The effect of habitat structure on guild patterns and the foraging strategies of insectivorous birds in forests

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In order to investigate the role of habitat heterogeneity on the foraging ecology of birds and overall guild patterns, two structurally different forest habitats were studied. The first represented a heterogeneous old-growth forest in the Mala Fatra Mts, while the second a structurally homogeneous spruce silviculture in the Javorniky Mts, Slovakia. The observed guild structure patterns and the organization of foraging niches are significantly different. The cluster analysis of Euclidean distances revealed four main guilds in the primeval forest comprising 23 bird species: foliage gleaners, bark foragers, aerial foragers, and ground foragers, while in the silviculture only three guilds consisting of 11 species: foliage gleaners, ground foragers, and bark foragers were detected. Foraging niche breadth indices revealed that species occurring at both study sites had significantly broader niches in the old-growth forest. Possible causes of the absence of the aerial foragers in the structurally homogeneous habitat, and the effects of habitat deterioration on bird foraging ecology, and consequently on settlement patterns, are discussed.

Key words: foraging behaviour, habitat selection, guild structure, resource partitioning, primeval forest, habitat degradation, Šrámková NNR.

Introduction

The relationship between animal communities and habitats has held an important place in community ecology studies for several decades. According to optimization thinking it is assumed that traits of species have evolved to be adap-

tive to maximize evolutionary success (BROOKS & MCLENNAN, 1991; PRICE et al. 1997). Based on this assumption, one may expect species-specific preferences for a particular habitat type as a consequence of an historical relationship between species and their environment. The patterns of bird habitat relationships have been well docu-

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mented by numerous studies often revealing strong foraging preferences in some species for a particular tree species (HOLMES & ROBINSON, 1981; PECK, 1989; KORŇAN, 2000). This suggests that forests with high structural complexity offer birds diverse microhabitats for foraging, nesting opportunities, and reduced predation (MACARTHUR & MACARTHUR, 1961; KARR & ROTH, 1971; MARTIN, 1993; PARRISH, 1995; GUNNARSON, 1996; WHELAN, 2001). However, studies of bird habitat selection have failed to provide unequivocal evidence of either floristic or structural habitat preference selection patterns (e.g. CODY, 1978; BERSIER & MEYER, 1994; see WIENS, 1989 for review). It is more appropriate to consider selection cues as a continuous scale, where one side is represented by birds dependent only on very rough habitat features and thus occupying rather wide scale of habitat types, while the second side represents highly selective species with narrow habitat amplitude. However, several studies have indicated that habitat selection patterns are very sensitive to the spatial scale on which they are viewed. WIENS et al. (1987) showed that habitat selection patterns of several shrub steppe bird species varied in relation to features of habitat structure at a biogeographic scale. Based on this, structural diversity coupled with tree species richness is still believed to influence how successfully a bird species can exploit a particular habitat. This is an important topic for conservation, especially when viewed in the light of current forest management practices.

The main aim of this paper is to describe species-specific foraging preferences in two structurally different habitats, and to show how these species exploit and divide resources as a possible explanation for their coexistence. The first site represents an old-growth beech-fir forest without regular forest management, the second a spruce silviculture maintained by forest management. We assume that habitat heterogeneity significantly influences both the breadth and structure of foraging niches as well as the diversity and abundance of those species which can successfully utilize the given habitat.

Study sites

Old-growth forest
A 27.5 ha study plot was located in the Šrámková National Nature Reserve, the Malá Fatra Mts (NW Slovakia) (48°11′ N, 19°06′ E). The reserve lies in the Bystrička valley at an altitudinal range of 800–1250 m a.s.l. and has an east to southeast slope orientation. The study plot experiences temperate cold

to cold climate conditions with an average annual rainfall of 900–1000 mm. The geological bedrock is formed from granodiorite, and at higher altitudes limestone (VYSKOT, 1981). The contemporary forest structure has a near-natural composition of tree species with a considerable proportion of snags and logs. The age of the oldest trees is 250–300 years. The forest is dominated by beech *Fagus sylvatica* (comprising 44.8%), fir *Abies alba* (20.2%), spruce *Picea abies* (4.8%), sycamore *Acer pseudoplatanus* (4.3%) with an admixture of elm *Ulmus montana* (2.9%), and rowan *Sorbus aucuparia* (2.4%). The shrub layer is composed of hazel *Corylus avellana* (5.9%), elder *Sambucus nigra*, and young saplings of beech, fir, and spruce. The herb undergrowth consists mainly of *Rubus hirtus, Oxalis acetosella, Dryopteris filixmas, Dryopteris austriaca, Vaccinium myrtillus, Homogyne alpina, Luzula nemorosa* (VOLOŠČUK, 1986). The forest interior has considerable horizontal and vertical heterogeneity caused by abundant treefall and subsequent microsuccession. According to the Braun-Blanquet classification (MICHALKO, 1986), the study plot belongs to the submontane to montane acidophilous beech forests (the alliance *Luzulo-Fagion*).

