a cinegék közül a legnagyobb niche szélességűnek a kékcinegét, míg a legkisebbnek a széncinegét találtuk. A harkályguilden belül a legnagyobb niche szélességű a csuszka, míg legkisebb a közép fakopáncs volt. Habár a madarak táplálékkereső viselkedésének hasonlósága évszakonként változott, a cinegéknel 4 dimenzióban és harkályoknál mind az 5 dimenzióban a legnagyobb hasonlóságot a fészkelési időszak alatt tapasztaltuk.

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during one year, and here the residents of that study is reported. The following topics are examined: (1) the seasonal variation in foraging sites and techniques of species; (2) the sexual differences in foraging behaviour of Great Spotted Woodpecker; (3) delimitation of guilds by Principal Component Analysis; (4) the seasonal niche breadth and overlaps of species.

2. Methods

2.1. Study site

The field work was carried out in the Sikfókút Forest of the Bükk Mountains National Park (47°55' N, 20°28' E), which is 6 km from the town of Eger in Northeast Hungary. The elevation of study site is between 320 m and 340 m. The 64 hectare oak forest has two species of oak, the Sessile Oak (*Quercus petraea*) and the Turkey Oak (*Quercus cerris*). The total density of trees is 816 stems/hectare, while the ratio of Sessile Oak to Turkey Oak is 5.42. The average heights of Sessile Oak and Turkey Oak are 17.2 m and 18.7 m, respectively. Sixteen species of shrub are found in the forest, e.g., *Cornus mas*, *Acer campestre*, *Ligustrum vulgare*, *Euonymus verrucosus*. The height of trees is 15-20 m, and that of the shrubs varies between 1 and 4 m. The description of area is detailed in Jakucs (1985).

2.2. Field work

The observations on foraging behaviour were made in five niche dimensions. For each observation we recorded height, substrate, posture, foraging method and tree species. Height was estimated to the nearest meter. As substrate categories we used branches, leaves, acorns and litter, whereby branches were subdivided by diameter size in categories of 5 cm: 0-4.9 cm, 5-9.9 cm, etc. For 'posture' we recorded the foraging positions, e.g., perching, hanging, hovering, climbing upwards and climbing downwards. The foraging methods considered were searching, pecking, drilling, peeling, food and flycatching.

We separated searching (exploitation of food) and pecking (foodcatching and handling) which are usually combined as gleaning (Holmes et al. 1979). The fifth dimension, e.g., tree species includes the two oak species (Sessile Oak and Turkey Oak) and the shrubs. Because the exact identification of shrubs on which the birds foraged was difficult due to dense vegetation, we combined all of the shrubs into one category (see details in Székely 1986a, Székely 1987).

Data were collected at 15 second intervals for each of the five dimensions simultaneously. The fifteen seconds included 10 seconds of data recording and a slow counting up to five. That kind of observation was collected by other researches as well (Alatalo 1982a, Landres & MacMahon 1980). We followed the bird with a maximum limit of 20 consecutive records, but due to the fast movement of birds more than 5 records were rarely made. Due to the consecutive records we could avoid the effect of different bird detectability in various vegetational layers (Seather 1982, Wiens 1983).

Observations were collected from November 1983 to October of 1984. Three time periods were used: winter containing data from November-March, breeding season from April-July and autumn from August-October. For the niche measures both the winter and breeding season were split into two subseasons. In the latter case early winter included data from November to January, the late winter data from February to March, the early breeding data from April to May, the late breeding data from June to July and the autumn data from August to October.

We examined the most common and easily observable species throughout the year: Great Tit (*Parus major*), Blue Tit (*P. caeruleus*), Marsh Tit (*P. palustris*), Goldcrest (*Regulus regulus*), Long-tailed Tit (*Aegithalos caudatus*), Great Spotted Woodpecker (*Dendrocopos major*), Middle Spotted Woodpecker (*Dendrocopos medius*), Lesser Spotted Woodpecker (*Dendrocopos minor*), Nuthatch (*Sitta europaea*) and Treecreeper (*Certhia* sp.). As the two treecreeper species living in this area (*Certhia brachydactyla* and *C. familiaris*) are difficult to identify even in hand (Kuitunen 1986), we took the observa-

Tab. 1. The species studied, and the number of observations in each of the periods. Asterisks indicate data which have not been used in our analyses. (W = winter, B = breeding, A = autumn).

