

Bird community changes in different-aged oak forest stands in the Buda-hills (Hungary)

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Bird community parameters were analysed in six stages of oak forest succession from brushwood to climax. Bird data were collected in the breeding season with the modified I.P.A. method, which gives density estimations for 100 m radius circles. Community diversity, expressed in relative density and rarefaction species number was greatest in the fourth stage of succession, in 61-80 year old forest stands. Open forest birds and hole-nesters reach their maximum densities here. A sharp difference was found between the community structure of the initial, open brushwood and the older, closed forest stages. This pattern emerged both from comparisons of the whole community and of different ecological groups of birds based on primary feeding, nesting and migratory habits. Different speciation and adaptation mechanisms in the open and closed habitats are supposed to be responsible for this difference. No clear pattern emerged from the analysis of the degree of specialisation within families.



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1. Introduction

Succession is the process whereby plant and animal communities succeed each other in time. Secondary succession takes place where some vegetation has existed before but has been removed. The earlier vegetation might be removed by either a natural (e.g., fire, wind, snow) or human action (clear-cutting). The study of secondary succession may follow two general methods. One of them is long-term, as is to examine the development of vegetation at the same place for a long time (direct method). The other is short-term, when we suppose that communities of different composition or age are members of a successional process and study them separately in the same year or within a few years (indirect method). Both of the methods are widespread among studies of animal communities.

Several hypotheses suggest that vegetation has the most significant role in forming bird community structure, through either its physiognomy (MacArthur 1964, MacArthur & MacArthur 1961, MacArthur et al.

1962) or its floristics (Rotenberry 1985). Whether general characteristics of succession such as an increase in diversity, density, stability and specialisation stated by Margalef (1968) and Odum (1969) can apply to birds or not is not yet unequivocal. In addition there is a strong bias in bird community studies towards north-temperate forests, so the possibility of making generalisations from the results is rather restricted.

This paper analyses the bird community structure of a typical central-european oak forest secondary succession. To avoid biases caused by small study area size and subjectively chosen successional stages, I divided the whole successional sere into 20-year intervals and applied a method which enabled me to survey comparatively large areas. The method and number of study plots were chosen so that the results could be comparable to those previously obtained in a nearby beech sere (Moskát 1988, Moskát & Székely 1989). The multivariate analysis of the vegetational and bird species composition of the two series will be the topic of another paper (Moskát & Waliczky MS).

Tab. 1. Vegetation variables of the successional stages.

Variable	Successional stages					
	A	B	C	D	E	F
Grass cover (%)	21	66	66	71	60	36
Shrub cover (%)	82	11	39	23	41	65
Canopy cover (%)	0	78	74	71	71	71
Tree height (m)	0.00	11.50	14.30	16.70	15.50	17.50
Shrub height (m)	2.49	1.39	1.30	1.55	2.57	2.98
Tree distance (m)	0.00	1.37	2.06	2.76	2.36	2.52
Shrub distance (m)	0.45	1.04	0.51	0.83	1.39	1.06
DBH (cm)	4.00	13.70	17.30	25.70	26.00	30.50
Number of tree species	4	3	6	8	3	8

Here I will discuss only the patterns of bird community parameters (species numbers, composition and density).

2. Study area

The study area is situated in the Buda-hills near Budapest, North-central Hungary (47°35' N, 18°90' E). The hills lie between 215-529 m a.s.l. Average yearly precipitation is 650 mm, average temperature is 8.7°C (Pécsi 1958).

Different-aged oak forests were chosen to represent the whole spectrum of secondary succession from the brushwood stage to the climax. The study plots were later grouped into six evenly aged stages, each with a 20-year interval. These stages can be characterized as follows:

Stage A: brushwood stage (<20 years old). Very dense, shrub-like stands of primarily Sessile Oak (*Quercus petraea*). The percent coverage of several shrub species, mainly Dog Rose (*Rosa canina*), Common Hawthorn (*Crataegus monogyna*), Common Privet (*Ligustrum vulgare*), Wart-cress (*Euonymus verrucosus*) is very high in these stands.

Stage B: young forest stage (21-40 years old). These are homogenous, dense, closed-canopy Sessile Oak-Turkey Oak (*Quercus cerris*) stands. Canopy cover is highest, shrub cover is lowest here.

Stage C: thinwood stage (41-60 years old). These forests are almost homo-

genous plantations of Sessile or Turkey Oaks, with scattered Wild Cherry (*Prunus avium*), Field Maple (*Acer campestre*) and Flowering Ash (*Fraxinus ornus*) trees. More open stands with moderate shrub cover consisted of mainly low (<1m) shrubs.

Stage D: high forest (61-80 years old). This includes the most open stands with low shrub cover and lowest tree density. Tree species besides the two oaks are Field Maple, Wild Service Tree (*Sorbus torminalis*) and European Ash (*Fraxinus excelsior*).

Stage E: preclimax stage (81-100 years old).

Stage F: climax stage (>100 years old, mostly between 101-120 years). The older stands are similar in appearance, though the oldest ones have higher shrub cover and taller shrubs in average. In these stands there are a few montane tree species like Beech (*Fagus sylvatica*), Sycamore (*Acer pseudoplatanus*), Norway Maple (*Acer platanoides*) and European Ash.

The physiognomical parameters of each successional stage can be consulted on Tab. 1, number of study plots and size of study area on Tab. 2.

3. Material and Methods

3.1. Bird data

Tab. 2. Main bird community parameters of the six phases of secondary oak succession. S : species number; Sr : rarefaction species number; N : total number of individuals in each phase; D : density (pairs/10 ha); n : number of study plots; A : study area (total coverage of study plots) (ha).

Phase	S	Sr	N	D	n	A
A	19	19.0	129	46.36	9	28.26
B	24	21.2	185	45.32	13	40.82
C	29	22.2	454	60.24	24	75.36
D	28	24.1	510	70.62	23	72.22
E	24	24.0	175	61.92	9	28.26
F	26	23.1	279	63.47	14	43.96

Bird density estimations were made in the spring of 1988 on each of the 92 plots. The method applied was the modified I.P.A. method (Moskát 1987). This is a point-count survey with a fixed, 100 m radius. All birds detected - heard or seen - have to be recorded within a 10 minute interval in each plot. The count has to be done twice in the breeding season at the same place, preferably once in April and once in May. This aims to survey the whole bird community, the early as well as late breeders. For every species recorded the higher estimate has to be accepted. Compared to the territory-mapping method this census gives an approximately 71% efficiency (Moskát 1987) in estimating bird densities on a community basis.

For the sake of censusing on exactly the same plots, big, yellow numbers were painted on selected trees, marking the centres of plots. The painting work and

selection of study plots was carried out in early spring, in February-March.

3.2. Vegetation data

The physiognomical variables recorded were as follows: grass cover, shrub cover, canopy cover, tree height, shrub height, tree distance, shrub distance, diameter of breast height (DBH), number of tree species. Grass, shrub and canopy cover were estimated by eye on each plot. Data on tree height, DBH and number of tree species were collected from the data bank of the Forestry Commission. Shrub height, tree distance and shrub distance were measured on at least twenty shrub and tree individuals around each plot center and later averaged.

3.3. Statistical analysis

Tab. 3. Species which have the highest dominance in different phases of oak succession (numeric dominance is over 10 percent of the whole community).

Species	Dominance (%) in stage					
	A	B	C	D	E	F
<i>Sylvia atricapilla</i>	15		11			
<i>Phylloscopus collybita</i>	15					
<i>Luscinia megarhynchos</i>	13					
<i>Fringilla coelebs</i>		13	11	11		
<i>Emberzia citrinella</i>		11	13			
<i>Parus major</i>					11	13
<i>Sitta europea</i>					10	
<i>Sturnus vulgaris</i>						14

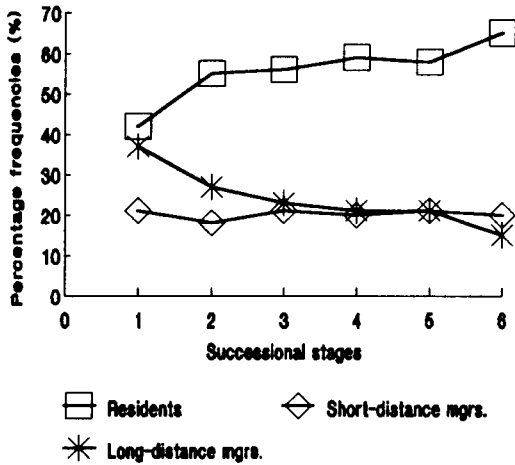


Fig. 1. The contribution of residents, short-distance migrants and long-distance migrants to the whole community in the successional stages in terms of species richness.

Because of the negative affect of different-sized study plots on diversity calculations (Wiens 1989), a rarefaction method was applied to estimate expected species number on plots of equal size (James & Rathbun 1981). This method has advantages over diversity indices (Wiens 1989) and gives a more accurate picture of community heterogeneity over different areas. The program RAREFACTION (Ludwig & Reynolds 1988) was applied for performing calculations. The formula is that of Hurlbert (1971):

$$E(S_n) = \sum_{i=1}^S \left\{ 1 - \left[\frac{\binom{N-n_i}{n}}{\binom{N}{n}} \right] \right\}$$

where n_i is the number of individuals of

the i th species, N is the total number of individuals and S is the species number when the sample contains n individuals.

For measuring similarity between bird communities in different successional stages the Sørensen's similarity index was used:

$$C = 2j / (a + b)$$

where j : number of species common to the two samples; a , b : total number of species in samples a and b .

4. Results

4.1. General community parameters

The absolute number of species is highest in stage C; the total number of individuals, average density per 10 ha and rarefaction species number is highest in stage D (Tab. 2.). The lowest number of species and individuals was found in stage A, the lowest density in stage B (Tab. 2).

The dominant species (over 10% of the total number of individuals) of each successional phase and their numerical dominance values can be consulted on Tab. 3. Species, which are dominant in more than one phase are Blackcap (*Sylvia atricapilla*), Chaffinch (*Fringilla coelebs*), Yellowhammer (*Emberiza citrinella*) and Great Tit (*Parus major*).

4.2. Community similarity

Tab. 4. shows that community similarity is

Tab. 4. Sørensen's similarity indices for the comparison of bird communities in different successional stages in oak secondary succession.

	A	B	C	D	E	F
A	1.000	0.500	0.531	0.500	0.500	0.435
B		1.000	0.830	0.808	0.833	0.760
C			1.000	0.912	0.830	0.764
D				1.000	0.885	0.852
E					1.000	0.880
F						1.000

Tab. 5. Grouping of bird species in each successional phase according to their primary nesting habits. Species numbers, numeric dominance in parentheses (percentage).

Breeding habit	A	B	C	D	E	F
Ground-nester	5 (26)	6 (25)	7 (24)	6 (22)	5 (21)	5 (19)
Shrub-nester	9 (47)	4 (17)	5 (17)	4 (14)	3 (12)	3 (12)
Canopy-nester	3 (16)	4 (17)	4 (14)	4 (14)	5 (21)	5 (19)
Hole-nester	2 (11)	10 (41)	13 (45)	14 (50)	11 (46)	13 (50)

lowest between stage A and all of the other stages, especially stage F. Other stages show a high similarity to each other in terms of species; the indices are lower for B-F and C-F comparisons.