Spruce silviculture
A 10.1 ha study plot was established in the Hlinická valley in the Javorníky Mts near the town of Bytča (49°16′ N, 18°35′ E). The study plot lies at an altitude of 330 m a.s.l. The area is characterized by a moderately warm climate with an average annual rainfall of 700–800 mm and an average annual temperature of 7.3 °C. The age of the forest was estimated at 80 years. In contrast to the Šrámková study plot, this forest structure is very homogeneous. The current tree species composition has been drastically changed by forestry activities. The plot is dominated by spruce *Picea abies* with a dominance of about 90%. An admixture of *Fagus sylvatica, Fraxinus excelsior, Quercus robur*, and *Alnus glutinosa* on the edge of the plot originates from the successional growth of native forest. The shrub layer is composed of *Ligustrum vulgare, Corylus avellana*, and *Crataegus* spp. The herb/forb layer is composed of *Dryopteris filixmas, Angelica sylvestris, Asarum europaeum, Dentaria bulbifera, Fragaria vesca, Hepatica nobilis, Rubus hirtus, Rubus idaeus, Vaccinium myrtillus, Carex sylvatica, Luzula pilosa,* and *Luzula sylvatica* (SABOVÁ, 1992).

Material and methods

Data collection
Bird foraging behaviour was investigated during the breeding season from the middle of May to the end of July in 1997. In the Šrámková study plot, data were also collected during the breeding season in 1998. The study plots were systematically walked from morning (5:00 CET) to evening (19:00 CET) and foraging birds were observed. Individual foraging birds were recorded on the data sheets with a standardized set of variables.

The following information was recorded: species, sex, day time, duration of foraging, foraging height, direction of foraging movement on substrate (horizontal or vertical), substrate type, and foraging strategy (for detailed description of the variables, see Appendix 2). We used only initial observations of foraging birds (1 tree 1 record) in order to avoid pseudoreplication bias. Altogether, 39 variables were recorded, which were subsequently used for statistical analyses.

The classification schemes of foraging behaviour according to both HOLMES et al. (1979) and REMSEN & ROBINSON (1990) were applied as follows: glean – a manoeuvre in which a stationary prey was picked from the substrate by a hopping or standing bird (including reach); hover – a manoeuvre in which a hovering bird picked the stationary prey from the surface of the substrate (usually for short distance); sally (flycatch) – a manoeuvre in which a bird makes a fluid lunge in the air or substrate to pursue a flying or stationary prey; probe (peck, drill or hammer) – a manoeuvre in which a bird's bill penetrated the substrate pursuing subsurface prey.

More information on the classification background of this scheme is given in KORŇAN (2000). Birds were divided into guild categories after statistical analyses. In describing the foraging guilds we followed the approaches of KORŇAN (1998) and TOMIAŁOJC et al. (1984) as follows: foliage gleaners – bird species mainly foraging on leaves and twigs in the canopy or shrub layers using mainly the gleaning and hovering strategies; ground foragers – bird species that glean prey from the ground; bark foragers – bird species which usually probe and peck on tree trunks and thick branches using vertical foraging movement; airspace foragers – bird species which usually flycatch prey in the air (also hawk or screen) on various substrates.

Data analyses
2,272 observations of feeding birds were taken over two years which were used for further data processing. The sheet observations were transformed into databases using MS Access™ 8.0 and MS Excel™ 8.0 platforms. The databases were used for creating data matrices 23 × 38 and 11 × 21 for statistical analyses. The variables in the data matrices were expressed as proportions based on the foraging frequencies of individual species in the set of variables. Species with less than 15 observations were excluded from further analyses. Because some variables had different units of measurement, the data matrices were standardized by range of rows. To analyze 23 × 38 and 11 × 21 data matrices, hierarchical cluster analysis of Euclidean distances (UPGMA) was used to illustrate the relationship among species in a multivariate space. All analyses were carried out using the statistical packages Nucosa 1.05 (TÓTHMÉRÉSZ, 1993), Syntax 5.0 (PODANI, 1993), and NCSS 97 (HINTZE, 1997). Niche breadth was calculated by Shannon's formula as follows:

$$H' = -\sum p_i \ln p_i,$$

where: $p_i = n_i/N$, n_i – number of foraging observations for each foraging substrate (type) "i", N – total number of foraging observation on all foraging substrates (types).