Species	W	B	A
<i>Parus major</i>	751	440	364
<i>Parus caeruleus</i>	869	524	384
<i>Parus palustris</i>	120	116	116
<i>Aegithalos caudatus</i>	170	12*	41*
<i>Regulus regulus</i>	211	29*	6*
<i>Dendrocopos major</i>	1051	924	697
<i>Dendrocopos medius</i>	637	166	123
<i>Dendrocopos minor</i>	345	54	31*
<i>Sitta europaea</i>	823	559	379
<i>Certhia</i> sp.	871	278	220
<i>Phylloscopus collybita</i>	-	165	26*
<i>Phylloscopus sibilatrix</i>	-	105	41*
<i>Ficedula albicollis</i>	-	71	-
<i>Muscicapa striata</i>	-	48	13*
Total	5848	3491	2441

tions for one species, *Certhia* sp. This might be resulted in broader niches than it is. Moreover, in the breeding season we observed another 4 species: Chiff-Chaff (*Phylloscopus collybita*), Wood Warbler (*P. sibilatrix*), Pied Flycatcher (*Ficedula albicollis*) and Spotted Flycatcher (*Muscicapa striata*). To reduce the subjective bias in the field work, only one of us (T. S.) collected the material. The observations were collected during 6 or 8 days per

month. Days with heavy rainfall, snowfall or stormy weather were avoided. During the year 400 hours of field work were completed. In this paper we examine only species of which we have more than 50 observations in a period. We made an exception only with Spotted Flycatcher on which we had 48 observations during the breeding period. The number of observations are listed in Tab. 1.

2.3. Multivariate analysis

We wanted to demonstrate changes of relative positions of species in the niche space during the year, therefore we carried out Principal Component Analysis (PCA) on the data set including all categories of the 5 dimensions as separate variables. The calculations were made by the BMDP programmes package (Dixon 1981). Eigenvalues greater than 1 were used to calculate the new orthogonally rotated Varimax variables. For the resident birds the three periods were analyzed simultaneously regarding the species as different units in each of the three periods (data-set 1). However, when we added four migratory species to the resident ones, the analysis was based only on data of May and of June (data-set 2).

2.4. Niche measures

We measured niche breadth by the Levins formula (Levins 1968):

$$B = \frac{1}{\sum p_i^2}$$

Tab. 2. Foraging height and diameter of branches of tits and Goldcrest during three seasons (means \pm S.D.).

	<i>P. major</i>		<i>P. caeruleus</i>		<i>P. palustris</i>		<i>A. caudatus</i>		<i>R. regulus</i>	
Height (m)										
Winter	4.93	± 4.77	8.48	± 4.95	5.91	± 5.02	6.16	± 5.16	3.10	± 3.58
Breeding	7.89	± 3.90	8.98	± 3.65	5.72	± 4.10	11.70	± 5.16	9.87	± 3.41
Autumn	7.88	± 3.56	8.87	± 2.94	7.40	± 3.30	5.36	± 3.12	5.60	± 6.20
Substrate (cm)										
Winter	3.27	± 3.85	2.70	± 2.09	2.74	± 1.68	2.48	± 0.39	2.62	± 0.91
Breeding	2.85	± 2.00	2.61	± 1.22	2.45	± 0.90	2.45	± 0.00	2.45	± 0.00
Autumn	2.73	± 1.64	2.46	± 0.26	3.47	± 3.13	2.57	± 0.78	2.45	± 0.00

Tab. 3. Percent observations of substrate when tits or Goldcrest was seen on leaves, or on the ground (see the number of observations in Tab. 1.).

	<i>P. major</i>	<i>P. caeruleus</i>	<i>P. palustris</i>	<i>A. caudatus</i>	<i>R. regulus</i>
On leaves					
Winter	2.8	2.4	0.0	0.0	5.7
Breeding	15.9	21.0	11.2	0.0	6.9
Autumn	4.4	2.6	9.8	0.0	16.7
On the ground or on snow					
Winter	26.9	2.2	13.3	4.7	25.1
Breeding	1.6	0.4	1.7	0.0	0.0
Autumn	6.0	0.3	0.0	0.0	0.0

where p_i is the relative frequency of the i th category.