4.3. Ecological groups

Grouping the species in each seral community according to their primary nesting habits we see that ground-nesters and foliage-nesters have similar ratios in every stage. Shrub-nesting species predominate in stage A then fall sharply and remain in a fairly constant ratio in closed-canopy stands. For the hole-nesters the situation is reversed, they have the lowest contribution to the whole community in stage A and predominate in all of the stages from B to F (Tab. 5).

For the groups using similar feeding places the ground-feeding group has the highest contribution to total species number in stage A then stabilizes at a lower level from stage B on. The foliage-gleaners have a fairly constant ratio in the whole sere. There are no bark-foragers in the initial stage, from B on their ratio is very similar to those of ground-foragers (Tab. 6).

4.4. Migratory status

Rarefaction species numbers were estimated on 27.1 ha (the area of the smallest number of study plots in a stage) according to their status of being sedentary, short-distance migrant or long-distance migrant. Short-distance migrants have a low and stable ratio in the whole sere (Fig. 1). On the same figure long-distance migrants and sedentary species show a reversed ratio: starting from almost the same position the former increases, the latter decreases in the course of succession.

For densities of the same groups we see very similar results with the difference that long-distance migrants have the lowest ratios in every stage and the short-distance migrant group has intermediate position (Fig. 2).

4.5. Specialization in genus and families

The highest species/genus ratio was calculated for stage C, and the highest species/family and genus/family ratios were found in stage A. In each case stage D has the lowest indices (Tab. 7).

5. Discussion

5.1. General community parameters

Tab. 6. Grouping of bird species in different stages of forest succession according to their primary feeding habits. Species numbers, numeric dominance in parentheses (percentage).

Feeding on	A	B	C	D	E	F
Ground	10 (53)	6 (25)	9 (31)	9 (32)	7 (29)	7 (27)
Foliage	9 (47)	12 (50)	14 (48)	11 (39)	10 (42)	11 (42)
Bark	0 (0)	6 (25)	6 (21)	8 (29)	7 (29)	8 (31)

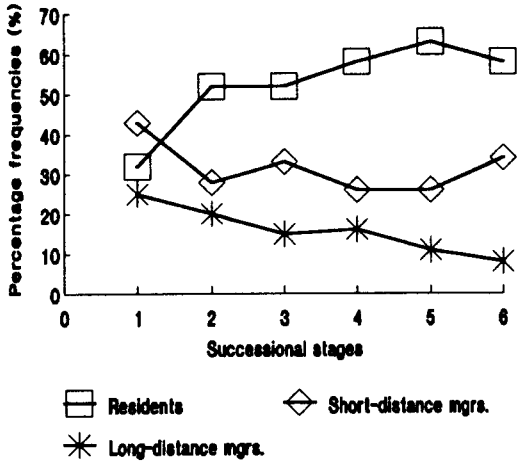


Fig. 2. The ratio of the three different group of birds based on migratory status in each of the successional stages measured in abundances.

Absolute species number was found to be highest in stage C (see results). The area is greatest here, so it may come from the species-area relationship proposed by Preston (1960, 1962). This predicts that the greater the area the higher the species number it supports. This bias in species numbers towards the larger areas can be eliminated by the application of the rarefaction method (James & Rathbun 1981). According to successional theory (Odum 1969) community diversity and stability increases during succession. For birds this is supported by a wealth of studies (e.g., Kendeigh 1948, Odum 1950, Johnston & Odum 1956, Karr 1968, Shugart & James 1973, Glowacynski 1975). However, this increase is not monotonic in every case. Smith & MacMahon (1981), for example, found that diversity peaked in the preclimax forest. According to the data of May (1982) in North America and Bejcek & Stastny (1984), Glowacynski & Weiner

(1983) and Moskát & Székely (1986) in Europe diversity and density show a two-peaked distribution in the course of succession. In Europe the decrease takes place between 30-40 years of age which is in agreement with my density data but not with the rarefaction species number. Moskát & Székely (1986) explained it as a consequence of a lack of both hole-nesters and shrub-nesters in these communities. The absence of high trees and a significant shrub level is also true for our study forests of this age.

My results that both density and rarefaction species number have their peaks in stage D do not fit the above-mentioned patterns. Several common species reach their maximum density here, namely Great, Middle and Lesser Spotted Woodpeckers (*Dendrocopos major*, *D. medius* and *D. minor*), Tree Pipit (*Anthus trivialis*), Collared Flycatcher (*Ficedula albicollis*), Chaffinch and Golden Oriole (*Oriolus oriolus*). In the habitat selection of these species either old trees or openness seem to play a significant role. The vegetational physiognomy of this stage satisfies these requirements as both canopy and shrub cover are low here. This follows from the forest management practice of selective thinning which creates a situation uncommon in natural succession. However, there are no great differences between rarefaction species numbers of the five closed forest stages.

This similarity of the later stages is expressed in the similarity indices, too. The same applies to ecological groups of birds. All these suggest that there is a sharp difference between shrub-like and closed-canopy forests. Analysing bird community data from successional seres of different localities over Europe Blondel & Farré (1988) found that the initial, open stages

Tab. 7. Degree of specialization in bird communities of different phases of forest succession in terms of species/genus, species/family and genus/family ratios.

Ratio	A	B	C	D	E	F
Species/genus	1.357	1.500	1.526	1.400	1.333	1.368
Species/family	2.111	2.000	2.070	2.153	1.714	1.857
Genus/family	1.555	1.333	1.357	1.538	1.286	1.357

differed much while old stages converged to each other. They explained this on historical grounds, namely, that the similarity of the European forest faunas is pronounced because these habitats were not fragmented during the Pleistocene. On the other hand, speciation in open and semi-open habitats were helped by the fragmentation of such habitats in the same time period. This hypothesis is also helpful when explaining the sharp demarcation found between bird communities of the initial stage A and closed forest stages in our study.

5.2. Migratory status

The ratio of long-distance migrants is highest in the initial brushwood phase and decreases towards the climax while that of the sedentary species show an opposite trend. This is true for both the species number and density. The difference between these ratios in the initial and later stages is statistically significant (Mann-Whitney U-test, $p < 0.05$). The same pattern has been obtained by many researchers for European forest successions (Bilcke 1984, Helle & Fuller 1988, Mönkkönen & Helle 1989), while a reversed ratio of tropical migrants were found in North American successions (MacArthur 1959).

There are three hypotheses explaining these observations. MacArthur (1959) proposed that the proportion of migrants is highest in places where the change between winter and summer food supply is greatest. Alerstam & Enckell (1979) hypothesize that migrants are better competitors in open habitats because birds with simple niches can more easily fit into an existing community in their winter quarters. Finally, Bilcke (1984) assumes that the proportions of migrants in the breeding area is determined by the proportion and geographic distribution of the vegetation types in the winter quarters. This latter hypothesis was strongly supported by Mönkkönen & Helle's work (1989). They showed that the first two hypotheses failed to explain intercontinental differences while that of Bilcke's was successful in doing so. The proportion of forested land is highest in South America, lowest in

Africa. The nesting habits of long-distance migrants follow this pattern: in North America they inhabit mainly forested habitats while in Europe they select open or brushy habitats more often. Though a rigorous test of this hypothesis is still needed, the arguments supporting it seem strong.

5.3. Specialization

The hypothesis that specialization as measured by species/genus, species/family or genus/family ratios increases during succession (Margalef 1968, Odum 1969) was not supported by our data. Because others reached the same conclusion (Głowacynski 1979, Helle 1985) either the method is wrong for measuring specialization or the hypothesis is false. A more promising method would be to actually measure diet or foraging microhabitat niche breadth of every species in the successive communities and calculate the actual ratio between specialists and generalists. Then we can conclude whether specialisation increases as succession progresses or not. In the absence of such data we cannot state that succession in our case would lead to greater specialization.

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Összefoglalás

Madárközösség-változások különböző korú tölgyesekben a Budai-hegységben

Jelen dolgozat a tölgyerdei másodlagos szukcesszió hatását vizsgálja a madárközösségek szerkezetére. A vizsgálat a szukcesszió hat fázisát foglalja magában, a sűrűség fázistól a klimaxnak tekinthető öreg erdőkéig. Az egyes madárfajok denzitásadatait az ún. módosított I.P.A. módszerrel becsültük, amely 100 m sugarú körökre szolgáltat adatokat. Összesen 92 mintavételi kör adatai szerepelnek az elemzésekben, ezek fázisonkénti megoszlása a sűrűségtől az öreg erdőig a következő:

9, 13, 24, 23, 9 és 14.

A legalacsonyabb fajszám a sűrűség fázisban, a legalacsonyabb denzitás a vékony rudas erdőben (B fázis) volt. Ez utóbbinak az oka valószínűleg a cserjeszint és az odúk szinte teljes hiánya ezekben az erdőkben. A legmagasabb denzitás és rarefaction-módszerrel számított fajszám a szálaserdőben (D fázis) mutatkozott, ami azzal magyarázható, hogy számos odúlakó faj (pl. harkályok, örvös légykapó) és nyílt, ligetes erdőket kedvelő faj (pl. erdei pityer) itt éri el a maximális denzitást. Ez a nyitott, kis cserjeszintű erdőszerkezettel hozható összefüggésbe, amit az erdőgazdálkodás a törzskiválasztó gyérléssel és az ezzel járó munkálatok utóhátsaival hozott létre.

A teljes közösségek és a fészkelési, táplálkozási és vonulási szokásokon alapuló ökológiai csoportok összehasonlításakor egyaránt kifejezett a különbség a cserjeszintű, fiatalos fázis és a többi, záródott fázis között. Ez a hipotézisek szerint a kétféle élőhelyen különböző módon lezajlott fajképző folyamatok és alkalmazkodási mechanizmusok következménye lehet. Az európai madárközösségek szukcessziójában általános vonás, hogy a nyíltabb élőhelyektől a zártabbak felé haladva csökken a közösségekben a hosszútávú, trópusi vonulók aránya. Bilcke (1984) hipotézise szerint, amelyet Mönkkönen és Helle (1989) is megerősített, ennek magyarázata az, hogy az afrikai telelőterületen nagyobb arányban található nyílt - szavannás, félsivatagi - élőhelyek.

Margalef (1968) és Odum (1969) hipotézisét, amely szerint a szukcesszió során a specializáció mértéke növekszik, a faj/nemzettség, faj/család, nemzettség/család arányszámok nem támasztották alá. Mivel más kutatók (pl. Helle 1985) is hasonló eredményeket kaptak, valószínű, hogy a módszer nem alkalmas a tényleges specializáció mértékének a megállapítására.