Statistical differences between foraging niche breadths of species were tested by Student's t-test (HUTCHESON, 1970). Because it is known that the diversity formula is sensitive to sample size we estimated the niche breadth by generating 1000 bootstrap subsample estimates of the greater data set to get the 95% confidence limits. The bootstrap estimates support the outputs of the t-tests (see the results below).

Results

Guild structure of the old-growth beech-fir forest
Based on the results of the cluster analysis of Euclidean distances, four main clusters at the dissimilarity level 0.39 (Fig. 1) can be distinguished. The foliage gleaner guild was represented by the highest species diversity, containing chaffinch *Fringilla coelebs*, wood warbler *Phylloscopus sibilatrix*, chiffchaff *Phylloscopus collybita*, willow warbler *Phylloscopus trochilus*, coal tit *Parus ater*, goldcrest *Regulus regulus*, crested tit *Parus cristatus*, marsh tit *Parus palustris*, and blackcap *Sylvia atricapilla*. This guild can be divided into two subgroups. Members of the first subguild (coal tit, crested tit, and goldcrest) preferred foraging on conifers ($\chi^2 = 69.9$; d.f. = 2; $P < 0.001$), while members of the other subguild (chaffinch, chifchaf, wood and willow warbler) preferred foraging on deciduous trees ($\chi^2 = 8.9$; d.f. = 3, $P < 0.05$). Within this guild, chaffinch and wood warbler have the most similar niches. The chaffinch foraged mainly on beech (*Fagus sylvatica*, 47% of observations), less on fir (15%), and spruce (10%), preferring none of the above mentioned tree species. The wood warbler significantly preferred beech ($\chi^2 = 6.6$; d.f. = 1, $P < 0.01$, Yates correction). The syngeneric chiffchaff fed mainly on Norway spruce ($\chi^2 = 71.4$; d.f. = 1, $P < 0.001$). The willow warbler had obviously different foraging preferences. It fed mainly on sycamore ($\chi^2 = 278.6$; d.f. = 1, $P < 0.001$), but, interestingly, avoided beech ($\chi^2 = 19.6$; d.f. = 1, $P < 0.001$), and fir ($\chi^2 = 4.0$; d.f. = 1, $P < 0.05$), respectively. The coal tit preferred: fir (40.5%), spruce (31%), and avoided beech ($\chi^2 = 30.8$; d.f. = 1, $P < 0.001$). The goldcrest, a typical conifer specialist, usually captured prey on fir and spruce, both at $P < 0.001$. The crested tit, another member of the conifer specialists subguild, foraged almost entirely on conifers: spruce 70% and fir 27%. The marsh tit commonly caught prey at an average height of 10.2 ± 5.9 m (SD, Tab. 1). Its pref-
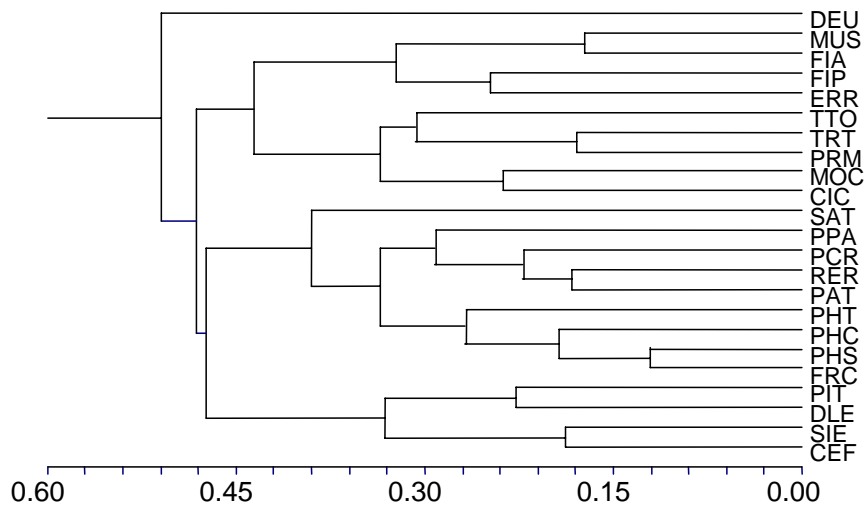
Fig. 1. Community dendrogram of foraging guilds of the old-growth beech-fir forest in the Šrámková National Nature Reserve. Cluster analysis revealed four clusters that correspond to foraging guilds in the following order from above to below: airspace foragers, ground foragers, foliage gleaners, and bark foragers. (For species codes see Appendix 1).

erences in foraging substrates were the following: beech 32%, fir 30.5%, spruce 15% and sycamore with 12.5%. The blackcap had a very dissimilar niche in the guild of foliage gleaners. It foraged at an average height of 5.6 m, mainly on beech (41%), fir (10%), sycamore (11%), and shrubbery (24.5%). The primary dissimilarity of its niche is probably due to its foraging in the lower strata which indicates some inclination to the guild of ground foragers.

