

# BIRD SPECIES DIVERSITY AND FORAGING NICHE SHIFTS IN URBAN PARK, OAK AND ACACIA FOREST

by

L. SASVÁRI

Eötvös Loránd University, Dept. of General Zoology, Budapest

Received on 20.01.1984

## Introduction

As cities and industrial zones encroach increasingly on the natural environment some bird species may be observed to adapt readily to new habitats. The recent ornithological literature clearly reflect the wide interest aroused by the process, but the first written reports were published as early as the last century (Marschal - Pelzen 1882; Patrizi - Montoro 1909).

In an artificial environment new habitats are formed for the birds, but despite the complexity of the new habitats the diversity of bird species is always inferior to that of the original, natural habitats. The man-made habitats are occupied by the most adaptive species without enriching the avifauna of the human environment (Erz 1966; Grimm - Theiss 1972). It was confirmed by comparisons in the compositions of bird communities between various man-made environments and forest habitats (Havlin 1975, 1980; Hudec 1976). Nevertheless the abundance of birds increases in the scanty bird community due to the colonization by graminivorous and hole-nesting birds (Lancaster - Rees 1979). Obviously the vegetation planted in an urban environment promotes an increase in the bird species diversity which resembles that of the desert and agricultural areas (Guthrie 1974, Vale - Vale 1976). However Emle (1974) found in the bird community of Tucson, that although the birds were more abundant in the town, the species diversity was lower there than in the original desert habitats. One of the aims of this study was to compare the bird communities of forest and parks of various sizes by means of a quantitative evaluation of the species diversity.

It is a well known fact, that, although diversity values inform us about the complexity of the community, but they do not give information about the connections between the species or the structure of the community. One of the available ways for detection of the interrelations between species and changes in the community is the niche analysis. Hence as a detailed investigation of the community structure was necessary for an evaluation of the bird community in the parks and oak and acacia forest by the analysis of the foraging width and overlap.

## Methods

### *Study areas*

Ten study areas were selected, ranging from the periphery to the centre of Budapest, so that all the characteristic types of squares and parks were represented. The parks are generally bordered by blocks of flats and housing estates as well as industrial areas without vegetation. The exception is Cemetery Park, of 185 ha the largest in the study, which is situated on the periphery of the city and bordered by a young acacia forest and arable fields. In order to obtain an appropriate ornithological evaluation of the parks a comparison was made with a part of an oak forest (*Quercus petraea*) and acacia forest (*Robinia pseudoacacia*) situated near Budapest. The oak forest was selected as an ancient original habitat in Middle Europe and the acacia was chosen as an artificial settled habitat in the 18. century. The area of these sites (50 ha) agreed approximately with that of Margaret Island (66.5 ha), one of the parks of Budapest, so that a direct comparison between the two was possible. The relative areas of the trees were selected so that the proportion of the sites covered by foliage and grass was also comparable with that of Margaret Island. All the parks contained trees which were 60–80 years old, and the age of the oak and acacia forest selected for comparison was the same. Since the bird communities in the newer parks reflect only an early stage in the development of the final bird populations they would not have been acceptable for comparison with mature parks. Therefore parks planted during the last five decades were disregarded. The extent of the shrub and tree foliage was measured as the area of ground covered by them.

The People's Park of 112 ha was chosen as study area and within that 9 dominant tree species were selected in which to measure the foraging niche width and overlap of the breeding songbirds and woodpeckers (Passeriformes and Piciformes), both by individual tree species and jointly in all nine, as a total park of mixed trees. The nine tree species were: *Quercus petraea*, *Robinia pseudoacacia*, *Platanus hybrida*, *Acer campestre*, *Populus alba*, *Populus italica*, *Aesculus hippocastanum*, *Fraxinus excelsior*, *Celtis occidentalis*. The bird species diversity calculated on songbirds and woodpeckers was also measured both on these nine tree species and jointly as total park. In the oak and acacia forest of 50 ha the foraging niche and species diversity for the songbirds and woodpeckers were also recorded. In the course of the observations the foraging niche was confined to the wooded areas, covered by foliage.

### *Census and data analysis for bird species diversity*

The census of 5 years was based on foraging birds. In all parks, as well as in the forest area selected for comparison, the traversing registration was adapted for the census. Where there was no extensive continuous foliage the minimum area of registration was a 100 m line of sight in each direction along the transect, and thus a total of 200 m could be covered. Where the

tree foliage or shrubbery was dense the distance covered in each direction was 25 m giving a total of 50 m. In practice this meant that starting at the border of a clump of trees the marginal area of the grove and the neighbouring clearing or meadow could both be observed, but within the grove a further transect was necessary in order to record fully the area under the trees. The narrow and wide survey belts altered irregularly and the direction of the traversing way according to the alterations was chosen. As a park of 120 hectares was surveyed for 3 hours, the time unit for the registration in all parks of more extension than 20 hectares and the compared forest area was 3 hours. In order to the largest park of 180 hectares should be surveyed for 3 hours the help of an assistant was always claimed. As the small squares were covered easily the unit of the registration on them was only 1 hour. The species observed and numbers of individuals were recorded directly on sketch maps of the parks and forest. From the middle of March to the end of June a census was conducted between 06.00 h and 11.00 h on 8–10 occasion in each park during one breeding season. Statements concerning the composition of species and individuals in this work refer to the mean values of these surveys. In winter the same method of sampling was used as at breeding time. Each park was surveyed on 8–10 occasions during one winter from December to the middle of March.