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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 breadthes of species was standardized in each dimension separately. Then the mean standardized niche breadthes 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 breadthes 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, than 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

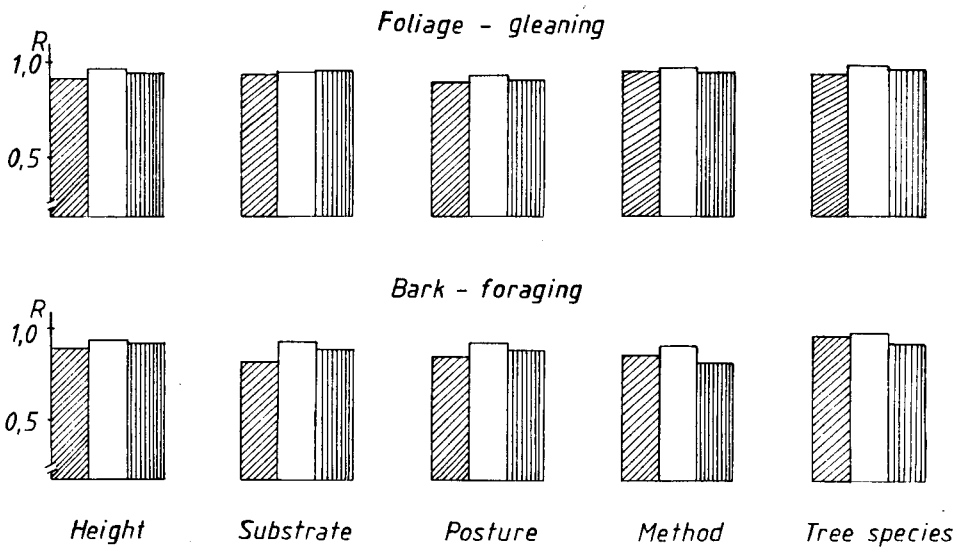


Fig. 6. Horn's indices of overlap of the two guilds for five niche dimensions. Symbols see in Fig. 1.

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. major</i> & <i>R. regulus</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

Tab. 8. Pairwise overlaps of bark-foragers for five niche dimensions. The intraspecific overlaps of male (♂) and female (♀) Great-Spotted Woodpecker are also indicated.

	<i>D. major</i> & <i>D. medius</i>	<i>D. major</i> & <i>S. europaea</i>	<i>D. major</i> & <i>Certhia</i> sp.	<i>D. major</i> & <i>D. minor</i>	<i>D. medius</i> & <i>S. europaea</i>	<i>D. medius</i> & <i>Certhia</i> sp.	<i>D. minor</i> & <i>S. europaea</i>	<i>D. minor</i> & <i>Certhia</i> sp.	<i>D. medius</i> & <i>Certhia</i> sp.	<i>D. minor</i> & <i>S. europaea</i>	<i>D. minor</i> & <i>Certhia</i> sp.	<i>D. medius</i> & <i>Certhia</i> sp.	<i>D. minor</i> & <i>S. europaea</i>	<i>D. minor</i> & <i>Certhia</i> sp.	<i>S. europaea</i> & <i>D. major</i>	<i>S. europaea</i> & <i>D. major</i>
Height																
Winter	0.81	0.67	0.83	0.62	0.74	0.69	0.52	0.50	0.33	0.79	0.92					
Breeding	0.88	0.44	0.83	0.80	0.41	0.86	0.36	0.87	0.42	0.90	0.91					
Autumn	0.79	-	0.80	0.75	-	0.59	-	0.56	-	0.89	0.87					
Substrate																
Winter	0.90	0.52	0.72	0.34	0.47	0.76	0.30	0.37	0.10	0.60	0.84					
Breeding	0.84	0.43	0.92	0.65	0.42	0.88	0.41	0.76	0.20	0.70	0.85					
Autumn	0.94	-	0.76	0.46	-	0.76	-	0.43	-	0.62	0.92					
Pesture																
Winter	0.74	0.80	0.57	0.41	0.75	0.65	0.59	0.58	0.34	0.51	0.95					
Breeding	0.83	0.88	0.74	0.54	0.78	0.84	0.73	0.67	0.50	0.64	0.92					
Autumn	0.80	-	0.72	0.39	-	0.87	-	0.53	-	0.55	0.93					
Method																
Winter	0.59	0.86	0.53	0.41	0.58	0.81	0.52	0.70	0.40	0.86	0.95					
Breeding	0.69	0.79	0.70	0.56	0.51	0.90	0.51	0.72	0.72	0.81	0.89					
Autumn	0.48	-	0.52	0.41	-	0.88	-	0.61	-	0.69	0.96					
Tree species																
Winter	0.84	0.92	0.94	0.92	0.78	0.90	0.87	0.92	0.85	0.98	0.97					
Breeding	0.95	0.98	0.97	0.89	0.97	0.98	0.97	0.93	0.89	0.92	0.87					
Autumn	0.87	-	0.95	0.62	-	0.90	-	0.75	-	0.66	0.95					

(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 Siskfókút 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 siskfókúti cseres-tölgyes erdőben. A madarak táplálékkereső viselkedését a keresési

magasság, ágvastagság, keresési irány és mód, továbbá fajaj alapján jellemeztük. Az állandó fajokat főkomponensanalízissel (PCA) két csoportba soroltuk. A cinegék (*Parus major*, *P. caeruleus*, *P. palustris*), az őszapó (*Regulus 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 cinegékénél 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 breath 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 sp.</i>	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 \pm 4.77	8.48 \pm 4.95	5.91 \pm 5.02	6.16 \pm 5.16	3.10 \pm 3.58
Breeding	7.89 \pm 3.90	8.98 \pm 3.65	5.72 \pm 4.10	11.70 \pm 5.16	9.87 \pm 3.41
Autumn	7.88 \pm 3.56	8.87 \pm 2.94	7.40 \pm 3.30	5.36 \pm 3.12	5.60 \pm 6.20
Substrate (cm)					
Winter	3.27 \pm 3.85	2.70 \pm 2.09	2.74 \pm 1.68	2.48 \pm 0.39	2.62 \pm 0.91
Breeding	2.85 \pm 3.00	2.61 \pm 1.22	2.45 \pm 0.90	2.45 \pm 0.90	2.45 \pm 0.00
Autumn	2.73 \pm 1.64	2.46 \pm 0.26	3.47 \pm 3.13	2.57 \pm 0.78	2.45 \pm 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

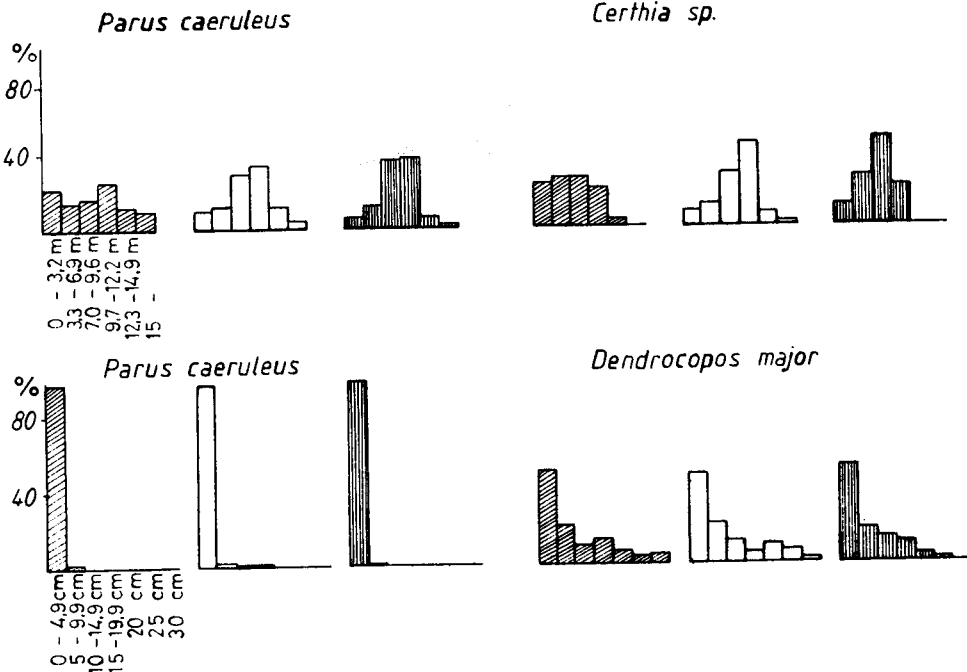


Fig. 1. Foraging height (upper row) and substrate (lower row) of some studied species in winter (▨), breeding (□) and autumn (▤).

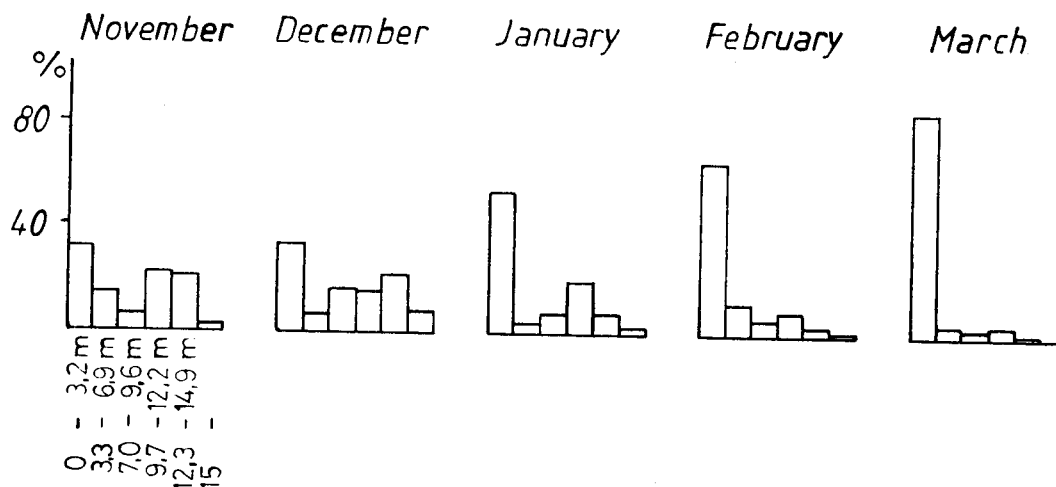
Parus major

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

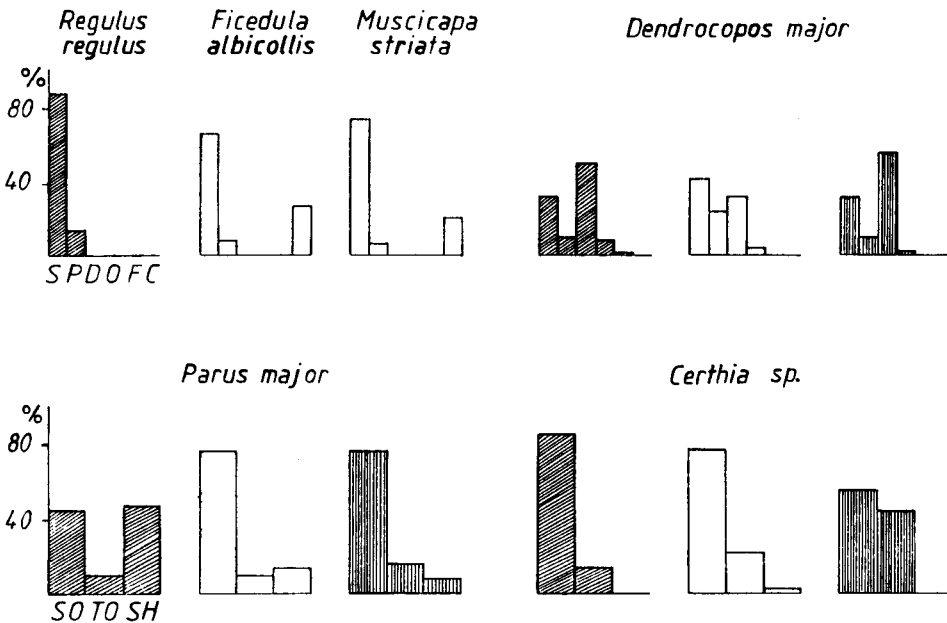


Fig. 3. Foraging method (upper row) and tree species (lower row) of some studied species in winter (▨), breeding (□) and autumn (▤). The abbreviations of categories as the follows: S = searching, P = pecking, D =drilling, O =peeling, F = food hiding, C = flycatching, SO = Sessile Oak, TO = Turkey Oak,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