The second cluster was interpreted as a guild of bark foragers and comprised four species: three-toed woodpecker *Picoides tridactylus*, white-backed woodpecker *Dendrocopos leucotos*, nuthatch *Sitta europaea*, and treecreeper *Certhia familiaris*. The nuthatch and treecreeper have the most similar niches. The nuthatch usually caught prey at a height of 13 ± 8.6 m (SD). It primarily foraged on fir (36%), beech (23%), dead trees (21%), and spruce (12%). The treecreeper foraged at an average height of 11 ± 8.5 m (SD). Potential inter-specific competition for resources might be possibly seen in foraging substrates: fir (34.5%), beech (18%), dead wood (17%), and spruce (14%). The three-toed woodpecker and white-backed woodpecker are connected at a dissimilarity level of 0.22. Both species used pecking as a main feeding strategy. The three-toed woodpecker fed mainly on dead trees (39%), fir (21%) and spruce (36%) at an average height of 11.5 ± 7.3 m (SD), whereas the white-backed woodpecker most frequently used fir

(30%), dead trees (26%), and spruce (13%) at an average height of 17.5 ± 9.2 m (SD).

The third cluster consisted of airspace foragers representing five species: red-breasted flycatcher *Ficedula parva*, collared flycatcher *Ficedula albicollis*, spotted flycatcher *Muscicapa striata*, house martin *Delichon urbica*, and, in comparison to the others, the very specific robin *Erithacus rubecula*. The spotted and collared flycatcher have the most similar niches in this guild. The first foraged at an average height of 19 ± 7 m (SD). In 67% of the total observations, it foraged in the air mainly by sallying (70%). The collared flycatcher captured prey at an average height of 16 ± 7.3 m (SD). The use of substrates is as follows: air (38%), beech (26%), and sycamore (19%). It mainly used sallying and less frequently hovering. The red-breasted flycatcher caught prey usually at 9 m, and it primarily foraged on beech (33%), air (28%), ground (13%), and sycamore (10%). This species usually sallied and hovered when catching prey. Probably the most interesting is the location of the robin in the multivariate space. It foraged at an average height of 2 m. The main foraging substrates were ground and beech (equally 25%), spruce (14%), and fir (10%). An important finding is that the robin used all techniques except probing. Gleaning and especially sally-pouncing (sensu REMSEN & ROBINSON, 1990) were used most frequently. The last species from this guild is the house martin, which was a non-breeder, but used

Table 1. Proportional use of coniferous vs deciduous tree species (pooled data) by foraging birds breeding in the mixed old-growth and coniferous forest.