Niche overlaps of species pairs were calculated by the Schoener index (Schoener 1968):

$$0 = 1 - \frac{1}{2} \sum |p_{xi} - p_{yi}|$$

where p_{xi} is the relative frequency of species x in category i while p_{yi} denotes the relative frequency of species y in category i .

Between more than two species the Horn's index of overlap was used (Horn 1966). This index can be applied for more than two species (Fekete & Précsényi 1981):

$$R = \frac{\sum (x_i + y_i) \log(x_i + y_i) - \sum x_i \log x_i - \sum y_i \log y_i}{(X + Y) \log(X + Y) - X \log X - Y \log Y}$$

where X and Y represent respectively, the total number of records of species x and y in the sample, while x_i and y_i represent the number of records made in the i th category in samples X and Y . The maximum value is zero.

We avoided comparing directly either the niche breadths or overlaps of different dimensions, because they based on various number of categories. Instead, we standardized the niche measures, than we calculated the averages of standardized measures of different dimensions. For example, when we wanted to compare niche overlaps of winter with those of breeding season in all of the five dimensions, at first

Tab. 4. Height and diameter of branches of woodpeckers, Nuthatch and Treecreeper (mean \pm S.D.)

	<i>D. major</i> ♂	<i>D. major</i> ♀	<i>D. medius</i>	<i>D. minor</i>	<i>S. europaea</i>	<i>Certhia</i> sp.
Height (m)						
Winter	9.78 (± 3.51)	9.97 (± 3.14)	10.65 (± 2.13)	11.92 (± 2.10)	8.11 (± 3.50)	6.40 (± 3.64)
Breeding	10.21 (± 2.34)	9.62 (± 3.39)	9.82 (± 2.25)	12.64 (± 2.05)	8.81 (± 3.14)	8.99 (± 3.30)
Autumn	9.01 (± 2.02)	9.48 (± 2.45)	10.05 (± 1.59)	11.72 (± 1.96)	7.91 (± 2.65)	7.37 (± 2.69)
Substrate (cm)						
Winter	8.14 (± 7.78)	9.17 (± 7.49)	9.52 (± 8.16)	2.80 (± 1.83)	14.19 (± 9.60)	22.72 (± 7.63)
Breeding	8.40 (± 7.52)	11.07 (± 9.47)	11.66 (± 9.75)	2.45 (± 0.0)	10.36 (± 8.84)	15.14 (± 8.64)
Autumn	7.38 (± 6.35)	8.22 (± 7.04)	6.91 (± 5.41)	2.61 (± 0.90)	11.27 (± 7.89)	17.18 (± 7.42)

Tab. 5. Foraging method of some studied birds (tits and woodpeckers) during the year indicated as percent observation (see Tab. 1. for number of observation; W=winter, B=breeding, A=autumn).

	<i>P. major</i>			<i>P. caeruleus</i>			<i>D. major</i>			<i>D. medius</i>		
	W	B	A	W	B	A	W	B	A	W	B	A
Searching	78.3	66.0	80.8	49.4	57.8	55.2	31.9	41.1	31.4	58.2	56.4	50.4
Pecking	21.4	33.6	19.0	50.2	42.0	44.5	9.0	23.9	9.9	23.4	39.4	43.1
Drilling	0.3	0.0	0.0	0.2	0.2	0.0	50.2	32.1	56.7	15.9	4.2	6.5
Peeling	0.0	0.0	0.0	0.2	0.0	0.0	8.2	2.9	2.0	2.3	0.0	0.0
Food hiding	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.2	0.0	0.0
Flycatching	0.0	0.4	0.2	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0

the standardized values were calculated separately in each dimension. Than the standardized values of winter (five values) were compared with those of breeding (five values). The standardizations were made as follows:

$$x' = \frac{x - \bar{x}}{s}$$

where x is the original variable, \bar{x} is the mean of original variables, s is the standard deviation of original variables, and x' is the standardized variable. The mean of the standardized variables in a particular dimension gives zero with the standard deviation of one. Since the statistical tests and comparison of niche measurements are