Bird diversity was calculated using Shannon – Weaver's (1949) equation:  $H' = -\sum p_i \log_n p_i$ ; where  $p_i$  is the proportion of the individuals of  $i$  species to the total number of individuals. Equitability was calculated using  $J' = \frac{H'}{H_{\max}}$  where  $H_{\max} = \log_n S$  ( $S$  = number of species).

#### *Census and data analysis for niche width and overlap*

The foraging habitat was selected for the niche dimension analysis and was divided into 20 categories of microhabitats (see Table 1). The Shannon – Weaver formula was used to estimate the niche breadth of each species in the feeding niche categories, and the overlap between the 2 species determined using an adaptation of the Whittaker (1960) index:  $C_{jk} = 1 - 0.5 \sum_i |p_{ij} - p_{ik}|$  where  $p_i$  is the proportion of foraging species,  $j$  and  $k$ , in the  $i^{\text{th}}$  category of microhabitats.

Since the average niche width and niche overlap were calculated using formulae suggested by Pielou (1975), the recording was carried out according to her method. In the course of a transect the number of „occurrences“ of the feeding songbirds and woodpeckers in the microhabitats was counted within a survey belt 50 metres wide. An „occurrence“ involved the presence of one or more individual(s) of the species, and no account was taken of the actual number of individuals involved. When feeding in groups it was possible that the birds might be recorded simultaneously in several microhabitats. In five years 1978–1982 the census was conducted between sunrise and late morning in each park tree species and compared forests on 70 to 80 occasions during the breeding season, and 50 to 60 occasions in winter.

Table 1.

Resource matrix for evaluating average niche width and overlap  
 niche-dimension = foraging microhabitats (B)

		j ..... e															
		shrubs and trees															
		0-3 m			3-10 m			10 m <									
		branch (diameter)			branch (diameter)			branch (diameter)			leaf, bud (berry) air						
		trunk	5 v cm	3-5 cm	3 ^ cm	leaf, bud (berry) air	trunk	5 v cm	3-5 cm	3 ^ cm	leaf, bud (berry) air	trunk	5 v cm	3-5 cm	3 ^ cm	leaf, bud (berry) air	
species (A)	l																
	.																
	.																
	.																
	i																
	.																
	.																
	.																
	r																
																$n_{rc}$	$n_r$
																$n_j$	
																$n_c$	
																$N$	

Notes to Table 1.

$n_{ij}$  = Number of occurrence of  $i$ th species in  $j$ th microhabitat.

$n_i$  = Number of occurrence of  $i$ th species in all microhabitats.

$n_{.j}$  = Number of occurrence of all species observed in  $j$ th microhabitat.

$N$  = Number of all occurrences.

For formulae for the evaluation of data, see Pielou (1975), Ecological diversity. In order to measure average niche width and overlap is derived from Brillouin's diversity index (1962):

$$H_{(AB)} = \frac{1}{N} \log \frac{N!}{\prod_i \prod_j n_{ij}!}$$

Based on this the species diversity:  $H_{(A)} = \frac{1}{N} \log \frac{N!}{\prod_i n_i!}$  and habitat

diversity:  $H_{(B)} = \frac{1}{N} \log \frac{N!}{\prod_j n_j!}$ .

The mean species diversity of occurrences within one kind of habitat averaged over all kinds of habitats:  $H_{B(A)} = \sum_j \frac{n_j}{N} \left\{ \frac{1}{n_j} \log \frac{n_j!}{\prod_i n_{ij}!} \right\}$ .

The mean habitat diversity of occurrences of one species averaged over all species:  $H_{A(B)} = \sum_i \frac{n_i}{N} \left\{ \frac{1}{n_i} \log \frac{n_i!}{\prod_j n_{ij}!} \right\}$ .

From the above, the average niche width  $W = \frac{H_{A(B)}}{H_{(B)}}$  and the average niche overlap  $L = \frac{H_{(B)}}{H_{(A)}}$  with  $0 \leq W < 1$  and  $0 \leq L < 1$ .

Since it is impossible to make calculations where  $N$  is high, Stirling's formula ( $n! \approx n^e e^{-n} \sqrt{2\pi n}$ ) and, based on it, logarithmic transformations had to be used so that the desired  $W$  and  $L$  values could be obtained. The average niche width indicates the proportion of exploitation of the feeding habitat, the average niche overlap indicates the degree of possible competition in the bird community. If each species is found in only one microhabitat then  $W = 0$ , and if each kind of microhabitat contains only one species then  $L = 0$ . If  $W$  and  $L = 1$  all species are feeding in equal distribution of individuals in all microhabitats.

## Results

### *Grass and foliage area dependent species diversity in the urban parks in comparison to the oak and acacia forest*

It was considered likely that species diversity is directly related to the area of plant cover. Therefore the diversity and equitability were evaluated as a function of the grass and foliage area. In Table 2 it can be seen that  $r$  values are higher as a function of grass area than as that of the foliage area. However, the differences between the  $r$  values for the grass and foliage areas were small, and since foliage area is a better measure of ecological value of urban parks, taking the highest and lowest  $r$  values the species diversity is detailed in relation to foliage area in Table 3.

The number of bird species and diversity found in the largest park were surpassed by that of the oak forest in each year, indicating that even the largest wood park, which should be closest to the natural environment, has not such a high ecological value as an oak forest. In the Margaret Island most closely related by size and vegetation cover to the oak forest 40 spe-

Table 2.