Species	N	Height (m)	SD (m)	Coniferous (%)	Deciduous (%)
Delichon urbica (L., 1758)	224	73.7	47.2	0	0
Muscicapa striata (Pallas, 1764)	63	18.6	7	15.8	15.4
Ficedula albicollis (Temminck, 1815)	53	15.7	7.3	9.4	49.1
Ficedula parva (Bechstein, 1794)	61	8.7	7.5	8.2	44.3
Erithacus rubecula (L., 1758)*	20	0	0	0	0
Erithacus rubecula (L., 1758)	52	2.2	3	23	30.8
Turdus torquatus (L., 1758)	20	0	0	0	0
Turdus merula (L., 1758)*	32	0	0	0	0
Pyrrhula pyrrhula (L., 1758)*	19	0	0	0	0
Troglodytes troglodytes (L., 1758)	55	0.4	0.7	7.2	10
Prunella modularis (L., 1758)	28	1.5	2.7	10.7	14.3
Motacilla alba (L., 1758)*	18	0	0	0	0
Motacilla cinerea (Tunstall, 1771)	44	0.9	2.2	0	2.3
Cinclus cinclus (L., 1758)	33	0	0	0	0
Sylvia atricapilla (L., 1758)	61	5.6	5.2	14.7	59.0
Parus palustris (L., 1758)	72	10.2	5.9	45.8	54.2
Parus cristatus (L., 1758)	17	10.8	8	97	0
Parus ater (L., 1758)	222	15.1	8.8	71.5	23
Parus montanus (Baldenstein, 1827)*	16	8.9	3.4	100	0
Parus major (L., 1758)*	28	6	1.9	89.3	7.1
Regulus regulus (L., 1758)	79	17.8	8.1	96.6	2
Regulus regulus (L., 1758)*	30	9.1	4.6	90	6.7
Phylloscopus trochilus (L., 1758)	79	9.2	4.7	25	67.8
Phylloscopus collybita (Vieillot, 1817)	105	10.7	9.7	47.7	48.6
Phylloscopus collybita (Vieillot, 1817)*	18	7.5	3.6	77.8	16.7
Phylloscopus sibilatrix (Bechstein, 1793)	152	10.7	8.2	15.2	82.3
Fringilla coelebs (L., 1758)*	30	10.4	3.8	100	0
Fringilla coelebs (L., 1758)	76	11.7	8.9	25.3	59.2
Picoides tridactylus (L., 1758)	33	11.5	7.3	57.6	3.0
Dendrocopos leucotos (Bechstein, 1803)	24	17.5	9.2	43	30.4
Sitta europaea (L., 1758)	86	13.1	8.6	48	30.0
Certhia familiaris (L., 1758)*	34	6.8	3.6	61.8	0
Certhia familiaris (L., 1758)	165	11.4	8.5	48	31.5

Key: The list is composed of species from both study sites; the spruce silviculture species are denoted with an asterisk; *N* – number of observations; height – average foraging height.

the airspace around canopy tops as a foraging site. Its average foraging height was 74 ± 47 m (SD). It strictly used air hawking (screening).

The last guild represents ground and lower vegetation strata foragers and consists of the following species: ring ouzel *Turdus torquatus*, wren *Troglodytes troglodytes*, dunnock *Prunella modularis*, grey wagtail *Motacilla cinerea*, and dipper *Cinclus cinclus*. The highest niche overlap in this guild was found between the wren and dunnock. The wren foraged at an average height of 0.4 m mainly on the ground (48%), fallen trees (25%), and herbs (20%) and mainly by glean-

ing. The dunnock foraged at an average height of 1.5 m mostly on the ground (35%). The other substrates such as litter, fallen trees, herbs, and beech counted equally for 12%. Gleaning was the most frequently used foraging strategy. The ring ouzel was a typical ground forager characterized by litter-gleaning and leaf-lifting foraging attacks. Both the grey wagtail and dipper, which are typical stream-associated species, had very specific niches. The dipper is a strict diver-gleaner on stream bottoms and a bank gleaner. In contrast, the grey wagtail foraged on wet stream banks by gleaning, hawking, and hovering.
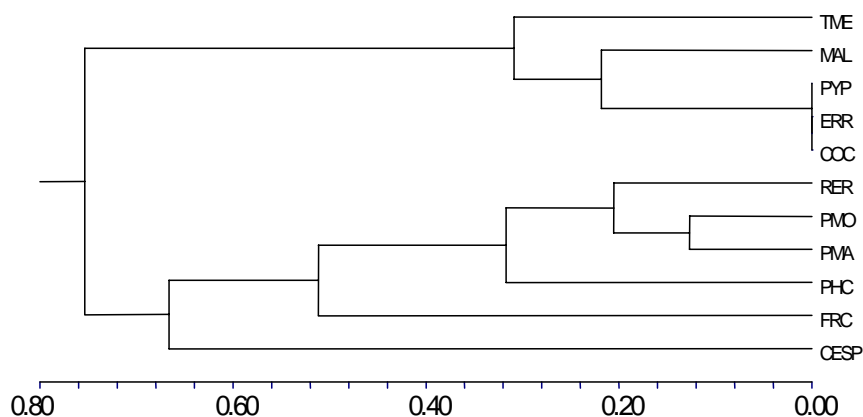
Fig. 2. Community dendrogram of foraging guilds in a spruce silviculture. Cluster analysis revealed three clusters – guilds in the following order moving downward: ground foragers, foliage, gleaners and bark foragers. (For species codes see Appendix 1).