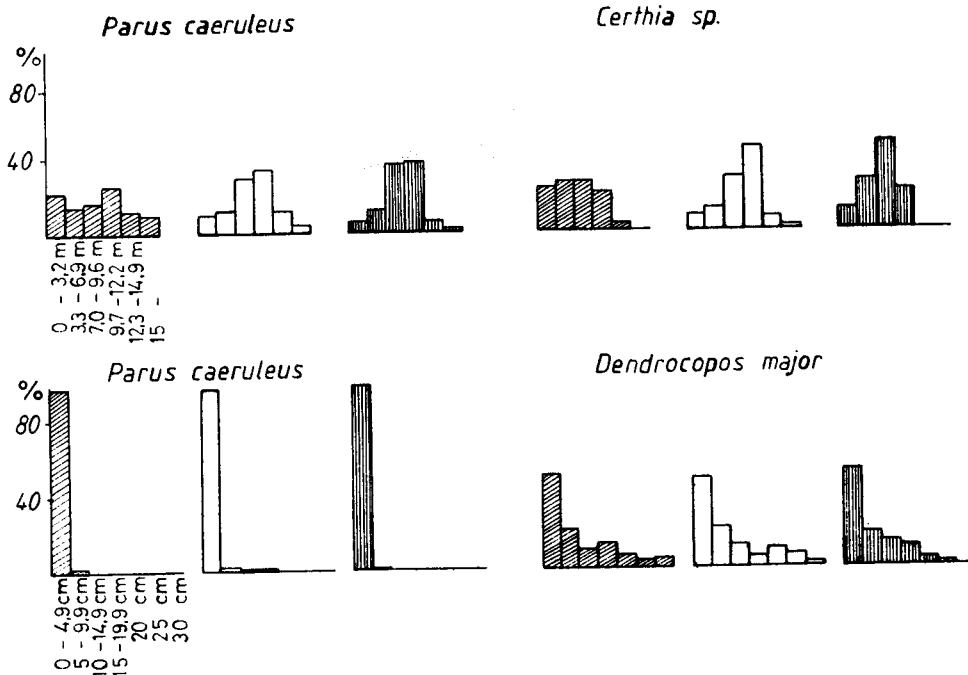


Fig. 1. Foraging height (upper row) and substrate (lower row) of some studied species in winter (▨), breeding (□) and autumn (▤).

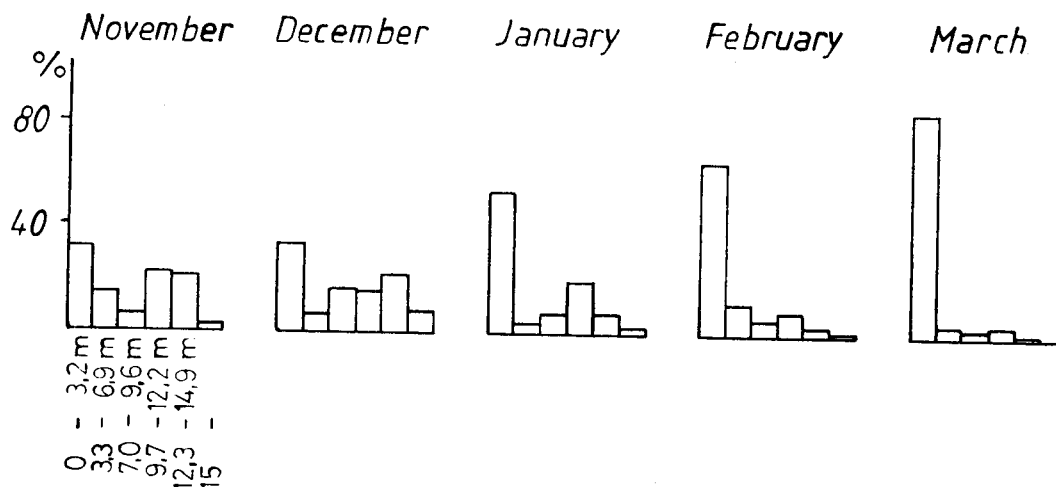
Parus major

Fig. 2. Relative frequency of foraging height of Great Tit in winter. The foraging height decreased from November to March. (Number of observations were 99, 114, 107, 212, 219, respectively.)

not straightforward (Hurlbert 1978), the standardized variables were used for statistical testing.