Correlation coefficients based on H' and J' values and areas covered by grass and foliage

		<i>r</i> values based on grass area		<i>r</i> values based on foliage area	
		calculated for all species	excluding pigeon, tree and house sparrow	calculated for all species	excluding pigeon, tree and house sparrow
H' In breeding season	1978	0.963	0.969	0.942	0.963
	1979	0.944	0.972	0.948	0.960
	1980	0.933	0.966	0.940	0.972
	1981	0.948	0.977	0.928	0.971
	1982	0.936	0.973	0.931	0.961
H' In winter season	1978	0.906	0.946	0.898	0.951
	1979	0.918	0.960	0.902	0.948
	1980	0.939	0.947	0.907	0.953
	1981	0.922	0.962	0.905	0.942
	1982	0.927	0.952	0.875	0.947
Significance of all <i>r</i> : $p < 0.001$					
J' In breeding season	1978	0.401	0.419	0.291	0.301
	1979	0.321	0.403	0.278	0.288
	1980	0.414	0.364	0.187	0.207
	1981	0.318	0.375	0.221	0.241
	1982	0.312	0.353	0.310	0.327
J' In winter season	1978	0.473	-0.701**	0.434	-0.677**
	1979	0.521	-0.652*	0.485	-0.612*
	1980	0.471	-0.668**	0.472	-0.624*
	1981	0.396	-0.708***	0.427	-0.684**
	1982	0.449	-0.661**	0.388	-0.656*

Significance: \*\*\*  $p < 0.001$  \*\*  $p < 0.02$  \*  $p < 0.05$ 

cies were found to feed in the breeding season 33 in winter and 25 species permanently resident. In the oak forest 63 species bred, 38 were found in winter and 25 were resident. The H' values were far lower than that of the oak forest but they were higher than in the acacia forest. Omitting the feral pigeon, house sparrow and tree sparrow from the calculations resulted in correlation coefficients being higher, and differences between them being lower in successive years. This suggests that the lower *r* values and higher differences between them were due to the fluctuation in numbers of individuals of pigeons and sparrows. In winter H' and *r* values are lower than in the breeding season.

*r* values related to the equitability were significant in winter when pigeons and sparrows were disregarded, negative correlations showed a decrease in equitability in relation to an increase in grass and foliage area.

In the small squares bird density was especially high because of the concentration of feral pigeon and house sparrow, but as a result of a more

Table 3.

## Bird density and species diversity in urban parks, oak and acacia forests

Size (ha)	In breeding season					In winter season			
	Grass area (ha)	Foliage area (ha)	H' values lowest highest		Density ind./ha $\bar{x}$ SD	Number of species	H' values lowest highest	Density ind./ha $\bar{x}$ SD	Number of species
Urban park	0.15	0.06	0.05	0.190 - 1.089			5 - 7	0.746 - 0.751	4 - 5
	0.24	0.13	0.06	1.085 - 1.061			6 - 7	0.602 - 0.637	4 - 5
	0.45	0.22	0.16	0.985 - 0.899			4 - 7	0.616 - 0.870	4 - 5
	1.6	0.8	0.68	1.338 - 1.481		218.1	7 - 10	2.007 - 1.800	11 - 15
						54.2		47.4	
	2.1	1.5	0.75	1.635 - 1.866		43.7	6 - 9	1.501 - 1.996	12 - 15
						5.3		8.2	
	22	16.05	6.05	1.698 - 1.992		24.4	18 - 22	2.017 - 2.434	23 - 28
						1.8		2.6	
	66.5	45	31.5	2.438 - 2.479		19.6	35 - 40	2.047 - 2.243	29 - 33
					5.7		5.3		
81.5	63	26.5	2.259 - 2.459		17.9	31 - 36	1.983 - 2.167	27 - 31	
					4.7		5.8		
112	81	73.5	2.738 - 2.963		16.2	44 - 49	2.654 - 2.664	30 - 36	
					3.3		2.9		
185	136	130	2.375 - 2.998		15.4	52 - 59	2.562 - 2.864	37 - 41	
					1.5		1.3		
Oak forest	50	48	42	3.649 - 3.804		22.7	49 - 53	3.142 - 3.276	36 - 38
					2.8		2.2		
Acacia forest	50	42	44	2.119 - 2.308		7.3	27 - 30	1.976 - 2.182	34 - 35
					1.6		1.3		

Table 4.

## Bird density and species diversity on various park trees in breeding season

	Density* (individual/ha) $\bar{x}$ SD		Diversity
<i>Quercus petraea</i> .....	21.6	3.8	2.445 - 2.643
<i>Robinia pseudoacacia</i> .....	16.2	4.3	1.802 - 1.934
<i>Platanus hybrida</i> .....	11.7	1.8	1.497 - 1.522
<i>Acer campestre</i> .....	18.4	2.7	2.276 - 2.388
<i>Populus alba</i> .....	19.3	4.1	2.091 - 2.311
<i>Populus italica</i> .....	14.3	2.7	0.776 - 0.985
<i>Aesculus hippocastanum</i> .....	13.1	1.7	0.488 - 0.593
<i>Fraxinus excelsior</i> .....	11.9	2.7	1.177 - 1.398
<i>Celtis occidentalis</i> .....	14.7	2.8	0.896 - 1.077

\* Density calculated from the means of each year.

favourable dispersion of the species, the bird density per hectare remained moderate in the larger parks. Nevertheless the bird density of a park of 66.5 ha was far higher than that of acacia forest, but it was lower than that of oak forest.