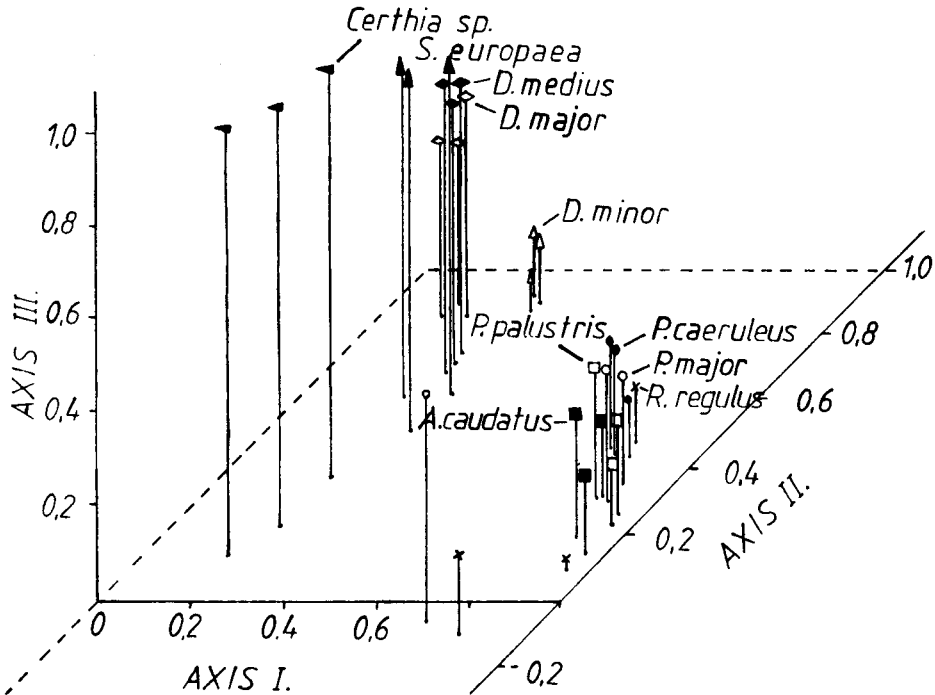


Fig. 4. Distribution of resident species along the three-dimensional principal component space in winter, breeding and autumn. The first component included 66.5% of the total variance, while the second and third ones explained 17.6% and 7.4% of total variance, respectively.

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 Tree-creeper. However, along the second principal component the Tree-creeper 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

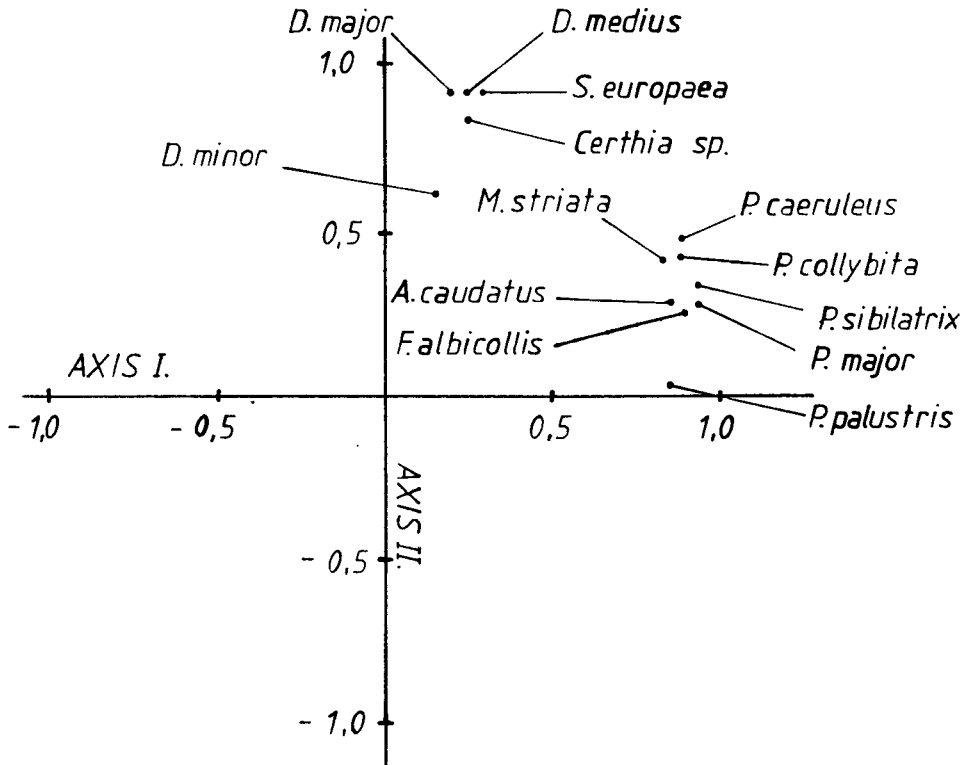


Fig. 5. Distribution of migratory species and resident ones along two principal components in May-June. The first two principal components included 69.1% and 15.7% of the total variance.

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

Effect of environmental factors on tits wintering in a Hungarian marshland

A. Báldi and T. Csörgő

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We studied Great Tits and Blue Tits during six winters in a marshland in Central Hungary. The number of wintering Tits increased during the study. Tits were found to be residents, immigrants and floaters. The number of immigrants decreased in mid-winter in both tit species, while the number of residents increased. The number of immature floaters changed parallel to that of immigrants, but the number of adult floaters was low and did not change considerably during winter. For both Great and Blue Tits the presence of nest-boxes and artificial feeding increased the overwintering numbers, and for the Blue Tit the effect of temperature was also significant.

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1. Introduction

Population fluctuations of tits and their regulating factors have puzzled ecologists for many years (e.g., Perrins 1965). There is a big 'surplus' of yearling Tits (*Parus* spp.) after fledgling, but only a small portion is able to survive until the next breeding season (Perrins 1965). The recruited portion mainly depends on winter survival (Perrins 1979, Ekman 1984, Tinbergen et al. 1985, Nilsson 1987, Orell 1989), therefore winter survival seems to be crucial in the regulation of Tit populations.

The available resources are probably sparse in winter. The mortality rate can increase because of food deficiency, low ambient temperature, snow cover, predation risk and competition (Balén 1980, Jansson et al. 1981, Ekman 1984, Desrochers et al. 1988). The influence of winter temperature and snow cover has indirect effects mediated by a weather-dependent food shortage (Svensson 1981, Källander & Karlsson 1981, Bejer & Rudemo 1985). Gibb (1960) found that the number of Tits and Goldcrest (*Regulus regulus*) changed

in parallel with the abundance of insects and invertebrates. An abundant beechmast crop enhanced the survival of Tits in winter (Perrins 1965, Balén 1980, Drent 1984, Bejer & Rudemo 1985), just as did artificial food provided by man (Balén 1980, Brittingham & Temple 1988, Desrochers et al. 1988, Orell 1989). The greater the winter survival the greater the breeding density of Tits in the consecutive spring (Perrins 1979, Balén 1980, Jansson et al. 1981, Drent 1984, Ekman 1984), although the reproductive success was lower in food added areas (Jansson et al. 1981).

Although the overwinter movements and population fluctuations of tits has been thoroughly studied in Scandinavia (Orell 1989), England (Perrins 1965, 1966), Germany (Croon et al. 1985) and the Netherlands (Balén 1980, Balén & Hage 1989), much less is known about Central Europe. Particularly, our knowledge is weak concerning tits living in less preferable habitats such as marshes or plantations.

In this paper we were interested in Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*) living in a marsh in Hungary.

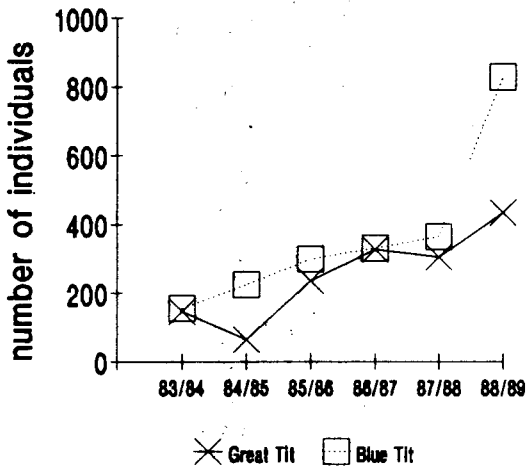


Fig. 1. Number of wintering Great and Blue Tits in the study area.

We analysed the data on the number of birds and composition of populations and also the effect of temperature, snow cover, artificial feeding and nestboxes on these populations.

2. Study area and methods

Field work was done in the Nature Reserve of Ócsa SE of Budapest in central Hungary (47°15' N; 19°15' E). There is a full successional sere of swamp vegetation in the area from open water to Alder (*Alnus glutinosa*) woods.

Area I. The main part of the study was carried out at the Bird Ringing Center of the Hungarian Ornithological Society, near Ócsa. The study area is situated between agricultural land and reedbeds (*Phragmites communis*). The vegetation in the ecotone is very variable, there are patches of reeds, Bullrush (*Typha angustifolia*), marshes, various willow bushes (*Salix alba*, *S. cinerea*, *S. caprea*), Elder (*Sambucus nigra*), and Poplar Trees (*Populus* spp.).

Data were collected in winters from 1983 to 1989. We used data from October to

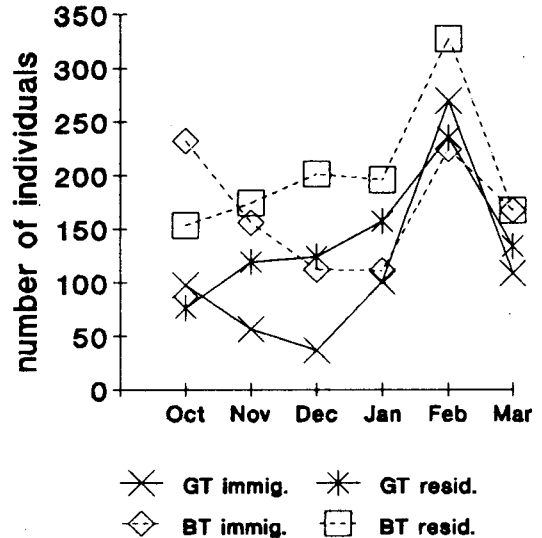


Fig. 2. Number of Tits in relation to time, based on pooled data of the survey.