3. Results

3.1. Foraging behaviour

3.1.1. Height and substrate

In winter the Goldcrest, Long-tailed Tit and tits tended to forage on the ground and on shrubs, except the Blue Tit (Fig. 1), this resulted in low foraging height (see also Tab. 2). The low foraging was most typical for Great Tit which foraging height decreased gradually from November to March (Fig. 2). The above mentioned species almost exclusively foraged on the thinnest branches. However, during the breeding season and autumn the tits foraged in the crown of trees, except the Marsh Tit. The tits searched for food frequently on leaves in spring (Tab. 3). The Chiff-Chaff, Wood Warbler and flycatchers

foraged in the lower crown.

Both the Great Spotted Woodpecker and the Middle Spotted Woodpecker foraged chiefly on thicker branches of the upper parts of the stems than the tits, but usually on thinner ones than 5 cm (Fig. 1). The Lesser Spotted Woodpecker could be spotted on thinnest branches of the upper crown. The Nuthatch and Treecreeper were characteristic on middle or lower parts of stems (Tab. 4). The Nuthatch was observed on leaves 6% of their times in the breeding season.

3.1.2. Foraging posture and method

Great Tit and Marsh Tit mainly perched, while the Blue Tit frequently hung in each of the periods. Only the Goldcrest hovered regularly, hovering was 8.3% of their time in winter. The typical foraging method of flycatchers was flycatching, but they pecked from the surface too.

The Great Spotted Woodpecker chiefly drilled and peeled off the bark (Fig. 3). The Middle Spotted Woodpecker was more mobile and it searched and pecked

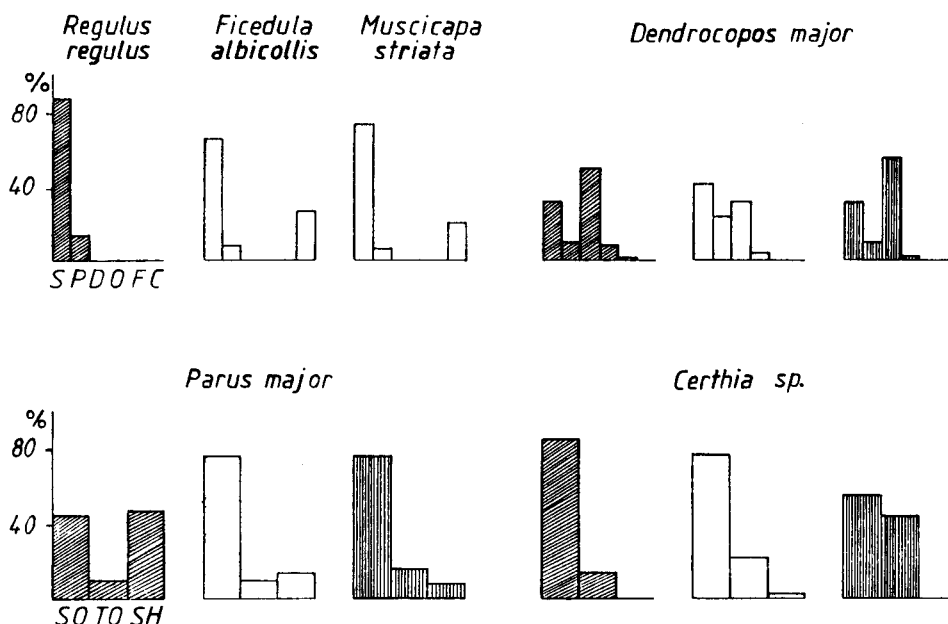


Fig. 3. Foraging method (upper row) and tree species (lower row) of some studied species in winter (▨), breeding (□) and autumn (▤). The abbreviations of categories as the follows: S = searching, P = pecking, D = drilling, O = peeling, F = food hiding, C = flycatching, SO = Sessile Oak, TO = Turkey Oak, SH = shrubs.

more frequently than the former species (Tab. 5). The Great Spotted Woodpecker searched more often in the breeding season than in winter or autumn (Fig. 3). The Nuthach pecked more rarely than the Great Spotted Woodpecker, and the Treecreeper was never observed drilling or peeling off the bark.

3.1.3. Tree species

The tits, Goldcrest and Long-tailed Tit foraged mainly on shrubs in winter (Fig. 3). However, in the rest of the year tits, warblers and flycatchers preferred the trees to the shrubs.