Table 5.

## Change of density of resident woodpeckers and songbirds in various seasons

Species	Urban park			Oak forest			Acacia forest		
	Breeding season	Winter season		Breeding season	Winter season		Breeding season	Winter season	
		above 0 °C	below 0 °C		above 0°C	below 0°C		above 0°C	below 0°C
<i>Picidae</i> .....	0.6	0.8	0.8	1.2	0.7	0.4	0.3	0.2	0.1
<i>D. major</i> .....	0.3	0.4	0.2	0.5	1.3	0.2	0.2	0.1	0.1
<i>Corvidae</i> .....	1.5	3.1	3.6	1.6	2.2	0.8	0.2	0.8	0.4
<i>P. pica</i> .....	0.5	0.6	0.2	1.3	0.8	0.3	0.1	0.2	0.1
<i>G. glandarius</i> .....	0.7	2.8	3.3	1.1	1.1	0.4	0.5	0.5	0.2
<i>C. frugilegus</i> .....	4.3	4.2	3.7	4.9	4.6	3.4	1.7	1.4	1.1
<i>Paridae</i> .....	2.4	2.4	2.8	3.5	2.8	2.4	0.9	0.9	0.7
<i>P. major</i> .....	3.2	5.4	2.6	5.8	3.4	1.2	1.4	1.3	0.2
<i>Turdidae</i> .....	2.9	3.2	2.4	3.6	2.4	0.9	1.2	1.1	0.1
<i>T. merula</i> .....	4.9	4.7	1.8	0.4	0.2	0.1	3.5	1.3	0.9
<i>Passer</i> spp .....	4.0	2.8	2.5	5.7	3.8	1.2	1.8	0.9	0.5
<i>Fringillidae</i> .....									

Notes: Density calculated from the means of each year in individual per hectare.



Table 6.

Niche breadth and overlap of the Picidae, *Sitta europaea* and *Certhia brachydactyla*\*

Niche breadth → ↓	In winter above 0 °C					In winter below 0°C								
	1.40 Pv	1.36 Dm	1.09 Ds	1.78 Dm	1.28 Dm	1.38 Se	1.30 Cb	1.98 Pv	1.92 Dm	1.51 Ds	1.20 Dm	2.09 Dm	1.92 Se	1.72 Cb
1.71 <i>Picus viridis</i>		.79	.72	.62	.47	.64	.46	.77	.70	.65	.42	.42	.42	.37
1.91 <i>Picus viridis</i>	×	.62	.67	.62	.44	.67	.48	.57	.61		.40	.60	.60	.42
1.40		.51			.35	.53		.51			.38	.42		
1.49	.77	.86	.86	.63	.85	.58	.75	.85	.85	.60	.83	.40	.40	.54
1.62 <i>Dendrocopus</i>	.68	×	.89		.82	.62	.55	.88	.88		.78	.60	.60	.41
1.11 <i>major</i>	.55				.48	.34					.40	.39		
1.18	.52	.84	×	.86	.94	.87	.61			.72	.90	.52	.50	
1.22 <i>Dendrocopus</i> <i>syriacus</i>	.78	.92	×		.61	.58	.53				.60	.57	.52	
1.40 <i>Dendrocopus</i> <i>medius</i>	.66	.67	.93	×	.90	.71	.59				.85	.67	.69	
1.61	.42	.81	.73		×	.90	.88				.79	.84	.84	
1.81 <i>Dendrocopus</i>	.45	.92	.70	.87	×	.84	.74				.73	.72	.72	
1.40 <i>minor</i>	.43	.62				.68					.55			
1.55	.61	.56	.52		.79	×	.94				.87	.88	.87	
1.81 <i>Sitta europaea</i>	.53	.65	.76	.86	.85	×	.90						.88	
1.32	.32	.56			.70									
1.59	.39	.54	.53	.61	.71	.92	×							
1.78 <i>Certhia</i> <i>brachydactyla</i>	.61	.65	.54	.61	.89	.93								

\* 3 values represent the niche breadths and overlaps of each species. First, second and third number one beneath the other show the values in urban park, oak forest and acacia forest.

In breeding season

Values for species diversity of the songbirds and woodpeckers in connection with the various tree species of the parks in breeding season are presented in Table 4. During the 5 years of this survey the highest  $H'$  value, in 1979, and the lowest  $H'$  value, in 1981, were found in the whole park, therefore they were chosen for the presentation of diversity of species associated with various tree species.

Species diversity was highest on the oak trees, it was followed by the diversities on *Acer campestre*, *Populus alba* and *Platanus hybrida* with much lower values. Diversity was lowest on the *Aesculus hippocastanum*.

*Niche breadth and overlap of the resident species  
within five guilds of the woodpeckers and songbirds*

To compare the niche structure of the woodpecker and songbird communities in various habitats, only the resident species were considered since firstly, even in the breeding season they represented the majority of individuals and secondly, variations in subsequent seasons could be assessed from their numbers. Consequently the analysis of the niche structure of the bird community of the three habitats was carried out on the 25 resident species which were common in the urban park and two forests.