April for this paper. The birds were mist-netted at bird tables. In the winters of 1983/84 and 1984/85 we fed the birds with sunflower seeds only when mist-netting was carried out. This was not enough however to influence the settlement of birds. In the following years we continuously provided a large surplus of artificial food, therefore we influenced the settlement of birds throughout the winter. The bird tables were placed among bushes and the mist-nets were placed around them in the shape of a triangle or square. Mist-netting was carried out only under fine weather conditions, when there was no rain, snow or wind. The different number of mist-netting days in different months were linked to an equal number of mist-netting days throughout the six winters. Nestboxes were put in the area in the spring of 1987.

Occasionally mistnets were placed in a reed patch both in the winter and breeding seasons.

Area II. The second part of the study was conducted in the same region, about 10 km from the Bird Ringing Center. The area was a small plot of alder wood (7 ha) with bushy surroundings. 100 nestboxes were placed in the forest patch in the spring

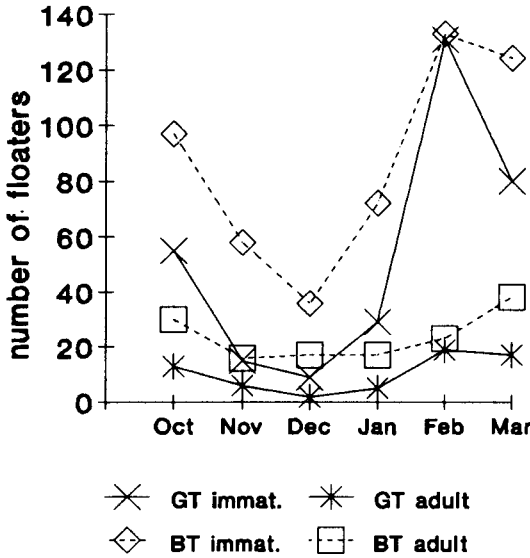


Fig. 3. Number of floater Tits in relations to time, based on pooled data of the survey.

of 1986. The nestboxes were visited at night every two weeks in the winters from 1986/87 to 89/90, to check the roosting tits. Beside the nestbox area bird feeders were put out and mist-netting was carried out.

Meteorological data (monthly mean temperature, snow cover and depth) were available from Monor, a village 20 km from Ócsa.

The recorded Tits were distinguished on the basis of their status, being floaters, immigrants or residents. Residents were those birds already captured in summer or in more winters, immigrants were the newly captured birds. Those birds captured only once were considered as floaters.

The data were analyzed with the SPSS/PC+ statistical program package (Norusis 1986). We applied multiple stepwise regression-correlation- and principal-component analyses. The multiple stepwise regression calculations were performed on the basis of summed monthly number of individuals, linked to an equal number of mist-netting days. The independent variables were monthly mean temperature, percentage of days covered

by snow in a month, number of bird tables and number of nestboxes.

3. Results

The number of captured tits increased in the six consecutive winters in both species (Fig. 1). The number of Blue Tits increased monotonously, but the increase in Great Tits broke down in the harsh winters of 1984/85 and 1987/88. The decrease was greater in the winter of 84/85, because in this winter there was no continuous feeding (see above).

The pooled data of the six winters showed that there were parallel changes in the number of birds between the resident and between the immigrant Great and Blue Tits (Fig. 2). Within the two species the number of individuals did not change in parallel between residents and immigrants. In all cases there was a peak in the number of individuals in February (Fig. 2).

The ratio of Blue Tit:Great Tit was 7:10 in summer and 30:12 in winter in the reeds. The difference between summer and winter proportions proved to be significant (Student test for proportions; $t=8.52$, $n=42$, $p<0.001$), that is the number of Blue Tits increased significantly in

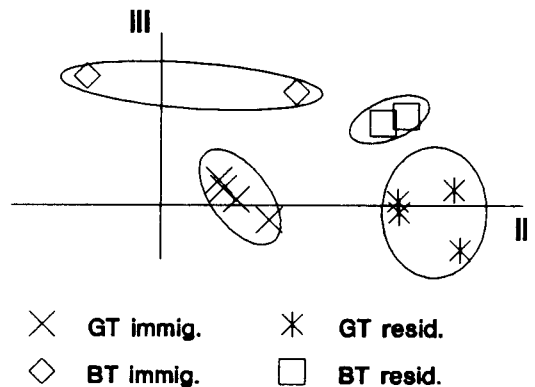


Fig. 4. Position of Tit groups on second (II) and third (III) Principal Component axes explaining 12.2% and 10.9% of the total variance, respectively. The second axis can be interpreted as status, the third as species.

Tab. 1. Pearson's correlation coefficients and its one-tailed significance (*: $p < 0.01$; **: $p < 0.001$) between the different groups.

	G.T. ad. male immig.	G.T. ad. fem. immig.	G.T. im. male immig.	G.T. im. fem. immig.	G.T. ad. male resid.	G.T. ad. fem. resid.	G.T. im. male resid.	G.T. im. fem. resid.	B.T. ad. immig.	B.T. im. immig.	B.T. ad. resid.	B.T. im. resid.
G.T. ad. male immig.	1	*	**	**	**	NS	**	**	NS	NS	*	NS
G.T. ad. fem. immig.		1	NS	**	NS	NS	NS	**	NS	*	NS	NS
G.T. im. male immig.			1	**	*	NS	**	**	NS	*	*	*
G.T. im. fem. immig.				1	*	NS	**	**	NS	*	NS	*
G.T. ad. male resid.					1	**	**	**	NS	*	**	**
G.T. ad. fem. resid.						1	**	**	NS	NS	NS	*
G.T. im. male resid.							1	**	NS	*	**	**
G.T. im. fem. resid.								1	NS	*	**	**
B.T. ad. immig.									1	**	NS	NS
B.T. im. immig.										1	**	**
B.T. ad. resid.											1	**
B.T. im. resid.												1

the reeds in winter.

The pattern of monthly fluctuations in abundance in both species was more vigorous in the change of the immature floaters (Fig. 3), while the number of adult floaters was low, and did not show considerable changes.

The principal-component analyses (PCA) separated four groups, namely resident Blue and Great Tits and immigrant Blue and Great Tits (Fig. 4).

Only the Great Tit data of Area II. were analysed here, because the sample size was too small for the Blue Tit. We divided the Great Tit population into two groups. In group F those birds were clustered, which were registered only at the bird feeders, by mist-netting. Group R consists of birds checked when roosting in the nestboxes, with no attention to whether they visited the feeders or not. The tendency to be resident (group R) or floater (group F) was significantly different between group F and R (chi-square test with Yates cor-

rection; $\chi^2=31.90$, $df=20$, $p < 0.05$) (Fig. 5). These findings supported the results of PCA, that is the status is one of the most important factors affecting winter population fluctuations in tits.

The correlations between the species, age, sex and status groups were significant only in the case of a positive correlation, that is the number of individuals of the different groups changed in parallel (Tab. 1).

Four environmental factors were analysed in the study, the temperature, snow cover, presence or absence of artificial feeding and the number of nestboxes. These factors showed different relationships with the groups of tit species, age, sex and status (Tab. 2). The results of the multiple stepwise regression analyses showed that artificial feeding had by far the greatest effect on the population fluctuations of the Great Tit, but the number of nestboxes had a significant effect, too (Tab. 2). In the case of the population

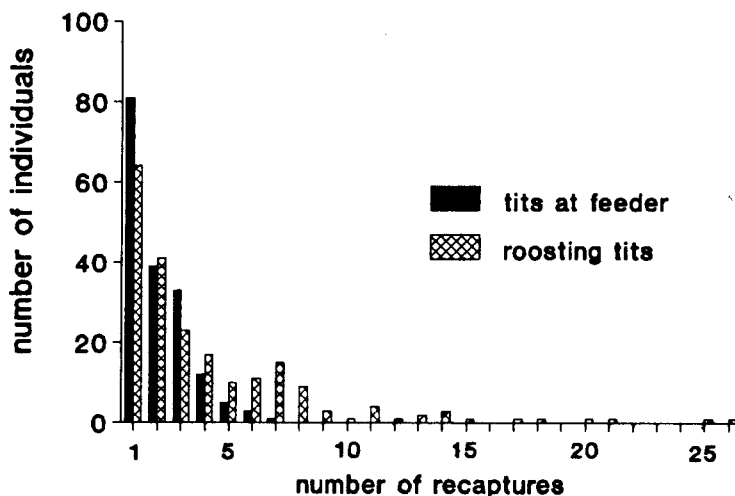


Fig. 5. Number of recaptures of Great Tits in area II, based on data of the consecutive winters.

fluctuations of Blue Tit, there were three significant factors, namely the number of nestboxes, temperature and feeding (Tab. 2).

4. Discussion

The number of recorded Tits increased during the study in Ócsa, like in several parts of Europe (Hildén 1987, Balen & Hage 1989, Winkel 1989). The number of wintering Great Tits dropped in the study area in hard winters. In Hungary Great Tits move to villages in winter, where human activity and farming may enhance the chance of survival (Sasvári 1978). Seasonal shifts in habitat use of the titmice seems to be common (Bilcke 1984, Møller 1984). This is contradictory to the findings of Perrins (1979), who showed that the Blue Tit moved to town, and the Great Tit stayed in forests in England.

The number of Blue Tits declined to a much lesser degree in cold winters. Hildén (1987) pointed out that the long-term increase in the abundance of Blue Tits in Finland is the consequence of the extending of the reed stands where the species forages in winter. The use of reed-beds was supported by this study, since the ratio of Blue Tit:Great Tit increased significantly in winter in the reeds.

According to Balen & Hage (1989) the increasing number of individuals during the study period may be the consequence of the decrease in the proportion of long-distance movements of the Great Tit, which might be caused by improved conditions in winter. In the Netherlands these improved conditions were due mostly to the enhanced proportion of artificial feeding (Balen 1980, Balen & Hage 1989).

Status is of crucial importance in determining the winter movements of individuals and thus the changes in winter populations of titmice. Clobert et al. (1988) reached similar conclusions, though they defined status in a slightly different way. It is not worth being floater (Smith & Arcese 1989).

The majority of the resident Tits were adult individuals, whereas floaters were mostly immatures. Adult floaters were scarce and might be residents in another part of the area, but they occasionally visited the feeders. The low number of resident immature individuals may be the consequence of the subdominant position of the immature Tits (e.g., Perrins 1979).

Artificial feeding provides very rich foraging patches, so it attracts birds from long distances, but the overcrowding, increased predation pressure, searching for emptied territories and better survival conditions led to the dispersion of transient

Tab. 2. Results of multiple regression calculations after stepwise elimination of insignificant variables. For significant relations R and significance of F are given (R (significance of F)).