Structure of foraging guilds in a spruce silviculture
The same approach was applied to guild determination in the spruce plantation study site. The hierarchical cluster analysis revealed three clusters – guilds at the Euclidean distances dissimilarity level 0.52, namely: foliage gleaners, ground foragers, and bark foragers (Fig. 2). The foliage-gleaning guild contained five species: blackbird *Turdus merula*, pied wagtail *Motacilla alba*, bullfinch *Pyrrhula pyrrhula*, robin *Erithacus rubecula*, and hawfinch *Coccothraustes coccothraustes*. Based on the output of the analysis, hawfinch, robin, and bullfinch had very similar foraging niches. This might have been caused by the relatively small sample size, so the observed results may not reflect any real pattern. All three species foraged on the ground using gleaning. The pied wagtail foraged on the ground and stones near streams using gleaning. The blackbird is the last species of this guild, and it is a typical ground forager using gleaning and probing into the ground.

The second cluster represents a guild of foliage gleaners consisting of goldcrest, great tit, willow tit, chiffchaff, and chaffinch. The most similar niches in this guild were those of great tit and willow tit. The great tit foraged at an average height of 6 ± 1.9 m (SD). The main foraging substrates were spruce *Picea abies* and, less frequently, beech *Fagus sylvatica*. The willow tit captured prey at an average height of 9 ± 3.4 m (SD). It foraged strictly on spruce, typically using gleaning from leaves or twigs. The goldcrest caught prey usually at 9 ± 4.6 m (SD). Similarly to the great tit, it foraged mainly on *P. abies* and, less frequently, on *F. sylvatica*. The lower strata were preferred by

the chiffchaff, which foraged at an average height of 7.5 ± 3.6 m. It mainly foraged on spruce (78%) and beech (17%). The chaffinch is the last member of the foliage-gleaning guild. It foraged at an average height of 10 ± 3.8 m exclusively on spruce; however, its use of foraging attacks was broader and included gleaning, hovering, and hawking.

The guild of bark foragers is represented only by the treecreeper, which foraged at an average height of 7 ± 3.6 m on the trunk where the foraging movement was vertically directed. In 62% of cases, it foraged on spruce, and in 38% of cases on dead trees using a gleaning strategy.

The niche breadth values for both study sites are given in Table 2. Differences in niche breadth were tested only between species that occurred at both sites, namely chiffchaff, treecreeper, robin, chaffinch, and goldcrest. These species have significantly broader niches under near-natural conditions when compared to the spruce silviculture (t-test, all comparisons significant at $P < 0.001$).

Discussion

What are the main structural differences in the overall guild structure between these two distinct habitats? The ecosystem of the old-growth beech-fir forest stands in contrast to the spruce plantation. If we analyze the average feeding heights and their standard deviations, it is evident that, in the case of the plantation, the vertical separation in guild structure is much simpler. In fact, the species are basically divided only into higher and lower strata foragers. The habitat monoculture is structurally simpler in the sense of verti-

Table 2. Niche breadth values and their pairwise comparison between primeval forest (Šrámková NNR) and spruce plantation (Hlinik) for five passerine species that occurred at both study plots.

			Spruce silviculture				
			PHC	CEF	ERR	FRC	RER
		H'	2.15	2.31	1.00	2.26	2.23
Old-growth forest	PHC	3.36	7.83*** d.f. = 83				
	CEF	3.15		9.82*** d.f. = 354			
	ERR	4.29			10.94*** d.f. = 169		
	FRC	3.64				39.43*** d.f. = 120	
	RER	2.85					9.36*** d.f. = 196

Key: Niche breadth was calculated following Shannon's formula (H'). Statistical differences between species were tested by Student t-test (* $P < 0.1$, ** $P < 0.05$, *** $P < 0.001$).

cal and horizontal diversity in comparison to the near-natural forest. This observation is indirectly supported by the values of niche breadth indices at both sites. When observing these values, some contrasting results are seen. For example, in the old-growth beech-fir forest, the robin reached the greatest value of diversity index, but in the spruce plantation, it had one of the lowest values. To answer the question why such great differences in niche pattern exist, one is tempted to conclude that it is a logical consequence of reduced habitat heterogeneity. It seems even more informative, however, to ask what are the costs for birds occupying such a deteriorated habitat. Several studies have underlined the role of habitat features as an environment for food gathering (coupled with foliage structure), and consequently as a key factor for species occupancy patterns (HOLMES & SCHULZ, 1988; PARRISH, 1995; WHELAN, 2001). It is quite possible that the elimination of some floristic and/or structural features can lead to the absence of certain bird species, and, as a consequence, such a habitat may function as a sink in the landscape (FRETWELL & LUCAS, 1970). The crucial principle of habitat selection at the level of the individual might be the individual's ability to recognize "true" habitat in order to maximize its reproductive success. Even though, HAILA et al. (1996) support the view that habitat selection is based more on avoiding than preferring habitats, indicating that more complicated patterns may exist than were previously thought (e.g. the model of STORCH & FRYNTA, 1999).