In the bark gleaning group consisting of *Picidae*, *Sitta europaea* and *Certhia brachydactyla*, the niche breadth of the *Dendrocopus major*, *Certhia brachydactyla* and *Sitta europaea* was less than that of the *Picus viridis* in both the breeding season and winter, since *P. viridis* fed often on the ground and the lower parts of the trees. The niche breadth of woodpeckers, *C. brachydactyla* and *S. europaea* was highest in oak forest and lowest in acacia forest, where the density of woodpeckers was also lowest. (See Table 5 and 6.) The differences in niche overlaps were consistent with that of body sizes since large overlaps between *Dendrocopus syriacus* and *D. major*, and *C. brachydactyla* and *S. europaea* and little overlap between *C. brachydactyla* and *P. viridis* were found. The niche breadth for woodpeckers reflected the amount of overlap, since the latter was highest in oak forest and lowest in acacia forest. In oak and acacia forest, the winter niche breadth of all woodpeckers increased with respect to that found in the breeding season. In winter, the density of woodpeckers and other species feeding on bark (*Parus spp.*) decreased so the individuals which did not leave the forest could feed more often on the foraging sites, where they fed more rarely in the breeding season because of the higher density of birds then present. Consequently, the niche overlap between species *Picidae*, *Sitta* and *Certhia* decreased in parallel with the increase in niche breadth. Conversely, in urban parks where the density of resident species increased, the woodpeckers, *Sitta* and *Certhia*, were forced to search for food in narrower microhabitats. However, within these narrower foraging microhabitats there was no segregation between the species as their overlap increased; that is, the high density of the winter communities involved higher competition between woodpecker species than was present in the breeding season. During adverse weather conditions, when the temperature was below 0 °C and the soil was covered with snow, the shift in the parks was in the opposite direction to

that seen in the forests. In the oak and acacia forests the decrease of available feeding places was followed by a decrease in density and, despite the low density, the competition resulted in niche segregation with low niche breadth and overlaps for the woodpeckers, *Sitta* and *Certhia*. In the parks, human maintenance and the dense shrub plants provide food for woodpeckers at ground level, even in the most adverse weather conditions, and they search for food in areas where they are absent at higher temperatures with no snow. Thus niche breadth increases and the overlap among the species within this group is decreased.

The situation is different, however, for the direction of the shifts between the five species of *Corvidae* and woodpeckers and *Sitta* and *Certhia*. In comparison to the breeding season, the winter niche breadth of four *Corvidae* species increased in the park and the increase continued when the temperatures were subzero, indicating that the high number of resident species did not influence their foraging pattern. (See Table 5.) The abundance of *Corvus frugilegus* exceeded all the other *Corvidae* and its density essentially determined the interrelations of the *Corvidae* species. In the oak and acacia forest the frequency of *Corvus frugilegus* was moderate, whilst *Garulus glandarius* and *Pica pica* fed in highest density and had the largest niche breadths in winter and the breeding season in oak and acacia forest respectively. In winter, the feeding sites of *Corvidae* species were concentrated on the ground and niche breadth was decreased in the two forest habitats. In both winter and the breeding season, the highest overlap values were determined by species dominance, such that, in the park, highest overlap values were found between *C. corone* and *C. monedula*, in acacia forest between *Pica pica* and *C. frugilegus*, and in the oak forest between *G. glandarius* and *C. corone*.

In the *Paridae* group (*P. major*, *P. caeruleus*, *P. palustris*, *A. caudatus*) *Parus major*, which fed on the ground as well as on foliage and bark, had the highest niche breadth, whereas *Aegithalos caudatus*, which fed only on leaves and thin branches, had the lowest. Species of higher niche breadths have higher interspecific overlaps; species of lower niche breadths have low interspecies overlaps. In the breeding season niche breadth and overlap of the *Paridae* species were lowest in the acacia forest. The directions of the niche shifts between the 3 specified seasons are consistent with the niche shifts of the woodpeckers.

Only three resident *Turdidae* species were common in the habitats studied and their niche breadths were highest in oak forest and lowest in acacia forest. Probably the decrease in winter niche breadth of *Turdus merula*, *Troglodytes troglodytes* and *Erithacus rubecula* in forests was due to their continued abundance and they were not able to expand their foraging sites as was possible for the woodpeckers and tits. In the forests when the temperature fell below 0 °C, their numbers diminished and the niche breadth of all three species decreased somewhat. The overlap values did not alter significantly in subsequent seasons, thus indicating a stable interaction between the species.

Of the *Ploceidae* and *Fringillidae* graminivorous group, *Passer montanus* and *Fringilla coelebs* foraged on the widest niche breadths and *Emberiza citrinella* fed in the narrowest. Their niche overlaps and breadths were highest in oak and lowest in acacia forest in subsequent seasons. The directions of the shifts between the 3 specified seasons were consistent with the niche shifts of the woodpeckers. The graminivorous one was the most abundant in all habitats because of the high number of *P. montanus* and *P. domesticus* in the park and *P. montanus* in acacia forest, and of *C. coccyzus*, *C. chloris* and *F. coelebs* in the oak forest, so these species obviously strongly influenced the structure of the community.