	Temperature	Snow cover	Feeding	Nestboxes
G.T. male ad. immig.	NS	NS	0.379 (0.023)	NS
G.T. female ad. immig.	NS	NS	NS	0.463 (0.004)
G.T. male im. immig.	NS	NS	NS	NS
G.T. female im. immig.	NS	NS	0.488 (0.003)	NS
G.T. male ad. resid.	NS	NS	0.588 (0.000)	0.649 (0.000)
G.T. female ad. resid.	NS	NS	0.420 (0.012)	NS
G.T. male im. resid.	NS	NS	0.594 (0.000)	NS
G.T. female im. resid.	NS	NS	0.645 (0.000)	NS
B.T. ad. immig.	0.379 (0.023)	NS	NS	NS
B.T. im. immig.	0.672 (0.000)	NS	NS	0.604 (0.000)
B.T. ad. resid.	NS	NS	0.614 (0.000)	0.525 (0.001)
B.T. im. resid.	NS	NS	NS	0.644 (0.000)

tits (e.g., Kluyver & Tinbergen 1953, Ekman 1984, Orell 1989, Sullivan 1989). Thus the winter population fluctuations of titmice is mostly due to floaters. The number of resident tits fluctuated less, because it was determined by the characteristics of the area, that is the food availability and presence of nesting cavities. Their fluctuation is probably the consequence of the changes in the frequency of feeder visiting. There was a great peak in abundance in February in all of cases, because this is the period of the spring territory occupations of the floaters (Balén & Hage 1989).

Ekman (1984) pointed out that the number of Willow Tit (*Parus montanus*) declined in winter and it had minimum value in February. The Willow Tit probably has a different wintering strategy than Blue and Great Tits. The former species winters in closed social units, whereas the two latter species winter in loosely organized systems (Ekman 1989, but see Saitou 1978). Furthermore, the Willow Tit is a hoarding species (Perrins 1979), therefore the pressure on this species to float or migrate in winter may not be as strong as is the case with Blue Tits and Great Tits.

Resident Great Tits had roosting sites in the area and nesting holes and they can

claim territories in spring. The resident individuals move from their territories to a much greater extent in winter than in spring. In winter we recorded resident tits at the feeders in area II, which have regularly bred and continuously roosted for four years in the nestbox area, about 700-800 m from the feeders. The territorial Great Tits leave their territories to a considerably lesser extent in the breeding season (Ydenberg 1984).

Competition is an important factor affecting the populations of Tits in the breeding season (Minot & Perrins 1986, Török 1987) and in winter (Dhondt & Eycerman 1980, Alatalo et al. 1986). The existence of competition assumes that when conditions deteriorate, the number of individuals in one species decreases, while the other increases. Similar patterns can be expected within species, too. This could be detected as negative correlations in the number of birds between species or within species, but we were unable to find such correlations, only positive ones. This led us to the conclusion that there was no significant competition between Tits.

Environmental factors had different effects on the Tits. Great Tits usually forage on the ground in winter (Perrins 1979, Székely 1985), therefore one might expect that the effects of snow, ice and frost are

significant for them through the availability of food (Svensson 1981, Bejer & Rudemo 1985). In spite of these expectations, there were no significant relationships between the population changes of Great Tit wintering in the study area and the weather. We supposed that the artificial feeding caused this lack of correlation, which is found in other studies (Grubb 1987). The roosting sites also had a significant effect on the population fluctuations of Great Tits besides the effects of artificial feeding, because cavities can be crucial for winter survival as protected roosting sites (Drent 1987).

Blue Tits are good competitors by exploitation (Minot & Perrins 1986, Török 1987) and they are able to adapt to survive in the reeds (Hildén 1987). Therefore, this species has a lesser demand for artificial food in winter. However, the weather has a great effect on the population fluctuations of Blue Tit through the availability of natural food (Gibb 1960). The number of available nestboxes was the most important factor that influenced their winter population fluctuations.

The different effects of the weather on the two Tit species in Ocsa is contradictory to the findings of others (Bejer & Rudemo 1985). We supposed that this result may be the consequence of the atypical habitat, where the Blue Tit forages and disperses in the marsh in winter, whereas the Great Tit depends on artificial feeding and moves into the village when the weather becomes harsh.

Acknowledgements. We wish to express our gratitude to the members of the Hungarian Ornithological Society who helped with field work. T. Székely, J. Török and Z. Waliczky made helpful comments on the manuscript.

Összefoglalás

Környezeti tényezők hatása télen egy magyarországi láp cinegére

1983-89 közötti hat télen vizsgáltuk a széncinegék és kék cinegék téli populációit az ócsai lápvidéken. A tanulmány ideje alatt a két faj egyedszáma növekedett, valószínűleg a rendszeres etetés hatására. A hat tél októbertől márciusig terjedő idő-

szakának összevont adatai alapján a bevándorlók száma mindkét fajnál lecsökkent tél közepére, az állandó cinegék száma viszont folyamatosan nőtt. A populációk téli ingadozását elsősorban a fiatal kóborló egyedek számának változásai okozták. Az öreg kóborlók száma igen kicsi volt. Az állandó és az újonnan bevándorolt cinegék egyedszám változása között (mindkét fajon belül) legalább olyan jelentős volt az eltérés, mint a két faj azonos helyzetű csoportjai között.

Négy abiotikus tényezőt vizsgáltunk: etetés, hőmérséklet, hótakaró és oduk száma. Az októbertől márciusig terjedő időszakban a legjelentősebb hatása az etetésnek és az oduknak volt mindkét cinege faj esetében. A növekvő etető illetve odu szám hatására az egyedszám szignifikánsan megnőtt. A kék cinegék populációméretére még a hőmérsékletnek is jelentős volt a hatása.

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Parti fecske (*Riparia riparia*) populáció egyedszámának és túlélési valószínűségének monitoringja a Felső-Tiszán

Szép Tibor

Szép, T. 1991. Monitoring of abundance and survival rate of Sand Martin (*Riparia riparia*) population in the upper reaches of the River Tisza, 1986-1990. — Ornis Hung. 1: 37-44. (In Hungarian, with English summary).



The size of the Sand Martin population along the 556 km long Hungarian reaches of the River Tisza was 33300 pairs in 1990 and 30% of this population bred in the studied 73 km river stretch (9438 pairs). The characteristics of this population allow for an accurate annual estimate of size and survival rates.

A computerized data bank has been developed to store and select surveying and ringing data which have been collected since 1986.

The highest survival rate for adults was 0.503 ± 0.0483 between the 1987-1988 breeding periods but since then this value has decreased to 0.294 ± 0.0399 (1989-1990) which is the same level as found in the 1986-1987 breeding period. The population size increased continuously from 1986 (6392 pairs) and reached its highest level (12071 pairs) in 1989. There were 9438 pairs in 1990. The Sand Martin's survival rate is also connected to weather conditions in African migratory and overwintering areas and monitoring work there would provide quantitative data not only for the population studied but also for the analysis of other species as well.

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1. Bevezetés

Az egyik legnagyobb probléma a vonuló énekesmadarak monitoring adatainak elemzése során annak tisztázása, hogy a fészkelő állomány nagyságában tapasztalt változások a fészkelőterület minőségében bekövetkezett változásnak, avagy a vonulás és a telelés során történeteknek esetleg mindkettőnek a függvénye. A védelmi munkák kidolgozása során alapvető fontosságú az egyedszámváltozást okozó hatások lokalizálása.

Lack (1966) felvetette, hogy a mérsékeltövi énekesmadaraknál a populáció szabályozása, limitáltsága a fészkelési időszakon kívüli érvényesül. A vonulás során történeteknek, mint a fészkelő állomány nagyságát alapvetően befolyásoló hatásnak megdöbbentő igazolását a 60-as évek végi nagy afrikai szárazság mutatta meg (Berthold 1973, Winstanley et al. 1974, Cowley 1979). Számos hosszútávon vonuló énekesmadárfajnál drasztikus állománycsökkenést tapasztaltak a Szahel-

övezetben az 1968-1969 során bekövetkezett szárazság idején. A parti fecske (*Riparia riparia*) állományát több éven keresztül vizsgáló tanulmányok is megállapították, hogy az Afrika középső részén a Szahel-övezet déli részén telelő parti fecske (Mead 1979a) rendkívül érzékeny a vonulás és főként a telelés során történetekre, amelyek a túlélési rátát nagy mértékben csökkentve a legjelentősebb állományszabályozó faktorok közé tartoznak (Kuhnen 1975, Cowley 1979, Svensson 1986, Jones 1987, Pearsson 1987a,b,c). Møller (1989) füsti fecskénél közel 20 éven keresztül végzett vizsgálata rámutatott arra, hogy a vonulás és a telelés során történet jelent a legfőbb pusztulási okot. Ezen mortalitás független az egyedszámtól (density-independent) és erős korrelációban van a vonulási és telelési időszak különböző környezeti faktoraival. Ugyanazon populáció nagyságának és az egyedek túlélési rátájának szimultán való folyamatos vizsgálata jelentős segítséget adhat a probléma megoldásához. A fészkelési idő-

1. Táblázat. Gyűrűzött madarak száma Tiszateinken.

Tab. 1. Number of ringed birds at the Tiszatelek colony.

Év	Gyűrűzött adult	Gyűrűzött juvenilis	Telepméret (pár)
Year	Number of ringed ad.	Number of ringed juv.	Size of the colony(prs)
1986	711	981	1574
1987	1197	191	1516
1988	1371	1000	1993
1989	1489	1142	2587
1990	1761	888	2118

szakok közötti túlélési ráta jól tükrözi a vonulási, telelési időszakban történt pusztulások hatását (Møller 1989) és így alkalmas e hatások mérésére.

Számos madárfaj esetében ismertek jól használható és megbízható adatokat szolgáltató állománybecslő módszerek. Azonban ezen madárfajok esetében csak rendkívüli költségek révén van alkalom megfelelő számú egyed egyéni jelölése révén a túlélési ráta, a ki- és bevándorlási viszonyok pontos becslésére. A probléma tisztázásának szempontjából alapvető túlélési ráta megbízható, pontos becsléséhez a megfelelő számú egyed jelölése mellett számos más feltételnek is teljesülnie kell (pl. a befogással kapcsolatos viselkedési reakciók - csapdafélénk, csapdabolond egyedek - alacsony szintje, a mintázott populációnak és a ki/bevándorlási jellegének viszonylagos stabilitása, stb.).

A Felső-Tiszán fészkelő partifecske-ál-

lomány nagysága, megismert jellegzetességei alapján egyike lehet azoknak a populációknak, ahol e szimultán monitoring vizsgálatokat folyamatosan végezni lehet Európában. Az e populációnál végzett vizsgálatok módszereit és eredményeit kívánom dolgozatomban bemutatni az első öt év adatai alapján.