The woodpeckers, Nuthach and Treecreeper were observed mainly on trees. Since the density of two tree species was known (see study site) it was possible to say when a bird preferred a tree to another.

The Great Spotted Woodpecker, Lesser Spotted Woodpecker and Nuthatch preferred the Sessile Oak to the Turkey Oak in all of the three periods, while the Middle Spotted Woodpecker and Treecreeper were neutral in their tree-choice or slightly preferred the Turkey Oak (Fig. 3) (Székely 1986b).

3.2. Guild structure

We analyzed the foraging behaviour of resident birds by Principal Component Analysis (data-set 1) simultaneously in each of the three periods. Three eigenvalues were greater than one, and we have accepted these three components following the general practice. The three components explained about 91.5% of the total variance. The most important variables of the first axis were perching, search-

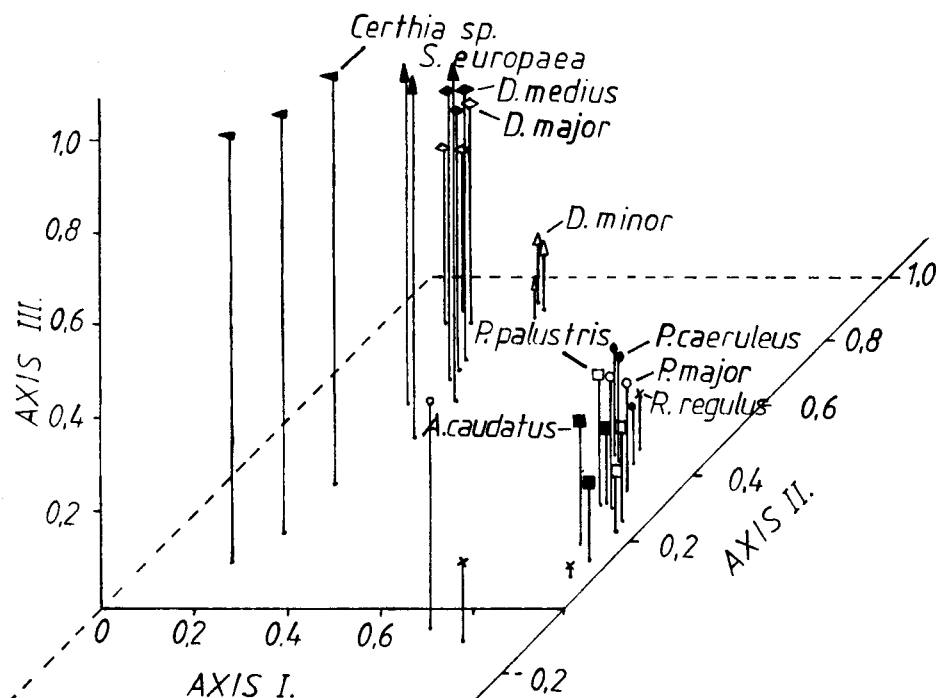


Fig. 4. Distribution of resident species along the three-dimensional principal component space in winter, breeding and autumn. The first component included 66.5% of the total variance, while the second and third ones explained 17.6% and 7.4% of total variance, respectively.

ing, and being on 0-4.9 cm of branch diameter. Along the first principal component the species were split into two guilds (Fig. 4). The foliage-gleaning guild included the tits, Goldcrest, and Long-tailed Tit, while the bark foraging guild involved the woodpeckers, Nuthatch and Treecreeper. However, along the second principal component the Treecreeper was among the foliage-gleaners, and in winter the Nuthatch was very close to the foliage-gleaners, probably because the major variables of second axis were drilling and being on Sessile Oak. However, we could not identify any single niche dimension as PCA axis. The foliage-gleaners formed a tight group in the three-dimensional space excluding the Great Tit and Goldcrest (Fig. 4). The latter two species were separated from the foliage-gleaners in winter, since they foraged more often on the ground than the others did (Tab. 3). In contrast to

foliage gleaners, the bark foraging species clearly separated from each other throughout the year.