*Average niche width and overlap of the bird community in urban park and oak and acacia forest*

Since in the breeding season 35 woodpeckers and songbirds fed in the parks, 36 species fed in oak forest and 24 fed in acacia forest, in order to evaluate communities of numerous species a standardised average measure was needed. The W values and their related H values were highest in oak forest and lowest in acacia forest, and the W value for the oak trees within the park was also lower than W for the oak forest while W for the acacia trees within the park was higher than W in the acacia forest. The highest W and H' values were both found for *Quercus petraea* and *Acer campestre* within the park. (See Fig. 1, Table 3 and 4.) The W values on the other tree species did not exactly follow the H values for the foraging birds. Species of the urban breeding bird communities which are adapted to the human environment, search for their food in a narrower range of foraging habitats than the species in the oak forest; however their range is wider than the species of the acacia forest.

During the breeding season the average niche overlap was lower in the urban park than in the oak forest and it was lowest in the acacia forest indicating that the differences of the L values between three habitats reflect that of the W and H values. The L value for the oak tree in the park was lower than the L value for the oak forest, and L for the acacia trees in the park was higher than L for the acacia forest consisting with the lower W value on the oak trees and high W value on the acacia trees within the park. The L was highest for the *Acer campestre* and lowest for the *Platanus hybrida* within the park.

The greatest differences in W values for the forests and urban parks were in the winter, when W values increased in the oak and acacia forest, but decreased in the parks in comparison with the values for the breeding season. Thus the niche shifts for the forests and urban environments were in opposite directions. Examining the W values in winter in relation to the extremes of weather conditions a considerable shift may be again found in opposite directions for the forest and urban environments. In oak and acacia forest between 0 °C and -10 °C, when the soil was covered by snow, the average niche width was lower than between 0 °C and +10 °C without snow. In the parks between 0 °C and -10 °C the average niche width was higher than between 0 °C and +10 °C.

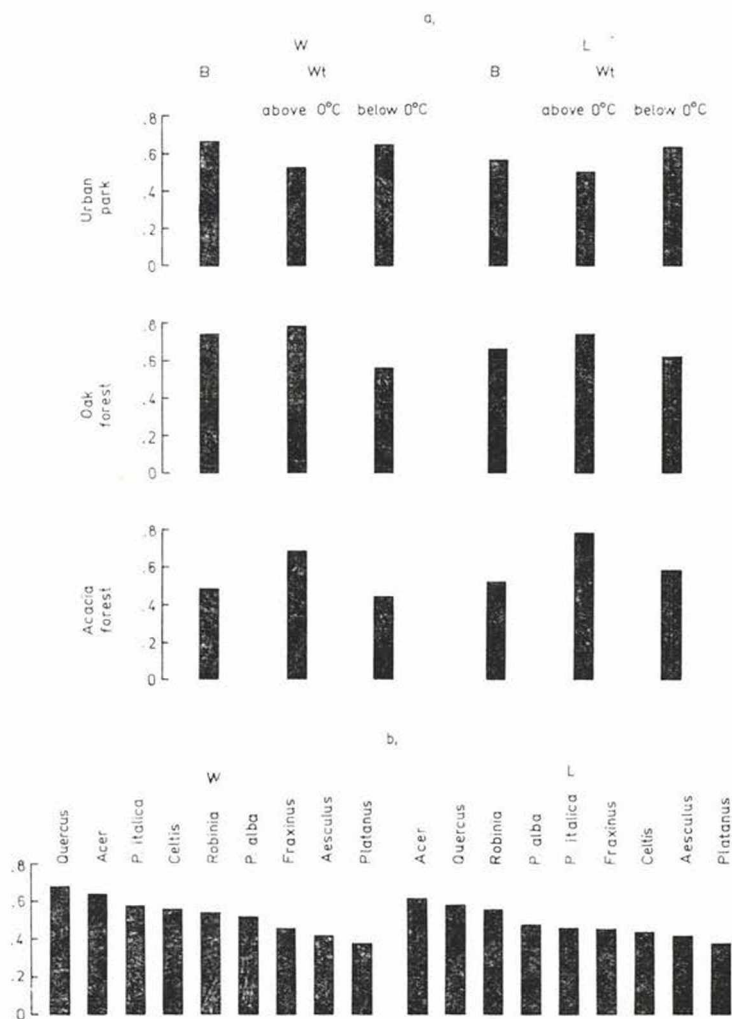


Fig. 1. Average niche width and overlap of the woodpeckers and songbirds in urban park and oak and acacia forest a) Values in various season, b) Values for trees within the park in breeding season.

notes: W = Average niche width.  
 L = Average niche overlap.  
 B = Breeding season.  
 Wt = Winter season.

Considering the L values calculated on data, a change in the tendency for change in opposite directions may be found if values for the forests and parks are compared. L values decreased in the oak and acacia forests at temperatures below 0 °C when the soil was covered by snow, that is, the

species segregated and foraged in narrower niches (see low  $W$  values) than they did at above  $0^{\circ}\text{C}$  in better weather conditions. However, the species in the urban parks were more often found to exploit wider feeding niches when temperatures fell below  $0^{\circ}\text{C}$  and snow covered the ground.

The direction of the shifts of averaged niche width of the bird communities in the three habitats is the same, as described in detail in the analysis of the groups of woodpeckers, tits and graminivorous species. Calculations of the data for average niche overlap found some differences in the shifts in relation to species overlap within the three groups. In winter,  $L$  values increased for the forest and decreased for the urban park. However, the overlaps within the woodpeckers, tits and graminivorous species decreased for the forest and increased for the urban park. In consequence of the high density, woodpeckers, tits and finches were pressed into narrower feeding niches in the park and the overlap increased between the species of a group while the segregation increased between the guilds. In the forest, the low density induced an opposite sequence of events and the average niche overlap among all species of the communities increased in parallel with the decrease of overlap between congeneric or near-related species.