The chaffinch holds a very specific position in the community structure. It is the most abundant species and may be regarded as a generalist. This view is supported by its high niche breadth index values at both sites. Its high ecological plasticity (broad habitat amplitude) is also supported by high-density values in most of the forest types in Central Europe (RANDÍK, 1981; TOMIAŁOJĆ et al., 1984; PAVELKA & PAVELKA, 1990; GŁOWACIŃSKI & PROFUS, 1992; KROPIL, 1993; KORŇAN, 1996; KORŇAN, in press; SANIGA, 1994, 1995; TOMIAŁOJĆ & WESOŁOWSKI, 1994). A similar trend can be seen for the chiffchaff and other birds, which also have one of the highest values of niche breadth at both sites. The niche breadth formula indicates that the robin, nuthatch, red-breasted flycatcher, and chaffinch have one of the widest foraging niches in the mixed old-growth forest. This approximately corresponds to the diet studies of KRIŠTÍN (1992, 1994). According to Krištín's data, the nuthatch, collared flycatcher, and robin have the broadest diet composition in a beech-oak forest in central Slovakia. Similarly, BUREŠ (1995) showed that the collared flycatcher is a typical polyphage (see also KORŇAN, 2000, for the entire flycatchers guild). It seems that no positive relationship between polyphagy and broad habitat amplitude exists for the flycatchers, which almost exclusively represent the guild of airspace foragers. Only this guild was absent in the spruce silviculture. However, this pattern is not surprising when we take into account the specific habitat requirements of flycatchers, which preferably occupy forest gaps and clearings (CRAMP & PERRINS, 1993). Their breeding densities have been reported to have a negative association with proportion of coniferous forests (ŠŤASTNÝ et al., 1996;

SÆTRE et al., 1999). Even in deciduous forests the simple scarcity of nest holes may be the cause for the unfavourability of any site. VIRKKALA (1988) pointed out the connection between tree species foraging preferences and population fluctuations that are related to broad-scale habitat changes in northern Finland. In particular, the Siberian tit *Parus cinctus* and Siberian jay *Perisoreus infaustus*, tied by foraging ecology to coniferous forest, showed decreasing population trends when coniferous forests were replaced by deciduous. In contrast, the willow warbler preferred foraging on deciduous trees and evidently benefited from such broad-scale habitat changes. It is possible that species-specific responses to habitat changes may be indirectly influenced by lower foraging success and/or increased stress in a particular habitat type (BROTONS et al., 1998).

Similarly to the airspace forager guild, the bark foragers were almost absent in the community analysis for the spruce silviculture. Their very low densities at the study site (VOJTEK & ADAMÍK, unpublished data) prevented us from collecting a sufficient number of observations. Although we occasionally observed the nuthatch and great-spotted woodpecker, these individuals nested in the adjacent oak-beech forest. It seems that the availability of standing dead trees significantly influence the "attractiveness" of the habitat for bark foraging birds. These requirements are in conflict with current forest management practices (ANGELSTAM & MIKUSIŃSKI, 1994; MIKUSIŃSKI & ANGELSTAM, 1997; WEIKEL & HAYES, 1999).

From the preliminary results of the study, the following forest management recommendations can be given. Forestry practice may lead towards near-natural bird diversity when suitable management methods are applied. The most suitable approach seems to be to maintain forests close to the original tree species composition and structure. This will make available similar foraging substrates that can support similar foraging base required by more nutritionally-specific bird species. This approach should not affect generalists because of high food availability in secondary natural forest and/or because of their widely adaptive feeding tactics that enable them to switch to other types of food resources. A second important aspect is stand structural complexity that creates wide scale of microhabitats, e.g. open canopy places, close canopy places, treefall gaps, places with dense understory vegetation. However, the spatial proportion of these microhabitats should reflect their occurrence in natural conditions, otherwise a bird community with changed density/dominance

structure may occur. From the timber production point of view, the best thinning regime seems to be the selection of individual trees in combination with clear-cutting of small patches not exceeding 1 ha with a few old standing trees producing seed. This regime leads to the development of an extremely complex stand structure characterized by several layers of foliage due to a mixture of different age classes. According to our experience, this forest management strategy may support the development of a near-natural forest of high ecological value for most of the native forest breeders while preserving not only the natural species composition, but also the density/dominance and dispersal patterns.