2. Anyag és módszer

2.1. Vizsgált terület

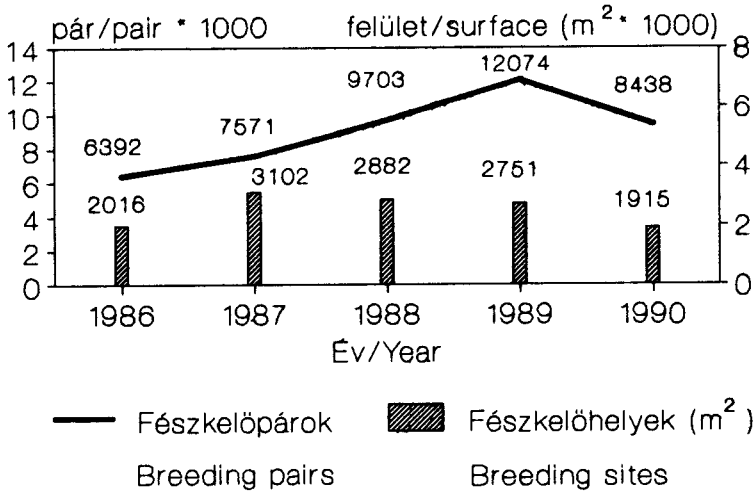
Az egyedszám és túlélési ráta szimultán monitoring vizsgálatához a Tisza Tuzsér-Tokaj szakaszán (617-544 fkm) végeztem adatgyűjtő munkát 1986-1990 során, fészkelési időszakban.

A vizsgált Tisza-szakasz a Tisza egyik parti fecskék által legsűrűbben lakott része, ahol a fészkelésre alkalmas partfalfeület nagyságában drasztikus változások nem történtek a vizsgálati időszakban. Az 1990-ben a Tisza közel egész magyarországi szakaszára (720 fkm - 164 fkm) kiterjedő felmérésem alapján (Szép, in press) a 33300 párra tehető tiszai állomány kb. 30%-a, 9438 pár, fészkel a vizsgált 73 kilométeres szakaszon. Az itt tapasztalt változások nem egy perifériás helyzetű populáció nehezen értelmezhető ingásai, hanem a Kárpát-medence partifecske-állománya szempontjából központi helyzetű populáció változásai. A Marián (1968) által a Tiszán végzett felmérések adatait is felhasználó Cramp (1988) európai állományokat összehasonlító munkájában láthatjuk, hogy a tiszai állomány, az ismert állományok közül egyike a legjelen-

2. Táblázat. Adult partifecskek túlélési rátájának becslése az St,Pt modell alapján. (Tiszateinken végzett gyűrűzési adatok alapján).

Tab. 2. Estimated survival rates of birds ringed as adults at the Tiszatelek colony using the St,Pt model.

Időszak	Túlélési ráta	Visszafogási ráta
Period	Survival rate	Recovery rate
1986-1987	0.309 ± 0.0571	0.187 ± 0.0659
1987-1988	0.503 ± 0.0483	0.219 ± 0.0259
1988-1989	0.436 ± 0.0396	0.186 ± 0.0239
1989-1990	0.294 ± 0.0399	0.359 ± 0.0327



1. Ábra. Potenciális fészkelőhelyek felülettének (m^2) és a fészkelőpárok számának (pár) változása a Felső-Tisza vizsgált szakaszán (617-544 fkm) 1986-1990 során.

Fig. 1. The surface of potential breeding site (m^2) and number of preeding pairs along the upper part of the river Tisza (617-544 km section) during 1986-1990.

tősebbeknek a holarktikus régióban.

A túlélési ráta becslése céljából a Tiszatelek térségében lévő (580 fkm), 1990-ben 2100 párból álló telepen, fészkelési időszakban (június vége-július eleje, első fészkalj) gyűjtött gyűrűzési és visszafogási adataimat használtam fel (1. Táblázat). Ez az egyik legnagyobb ismert partifecske-telep az irodalmi adatok alapján (Cramp 1988). A telep nagysága, stabilitása révén elegendő mennyiségű és a becslés szempontjából megfelelő minőségű adat gyűjtésére nyílt lehetőség.

2.2. Populáció egyedszámának felmérése

Az évente történő felmérések során azonos módszereket alkalmazva az alábbi paramétereket mértem, illetve becsültem:

- Potenciális fészkelőhely helye, hossza, felülete.

- Fészkelőtelep helye

-lakott és nem lakott fal hossza, felülete

-üreges száma, párok száma

Potenciális fészkelőhelynek tekintettem minden olyan függőleges partfalat, amelynek magassága a 0.5 m-t elérte. A több éve végzett felmérő munka alapján ez a faltípus bizonyult a legalacsonyabbnak, ame-

lyet a fecskék még fészkelésre használtak. E fészkelőhelyek pozícióját az 1:10000 léptékű Tisza atlasz felhasználásával határoztam meg, 0.1 fkm pontossággal. A falak hosszát és magasságát becsléssel állapítottam meg, 1m, 2m, 3m, 5m, 10m, stb., illetve 0.5m, 1m, 2m, stb. kategóriák alkalmazásával. A tiszai potenciális fészkelőhelyek ember általi zavartságának mértéke lényegesen alacsonyabb volt a homokbányákéhoz viszonyítva.

A telepen lévő üregek számát egyesével számolva állapítottam meg. A számolásnál azévi üregnek tekintetem minden olyan üreget, amelynek a végét kívülről nem lehetett látni (5 cm-nél hosszabb), a bejárata alapján használtnak minősíthető volt (kör vagy nem nagyon lapított ellipszis alakú bejárat, pókháló nélkül). A számolókat a faltól 5-10 m távolságban csónakból végeztem.

Használt falfelületnek a partfal azon részét tekintetem, amelynek legialább 2 m hosszán egy fészek volt.

A fészkelőpárok számának megállapításánál az irodalomban és a saját korábbi munkáim alapján használt 60% pár/üreg értéket alkalmaztam (Svensson 1986, Persson 1987a, Szép 1986, in press). E

becslés különösen jól alkalmazható a nagyobb telepeken (Szép, in press).

2.3. Populáció túlélési rátájának becslése

A parti fecskénél végzett jelölés-visszafogás egyedszámbecslések tesztelése során látható, hogy a madarak hálózása és gyűrzése nem módosítja a jelölt madarak későbbi befoghatóságát (Szép 1986, in press). Ez alapvető fontosságú feltétel a jelölés-visszafogás alapú túlélésirata-becslő módszerek alkalmazásához (Seber 1982). A napjainkban rendelkezésre álló rendkívül sokoldalú és nagy pontosságú számítógépes programcsomagok közül a SURGE-t (Clobert et al. 1985, 1987) alkalmaztam. A SURGE révén különböző túlélési rátát becslő modellek tesztelésére van mód. Az input adatok struktúrájának bonyolultsága többéves adatsor esetén rendkívüli módon megnehezíti az adatok manuális módon való előkészítését. Ezen

3. Táblázat. Juvenilis korban jelölt parti fecskék túlélési rátájának becslése a Sat,Pt modell alapján (Tiszatelek).

Tab. 3. Estimated survival rates of birds ringed as juveniles at the Tiszatelek colony using the Sat,Pt model.

Gyűrűzés éve	Túlélési ráta 1-2. év között
Year of ringing	Survival rate (1st-2nd year)
1986	0.188 ± 0.377
1987	0.279 ± 0.553
1988	0.266 ± 0.198
1989	0.095 ± 0.237

Túlélési ráta 2 évesnél idősebb korban.

Survival rate of birds aged two years or older.	
1987-1988	0.470 ± 1.70
1988-1989	0.557 ± 1.80
1989-1990	0.398 ± 0.54

Időszak	Visszafogási ráta
Period	Recovery rate
1986-1987	0.125 ± 0.376
1987-1988	0.150 ± 0.385
1988-1989	0.155 ± 0.165
1989-1990	0.338 ± 0.325

probléma kiküszöbölésére fejlesztettem ki a PROSUR (PROgram for SURvival estimation) programcsomagot, amely a terepen dolgozó számára is könnyen előkészíthető, egyszerű adatstruktúrából képes generálni nemcsak a SURGE, hanem más, pl. a JOLLY (Brownie et al. 1986), a CAPTURE (Otis et al. 1978) rátabecslő programcsomagok számára a bemenő adatokat. A PROSUR révén mód van generálni egy általunk megadott egyedszámú, túlélési rátájú, visszafogási valószínűségű populáció jelölés visszafogás adatait, majd tesztelni ezeken az adatokon a különböző becslő módszerek hatékonyságát.

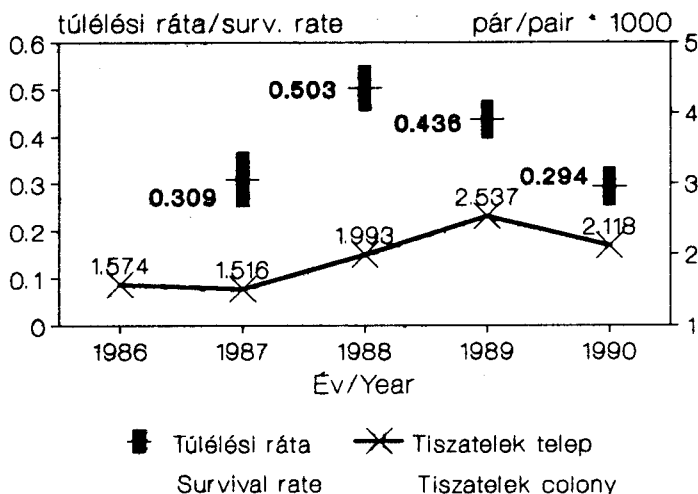
A vizsgált területen 1986-1990 között gyűjtött 26000 fogási adat manuális módon való kezelése, feldolgozása szinte lehetetlen volna. A meglévő és a további években gyűjtendő adatok gyors kezelése céljából a Magyar Gyűrűzési Adatbankkal (Szép 1988) kompatibilitást lehetővé tevő adatnyilvántartó programcsomagot (CAPIN, CAPture data INputing and checking program) fejlesztettem ki. A CAPIN révén létrehoztam a Tiszán és körzetében végzett partifecske-jelölési adatok számítógépes adatbankját, amely naprakészen tartja nyilván a 26000 fogás adatait. A CAPIN segítségével közvetlenül lehet adatokat kigyűjteni a fentebb ismertetett PROSUR számára, s így a különböző becslő eljárásoknak is.

3. Eredmények

3.1. Populációnagyság alakulása

Mint az a 1. ábrán látható, a vizsgált Tiszaszakaszon egyre erősödő növekvő tendencia volt tapasztalható 1986-1989 között. A növekedés nagysága különösen 1987-1988 és 1988-1989 között volt erőteljes. A fészkelésre alkalmas falfelület nagyságának alakulása eltérő tendenciát mutat, ami valószínűsíti azt, hogy a tapasztalt egyedszámváltozás nem a fészkelésre alkalmas felületek változására adott válasz.

A túlélési ráta becslése során vizsgált tiszateleki telep nagysága az egész területen tapasztaltakhoz hasonló változást mutatott (1. és 2. Ábra). Az 1986-1987 során



2. Ábra. Fészkelőpárok számának (pár) és a költési időszakok közötti túlélési rátájának változása Tízszatelken 1986-1990 között.