### Discussion

The vegetation of urban parks consists of various introduced plant species in an isolated and intensely disturbed environment. This is a new area of adaptation for birds, within which they meet new types of microhabitat, with vertical and horizontal arrangements differing from their original ones. Consequently the roles and interrelations between the visiting species and those permanently resident in the parks is different from the original community, which were essentially those characteristic of the oak forest bird communities. The lesser area of vegetation will only be preferred by those non-typical forest species best adapted to the man-made environment. Correlation between the high diversity of foliage and bird diversity (MacArthur and MacArthur 1961) is valid for both urban parks and forests, but if the total area of vegetation is small even the mature trees with a high area of foliage do not offer suitable habitats in the parks for the development of the forest bird community. Consequently, the colonization of the parks by birds theoretically corresponds to the colonization of islands, which is dependent upon the distance from the original habitats (Diamond 1970); here it is from the forest and areas. The area dependent bird species diversity have been described (Sasvári 1981, 1983), but the effect of distance from the oak forest cannot be examined here because the parks are too close to one another, and are at similar distance from the forests.

It was shown by the low  $H'$  and  $W$  values that the urban parks do not offer such wide food resources for the breeding communities as the oak forests; however the number of species, diversity and average niche width for the parks is higher than for the acacia forest. The feeding birds have a wider niche dimension on the parkland acacias (higher  $W$  value) than in the aca-

cia forest. Acacia trees were planted in the 18th century in the Carpathian Basin, replacing the original forests cleared for pasture. As shown by the low number of species, density, H and W values, even after two centuries the acacia forests were not such a rich habitat for colonization by bird communities as was the original oak forest of Middle Europe. Because of their heterogeneous plant populations the parks, also man-made, are better for settlement by breeding birds despite continuous disturbance by humans, than the homogeneous acacia forest. Nevertheless it is suggested that because of the same direction of the niche shifts in both the oak and acacia forests, the structure of the bird communities in acacia forest developed over the course of two centuries as a result of the Middle European avifauna. Presumably the higher H and W values of the acacia trees in the park as compared with these in acacia forest are due to the heterogeneity of the park plants which increase the value of the acacia trees with respect to those in homogeneous acacia forest.

The shifts of foraging sites depending on the change of density were found in the urban parks and oak and acacia forests. The species segregated according to their food source to avoid interspecific competition in winter, though this occurred only in the forest and during adverse weather conditions when temperatures fall below 0 °C. In winter, in the absence of snow, and as a consequence of migration of the non-resident breeding birds and the presence of only a few individuals of winter guest species, bird densities in the forest declined, thus ensuring that food is available for the resident species. This is reflected by higher W and H values being found in these conditions than in the breeding season. In adverse weather, when temperatures were below 0 °C and the ground was covered with snow, the species separated resulting in lower niche breadths and overlaps. The segregation might occur as a result of large decreases in bird density in times of food shortage.

The opposite shifts in feeding niche structure in the park and forest can also be explained by changes in bird density. Comparing bird densities in the breeding season and during moderate weather conditions in winter, when temperatures are above 0 °C and there is no snow, the decrease in W and L values can be attributed to the far higher density of birds in the park than in the forests. The higher density is unchanged at temperatures below 0 °C and the species are forced to exploit all available food niches. In the park the niche width and overlap increase and become highest under these conditions than in the acacia and oak forests.

It is possible that the decrease in food supply is in parallel with an increase in segregation of the breeding bird species in the ecologically poor man-made environments. In bad weather conditions the winter bird community is benefited by the urban environment without the segregation. However, the competition among the species increases. Differences between the L values for the various parkland tree species were lower than those between W values; that is, the overlap of the bird species was nearly the same on each tree species, but the width of the feeding niche shifts noticeably on the various trees.

It can be stated theoretically that, where high bird species diversity is linked to high average niche width, a tree species is offering an optimal habitat for the bird community, since the high number and favourable distribution of individuals exploit all accessible foraging microhabitats, being equally dispersed within them. High  $H'$  and  $W$  values combined with a low  $L$  value would reflect the best habitat utilization combined with the lowest level of competition, but such an advantageous coupling of  $W$  and  $L$  is difficult since in practice they usually have very similar values. This interrelationship is presented in Table 7, where the tree species studied are arranged in order of decreasing  $H'$ ,  $W$  and  $L$  values calculated for the breeding season. By selecting the higher  $H'$  and  $W$  values the most favourable foraging habitats for the parkland birds can be determined. *Quercus petraea* is followed by *Acer campestre* (although the latter has the higher  $L$  value) and these are followed by *Populus alba*, despite their relatively low  $W$  value.

It is suggested that the analysis of niche structure on the basis of specific relations and the evaluation of the connections by the standardized niche characteristics regarding the communities as a unit can be useful in the evaluation of various habitats. A range of ecological values for artificial and natural habitats may be assessed in this way, in relation to their bird communities. This could be more generally useful in the development of a healthier human environment.

Table 7.