When we added four migratory species to the resident birds (data-set 2), only two components had greater eigenvalues than one. Therefore we have accepted the first two principal components. The two components explained about 84.8% of the total variance. The most important variables of first axis were perching, searching, and being on 0-4.9 cm branch diameter, while that of the second axis were being in 0-3.2 m height, and foraging on Sessile Oak. The basic separation between the two guilds was similar to the first analysis. Both the warblers and flycatchers were included in the foliage-gleaning guild (Fig. 5).

3.3. Niche measures

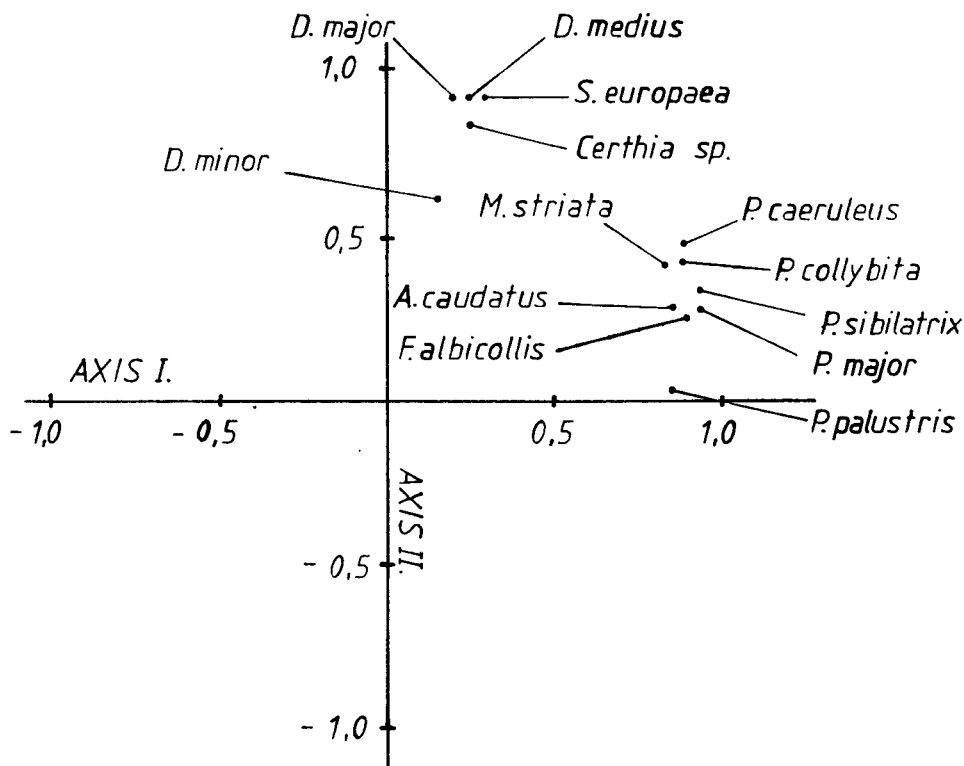


Fig. 5. Distribution of migratory species and resident ones along two principal components in May-June. The first two principal components included 69.1% and 15.7% of the total variance.

The species were separated into two guilds according to the PCA in both of the two data-sets (Figs. 4 and 5). Because the two guilds were highly separated from each other, we focused the niche measures within each of them.

3.3.1. Seasonal niche breadth of foliage-gleaners

In foraging height the Blue Tit had the widest niche breadth among foliage-gleaners during the winter (Tab. 6), while in the breeding season Great Tit had the widest one. The niche breadth of substrate were very similar among foliage-gleaners. The Goldcrest had an extremely wide niche breadth in posture in winter ($B=3.09$). The niche breadth of Chiff-Chaff and Wood Warbler was greater ($B=2.32$ and $B=2.24$ respectively) than that of the

other foliage-gleaners from the viewpoint of foraging method in the breeding season.

To reveal the typical niche-breadth for the foliage-gleaner species, the dimensions were standardized (see methods) and we compared the standardized niches of species. The Blue Tit had the widest standardized niche breadth (Tab. 6), the Great Tit had the smallest one, while that of the Marsh Tit was medium ($B=-0.02$). The average standardized niche breadths of species were not significantly different by paired t-test ($p>0.05$ for all possible combination of species).

3.3.2. Seasonal niche breadth of bark foragers

The niche breadth of Treecreeper was the widest in foraging height (Tab. 6), while in posture the Nuthatch had extremely wide