Some methodological comments should be made in connection with this study. First, single-site comparisons hold the risk of comparing idiosyncratic sites, thus generalization of revealed patterns may be misleading (MAC NALLY, 1994). Our ongoing research does not support this idea at least for the complex of mixed old-growth forest. Second, one may take exception that we compared structurally very different forests that automatically reveals different results. However, the goldcrest, for example, did not change its foraging preferences on coniferous trees at both study sites. The proportion of coniferous trees growing in the spruce plantation is 90% vs 25% in the old-growth forest. In contrast, chiffchaff preferred spruce in the old-growth forest but beech in the spruce silviculture, indicating that species-specific approach must be applied. The significance of such comparison is strengthened by the fact that in Slovakia the native forest composition has been replaced by spruce silvicultures at a broad landscape scale. This study is the first that investigates community organization through resource exploitation by birds in the region of the W Carpathians. The preliminary results show that much work is still needed to clarify several of the revealed patterns.

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CEF	*Certhia familiaris*		PPA	*Parus palustris*
CIC	*Cinclus cinclus*		PHC	*Phylloscopus collybita*
COC	*Coccothraustes coccothraustes*		PHS	*Phylloscopus sibilatrix*
DEU	*Delichon urbica*		PHT	*Phylloscopus trochilus*
DLE	*Dendrocopos leucotos*		PIT	*Picoides tridactylus*
ERR	*Erithacus rubecula*		PRM	*Prunella modularis*
FIA	*Ficedula albicollis*		PYP	*Pyrrhula pyrrhula*
FIP	*Ficedula parva*		RER	*Regulus regulus*
FRC	*Fringilla coelebs*		SAT	*Sylvia atricapilla*
MAL	*Motacilla alba*		SIE	*Sitta europaea*
MOC	*Motacilla cinerea*		TME	*Turdus merula*
PAT	*Parus ater*		TRT	*Troglodytes troglodytes*
PCR	*Parus cristatus*		TTO	*Turdus torquatus*
PMA	*Parus major*		MUS	*Muscicapa striata*
PMO	*Parus montanus*			

Appendix 2. List of variables used in statistical analyses.

No.	Variable description	Measurement unit
1.	Mean foraging height	meter (m)
2.	Standard deviation (SD) of foraging height	meter (m)
3.	Foraging movement in horizontal direction	frequency (%)
4.	Foraging movement in vertical direction	frequency (%)
5.	Foraging manoeuvre on beech *Fagus sylvatica*	frequency (%)
6.	Foraging manoeuvre on silver fir *Abies alba*	frequency (%)
7.	Foraging manoeuvre on Norway spruce *Picea abies*	frequency (%)
8.	Foraging manoeuvre on sycamore *Acer pseudoplatanus*	frequency (%)
9.	Foraging manoeuvre on elm *Ulmus glabra*	frequency (%)
10.	Foraging manoeuvre on rowan *Sorbus aucuparia*	frequency (%)
11.	Foraging manoeuvre on hazel *Corylus avellana*	frequency (%)
12.	Foraging manoeuvre on other live tree species	frequency (%)
13.	Foraging manoeuvre on litter	frequency (%)
14.	Foraging manoeuvre on bare ground	frequency (%)
15.	Foraging manoeuvre herb layer	frequency (%)
16.	Foraging manoeuvre on dead standing tree	frequency (%)
17.	Foraging manoeuvre on fallen dead tree	frequency (%)
18.	Foraging manoeuvre on or in water	frequency (%)
19.	Foraging manoeuvre on rock	frequency (%)
20.	Foraging manoeuvre in airspace	frequency (%)
21.	Glean from trunk	frequency (%)
22.	Glean from branch	frequency (%)
23.	Glean from twig	frequency (%)
24.	Glean from leaf	frequency (%)
25.	Glean in combination with other foraging substrate	frequency (%)
26.	Hover at trunk	frequency (%)
27.	Hover at branch	frequency (%)
28.	Hover at twig	frequency (%)
29.	Hover at leaf	frequency (%)
30.	Hover in combination with other foraging substrate	frequency (%)
31.	Probe or peck into trunk	frequency (%)
32.	Probe or peck into branch	frequency (%)
33.	Probe or peck into other foraging substrate	frequency (%)
34.	Hawk or sally at trunk	frequency (%)
35.	Hawk or sally at leaf	frequency (%)
36.	Hawk or sally at branch	frequency (%)
37.	Hawk or sally at twig	frequency (%)
38.	Hawk or sally in combination with other substrate (usually air)	frequency (%)