Trees ranked according to the  $H'$ ,  $W$  and  $L$  values of foraging woodpeckers and songbirds in breeding season

$H'$	$W$	$L$
<i>Quercus petraea</i>	<i>Quercus petraea</i>	<i>Acer campestre</i>
<i>Acer campestre</i>	<i>Acer campestre</i>	<i>Quercus petraea</i>
<i>Populus alba</i>	<i>Populus italica</i>	<i>Robinia pseudoacacia</i>
<i>Robinia pseudoacacia</i>	<i>Celtis occidentalis</i>	<i>Populus alba</i>
<i>Platanus hybrida</i>	<i>Robinia pseudoacacia</i>	<i>Populus italica</i>
<i>Fraxinus excelsior</i>	<i>Populus alba</i>	<i>Fraxinus excelsior</i>
<i>Celtis occidentalis</i>	<i>Fraxinus excelsior</i>	<i>Celtis occidentalis</i>
<i>Populus italica</i>	<i>Aesculus hippocastanum</i>	<i>Aesculus hippocastanum</i>
<i>Aesculus hippocastanum</i>	<i>Platanus hybrida</i>	<i>Platanus hybrida</i>

### Acknowledgements

I am grateful to Dr. Susan Totterdell and Debbie Clarke, Department of Pharmacology of Oxford University, for linguistic revision. This study was supported by the Biological Department of the Hungarian Academy of Sciences and the Eötvös Loránd University, Budapest.



### Summary

Species diversity, niche width and niche overlap were compared for oak forest, acacia forest and urban parks, as well as for various tree species within the park. The survey was based on records of individual birds feeding in various microhabitats during the breeding season and winter. Average niche width and niche overlap were assessed using formulae suggested by Pielou (1975) for standardized measures.

There was a highly significant positive correlation between the foliage area and bird species diversity in the parks. Bird diversity was lower in the urban park, with its mixed tree species, than in homogeneous oak forest, but higher than in homogeneous acacia forest.

During breeding season the niche width and niche overlap of the species were lower in the urban park than in oak forest, but they were lowest in acacia forest. It might be supposed that the decrease in number of breeding species is consistent with increased segregation of species in the poorer and poorer man-made environments. Acacia trees were planted in the 18th century in the Carpathian Basin, replacing the original forests cleared for pasture, and the structure of the bird communities in it developed over the course of two centuries as a typical species assembly of the Middle European avifauna.

In oak forest and acacia forest, when temperatures are between 0 °C and -10 °C, and the soil is covered by snow, the average niche overlap of the communities are lower than when temperatures are between 0 °C and +10 °C, without snow. This situation is reversed in the urban park. In bad weather conditions the winter bird community is benefited by the urban environment without the evolution of segregation, however the competition among the species increases.

High values for diversity, combined with a high average niche width and low values for average niche overlap reflect optimal habitats for the bird community. Thus *Quercus petraea*, *Acer campestre* and *Populus alba* are the best food sources for settling bird communities in the parks.

### REFERENCES

- Brillouin, L. 1962: Science and Information Theory. 2nd ed. Academic Press, New York.
- Diamond, J. M. 1970: Ecological consequences of island colonization by southwest Pacific birds. Proc. Nat. Acad. Sci. USA **67**: 529-536.
- Emlen, J. T. 1974: An urban bird community in Tucson, Arizona: derivation, structure, regulation. The Condor **76**: 184-197.
- Erz, W. 1964: Bemerkungen über Charakteristika in der Verstädterung westfälischer Vögel. Natur und Heimat, Münster, **24**: 107-117.
- Erz, W. 1966: Ecological principles in the urbanization of birds. Ostrich, Supplement **6**: 357-363.
- Guthrie, D. A. 1974: Suburban bird population in southern California. Am. Midl. Nat. **92**: 461-466.
- Grimm, H.-G. Theiss 1972: Die Vogelarten in Berlin-Stadtmitte. Falke **19**: 150-156.

- Havlin, J. 1975: Zur Erkenntnis der Artendiversität und Dominanz der Avifauna bei verschiedenen Typen menschlicher Siedlungen. Zool. Listy, Brno, **24**: 43–63.
- Havlin, J. 1980: Die Vogelwelt der städtische Landwirtschaftsobjekte. Folia Zoologica, **29** (4): 299–309.
- Hudec, K. 1976: Der Vogelbestand in der städtischen Umwelt von Brno und seine Veränderungen. Acta Sc. Nat. Brno, **10**(11): 1–54.
- Lancaster, R. K. – W. E. Rees 1979: Bird communities and the structure of urban habitats. Canadian Journal of Zoology **57** (12): 2358–2368.
- MacArthur, R. H. – J. W. MacArthur 1961: On bird species diversity. Ecology **42**: 594–598.
- Marschall, A. F. – A. Pelzen 1882: Vindobonensis. Wien.
- Patrizi-Montoro, F. 1909: Materiali per un Avifauna della provincia di Roma. Bull. Soc. Zoologico Italiano **4**: 1–103.
- Pielou, E. C. 1975: Ecological Diversity. John Wiley & Sons, New York.
- Sasvári, L. 1981: Bird Communities in the Parks and Squares of Budapest. Opusc. Zool. XVII–XVIII.: 121–143.
- Sasvári, L. 1983: Bird Abundance and Species Diversity in the Parks and Squares of Budapest. Folia Zoologica, in press.
- Shannon, C. E. – W. Weaver 1949: The mathematical theory of communication. University of Illinois Press, Urbana.
- Vale, T. R. – G. R. Vale 1976: Suburban bird population in west-central California. J. Biogeogr. **3**: 157–165.
- Whittaker, R. H. 1960: Communities and Ecosystems. MacMillan, New York.