Fig. 2. Number of breeding pairs and survival rates of adults at Tízszatelkek during 1986-1990.

az átlagtól elmaradó stagnálás, kis csökkenés, a teleptől 2 fkm távolságban ideiglenesen kialakult telep hatásával magyarázható.

3.2. Túlélési ráta alakulása

A SURGE által végzett modellszelekció alapján az adultként gyűrűzött madarak esetében a túlélési ráta becslésére az St,Pt

4. Táblázat. Tízszatelken 1986-1988 között gyűrűzött adult egyedek következő évi megkerülési helyének távolsága alapján az emigráció mértéke.

Tab. 4. Percentages of marked birds recaptured at various distances (km) between ringing site and subsequent year's recapturing site when the birds were ringed at the Tízszatelkek colony in 1986-1988.

Távolság (d) Distance	Adult	Juvenilis Juvenile
d=0	92.3%	59.2%
0 < d < 11	97.9%	63.3%
11 < d < 26	2.1%	22.5%
25 < d	0.0%	14.3%
Összesen/Total	195	49

modell - a túlélési ráta és fogási valószínűség évről évre változik - az, amely illeszkedik az adatokhoz, és relatíve kis számú becsült paramétere révén a legnagyobb pontosságot adó modell (Szép 1990) (2. Táblázat).

A juvenilisoként, a fogás évében kelt fiatal madarak esetében, az egyik legtöbb paramétert becsülő, s kis pontosságú becslést adó Sat,Pt modell illeszkedett - a túlélési ráta a madár korával és évenként változik (Szép, in press) (3. Táblázat). A juvenilis korú madaraknak a fészkekből való kirepülést követő napokon megkezdődik az igen nagy távolságra kiterjedő kóborlása. A Tízszatelken befogott juvenilisok származási helye igen változatos, így a gyűrűzött egyedek e telepre való következő évi visszatérésének valószínűsége igen heterogén lehet (4. és 5. Táblázat). A jelenleg használt módszerek ezt a heterogenitást nem tudják kezelni és ebből adódik a kis pontosságú becslés a juvenilis korban jelöltek esetében. A fiókák kirepülése előtti napokban, a fészkekben történő jelölése nagyban növelné a becslés pontosságát, azonban ezen jelölési módot számos módszertani probléma nehezíti. Az adult madaraknál végzett gyűrűzések alapján (1. Táblázat) az St,Pt modell alapján végzett becslés (2. Táblázat) szerint

5. Táblázat. A Tisza környéki homokbányákban 1980-1988 között gyűrűzött adult egyedek következő évi megkerülési helyének távolsága alapján az emigráció mértéke.

Tab. 5. Percentages of marked birds recaptured at various distances (km) between ringing site and subsequent year's recapturing site where the birds were ringed in sand-pit colonies near the river Tisza in 1980-1988.

Távolság (d) Distance	Adult	Juvenilis Juvenile
0<=d<11	76.8%	54.9%
10<d<26	16.7%	31.0%
25<d	6.6%	14.1%
Összes/Total	198	71

jelentős eltérést tapasztalunk a túlélési ráta és a populációnagyság alakulása között (2. Ábra). Látható, hogy bár 1987-1988 között a túlélési ráta rendkívül magas volt, az egyedszámban ez nem realizálódott teljes mértékben. Magyarozatként szolgálhat az 1987-ben, az átlaghoz képest későn megkezdett fészkelés. A minden év hasonló időszakában (június vége - július eleje) során végzett gyűrűzések alkalmával a fogott juvenilisek száma mindig lényegesen magasabb volt az 1987 évihez képest (1. Táblázat). Feltehető, hogy a másodköltségek száma és sikere is igen alacsony volt. Az adult madaraknál átlagos, kb. 0.20 - 0.35 és a juveniliseknél lévő kb. 0.1 - 0.2 túlélési rátából (Cowley 1979, Mead 1979b) feltételezhetjük, hogy a tapasztalt egyedszámnövekedés igen szoros kapcsolatban volt a túlélési ráta kiugróan magas értékével 1988 és 1989 során. Látható az is, hogy a rejtett fiókok számának lényeges szerepe lehet a kedvező körülmények realizálásában, de egy esetleges sikertelen fészkelési időszak esetén, egy kedvezőtlen vonulási szituációban könnyen kialakulhat drámai csökkenés is.

3.3. Ki- és bevándorlás

Mint azt a juvenilis madarak esetében láthatjuk, ha az egyedek fogási valószínűsége a későbbi években nagyon heterogén, úgy a túlélési ráta becslési pontossága igen ki-

csi lehet. Ilyen megfontolások alapján lényeges a gyűrűzött telepen fészkelő madarak ki- és bevándorlási jellegzetességeinek vizsgálata.

A 4. Táblázat alapján igen erős helyhűséget feltételezhetünk a tiszatelki telepen fészkelőknél, amely érték lényegesen magasabb az irodalmi adatoknál (Mead 1979a). A tiszamenti homokbányában fészkelő állománynál is kisebb ezen érték a tiszatelkihez képest (5. Táblázat). A magas helyhűség kedvező körülményeket teremt a túlélési ráta becsléséhez, amely nem elhanyagolható szempont.

A későbbiekben mód nyíthat a Tisza különböző telepein való jelölő munka révén a kolóniák közötti mozgások vizsgálatára, amely a populáción belüli és közötti migrációs jelenségek pontos feltárását teszik lehetővé.

4. Értékelés

A vonulás, telelés során történeteknek jelentős szerepük van a vonuló énekesmadarak fészkelőállományának változásában, ami szükségessé teszi ezen hatások nyomkövetését. E feladat megoldásának egyik leghatásosabb módja a fészkelőállományok nagyságának és túlélési rátájának monitoringja. Az ezirányú tervek realizálását sok esetben módszertani problémák nehezítik.

A parti fecske sajátosságai nagyrészt kiküszöbölik e problémákat, s így e faj alkalmas lehet sokoldalú monitoring vizsgálatokra. Különösen igaz ez a Tiszán fészkelő állományra, amely esetében számos olyan lehetőség áll rendelkezésre, amely Európában ma már nehezen fellelhető. A több tízezer párból álló, természetes élőhelyen élő, jól felmérhető populáció esetében mód van a túlélési ráta, ki- bevándorlási jellegek megbízható becslésére. Különösen fontos, hogy egy nagyobb régió állományának lényeges részét adó populációról van szó. Az elvégzett előzetes mérések, módszertani tanulmányok és a kialakított számítógépes adatbank megfelelő alapokat adhat egy hatékonyan működő monitoring munka számára. Az adatok nemcsak a hazai, hanem a nemzetközi természetvédelmi kutató- és tervezőmunka

számára is nagy jelentőségűek lehetnek.

A megkezdett adatgyűjtő, értékelő munka további folytatásához, fejlesztéséhez hatékony hazai és nemzetközi együttműködés, támogatás szükséges.

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Short communications - Rövid közlemények

Winter homing of Greenfinch (*Carduelis chloris*)

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During winter mortality levels of birds are high and may reduce many bird populations (MacArthur 1971). However the winter range of birds has received little attention as compared to a variety of other aspects such as breeding. The majority of the work on winter site fidelity refers to New World species (Loftin et al. 1966, Nickell 1968, Ralph & Mewaldt 1975, 1976, Woods 1975, Kennard 1976, Benvenuti & Ioalé 1980, Yunick 1983, Faaborg & Arendt 1984, Kricher & Davis 1986). We do have, however, some data about the wintering site fidelity of European species from the Mediterranean (Benvenuti & Ioalé 1980, Ioalé & Benvenuti 1983). Ralph & Mewaldt (1975) found that the sensitive period for the imprinting process for site tenacity lasts from the end of the migratory season to the beginning of wintering.

We chose the Greenfinch (*Carduelis chloris*) for our study of winter homing. This species breeds commonly in Hungary; part of the breeding population

winters in the Balkan Peninsula, and the resident population is increased by individuals which have migrated from Czechoslovakia and Poland. From December to March, between 1982 and 1986, we caught and banded Greenfinches weekly at an artificial feeder in a suburban habitat, a small town (Tamási) in the south of Hungary (18°25' E, 46°40' N).

3029 individuals were caught, 1663 (54.9%) males and 1366 (45.1%) females. (The sex ratio was notably similar to data obtained by Westphal (1981) in West-Berlin, where 53.2% males and 46.8% females were trapped over a period of 18 years.) There was no significant difference in recapture rate between the males and females (21.2% and 20.4%, respectively). Number of recaptures per birds caught repeatedly within the season were 1.24 (S.D.=0.51, n=265) of males and 1.26 (S.D.=0.54, n=268) of females. The rate of return was low. After the first year that the birds were banded, return percentages were 1.03% and 1.10% for males and

Tab. 1. The number of banded males (M) and females (F) of Greenfinch, the number and percent of returns by month of capture, and the number of returns by month of recapture

Month	Banded			Number of returns by month of capture			Percent of returns by month of capture			Number of returns by month of recapture		
	M	F	M+F	M	F	M+F	M	F	M+F	M	F	M+F
December	93	60	153	0	0	0	0	0	0	1	2	3
January	587	477	1064	8	6	14	1.36	1.26	1.32	15	11	26
February	785	671	1456	12	11	23	1.53	1.64	1.58	7	6	13
March	198	158	356	3	2	5	1.52	1.27	1.40	0	0	0
Total	1663	1366	3029	23	19	42	1.38	1.39	1.39	23	19	42

Tab. 2. Average differences in days between banding data and first recapturing data the subsequent winter

		One year later	Two years later
Males	n	15	8
	\bar{x}	-22.8	-15.6
	S.D.	26.9	25.7
Females	n	11	8
	\bar{x}	-21.0	-10.0
	S.D.	23.4	22.6
Average	n	26	16
	\bar{x}	-22.0	-12.9
	S.D.	25.0	23.6

females respectively, and after the second year of banding, percentages of returning birds were 1.66% and 1.73%. In the third year no individuals returned.

The number of returns analyzed by month of recapture was highest in that month in which the highest number of birds were banded, however the percent of returns did not differ between the months (Tab. 1). In the returns the number of birds banded at the beginning of winter was not higher than that of the birds banded at the end of winter. However, when we further examined the distribution of returns by month of recapture, we found that in the subsequent year the birds were recaptured earlier than would have been expected by the month of banding. In the first year after banding the Greenfinches returned three weeks earlier than when we had caught them in the previous year, and in the second year after banding they returned two weeks earlier than in the year of banding (Tab. 2).

Faaborg & Arendt (1984) argued that winter site fidelity is characteristic of species which winter regularly and they link the coexistence of the bird community with a stable abundance of food supply. Yunick (1983) suggested that *Fringillidae* species migrate only irregularly in North America and their presence in various habitats fluctuates widely; consequently they do not show a tendency to return to the same winter sites year after year.

Our findings suggest, that the Green-

finch, as a representative of European finches, is not a philopatric species in winter. Nevertheless, on the basis of the earlier recapture data it may be suggested that Greenfinches adapt through behaviour, which promotes the return to feeding places where they have occurred in previous years.

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