Folia Zool. – 56(1): 51–70 (2007)

A comparison of three different approaches for the classification of bird foraging guilds: an effect of leaf phenophase

Peter LEŠO and Rudolf KROPIL

Department of Forest Protection and Wildlife Management, Faculty of Forestry, Technical University in Zvolen, T.G. Masaryka 20, 960 53 Zvolen, Slovakia; e-mail: leso@vsld.tuzvo.sk, kropil@vsld.tuzvo.sk

Received 26 October 2005; Accepted 21 February 2007

A b s t r a c t . The study of foraging behaviour of 20 forest bird species was conducted during two different phenophases of a vegetation period in the West Carpathians oak-dominated natural forests. Using a standard and a modified *a priori* approaches, seven foraging guilds were distinguished, whereas only five significantly different guilds were clustered by a *a posteriori* approach. Four common guilds for all three approaches were quantitatively compared. The methods differed especially in the classification of foraging generalists. Differences in guild densities between *a priori* and *a posteriori* approaches emerged in both, the pre-foliage and the foliage periods, chiefly in the guilds of insectivores on ground surface (47.3–89.6%) and insectivores on buds/leaves and twigs (15.0–45.9%). The modified *a priori* method provided moderate densities of separate guilds. The modified *a priori* method with more detailed density calculation is recommended for the quantitative guild structure comparisons of different bird assemblages. The method takes into consideration proportional use of foraging substrates in combination with food type.

Key words: *a priori*, *a posteriori*, foraging strategy, foraging niche breadth, pre-foliage period, foliage period

Introduction

Knowledge of the bird foraging ecology is one of the keystones in successful management of species, communities and ecosystems. The abundance, distribution and availability of food resources are believed to be the principle factors influencing habitat suitability for birds (H o l m e s et al. 1979, W i e n s 1989, S u h o n e n et al. 1992, J o h n s o n & S h e r r y 2001, H i n o et al. 2002, A d a m í k & K o r ň a n 2004). Landscape habitat features and biotic interactions are both considered as most important factors determining birds foraging behaviour. The first factor is associated with an adaptation potential of certain species to specific habitat type in term of their morphology (the opportunistic theory). In accordance with the theory, it determines the number of species, which are able to survive in the certain habitat (O d u m 1945, M a c A r t h u r et al. 1962, J o h n s o n 1975, P e a r s o n 1975, B r a n d l et al. 1994). Differences in foraging adaptations determined by species-specific morphological traits were confirmed even between sexes of the same species (G u s t a f s s o n 1988, S u h o n e n & K u i t u n e n 1991). Providing that food is one of the most important factors determining bird distribution, then a bird assemblage forming may be influenced by a spatial distribution of food resources in a given ecosystem and its availability for particular foraging guilds (S u h o n e n et al. 1992). In accordance with the mentioned, H o l m e s et al. (1979) and recently H i n o et al. (2002) highlighted the possibility to predict qualitative and quantitative bird assemblage structure by the identification of food distribution factor within a certain site.

According to the foraging theory (Robinson & Holmes 1982), vegetation structure influences bird foraging behaviour mainly by means of food availability and the energetic constrains of its obtaining. Whelan (2001) supported this notion after analysing foraging preferences of three insectivorous species. He suggests that birds generally choose foraging strategy in order to minimize or at least decrease the need for more energetically costly aerial manoeuvres in contrast to non-aerial manoeuvres. He also supposes that foraging site selection in the wild, at least for some bird species, may often favour tree species (or parts of trees) that minimize the need for aerial foraging manoeuvres.

Interspecific and intraspecific competition as well as the risk of predation are the second factor leading to the development of individual-specific foraging strategies within a population and resource partitioning patterns among several sympatric species (MacArthur 1958, Pearson 1977, Alatalo et al. 1985, Suhonen et al. 1992, Kullberg & Ekman 2000, Hino et al. 2002, Jedlicka et al. 2006). Although the concept of species coexistence is usually based on the idea of minimum tolerance towards the co-occurring species, some authors stress the importance of positive interspecific interactions in structuring breeding bird communities (Mönkkönen et al. 1996, Forsman et al. 2002, Thomson et al. 2003). Dolby & Grubb (1999) confirmed also weather to be one of the factors influencing foraging strategies of birds. In fact, these interactions are complex and it could be rather misleading to consider the only one factor when studying foraging behaviour causality (Landres & MacMahon 1983, Whelan 2001).

Understanding ways and opportunities to obtain food (its real availability) including its occurrence and suitability is very important. That has led to the development of foraging guild concept in the last few decades. Two principal methodological approaches have been applied to determine foraging guilds: *a priori* and *a posteriori* (Jaksic 1981, Hawkins & MacMahon 1989, Wiens 1989).

The first is based on predefined guild categories and the consequential classification of birds into the existing guild categories (Karr 1971, 1976, Emlen 1972, Cody 1983, Tomiałojć et al. 1984, Alatalo et al. 1985, Kropil 1996a,b, 1998, 2004, Canterbury et al. 2000, Laiolo 2002, Bailey et al. 2004, Shirley 2004). In general, *a priori* approach is considered to be a rather subjective way of guild definition (Wiens 1989). Jaksic (1981) recommended that guilds should not be defined *a priori*. This approach requires relatively less-detailed field information and data obtained by various methods as well as literary data. Its application may be eligible for the broad evaluation of certain community units from the predetermined points of view.

A posteriori approach is based on field surveys and statistical evaluation of higher number of variables describing species foraging strategies (Holmes et al. 1979, Landres & MacMahon 1980, 1983, Holmes & Recher 1986, Krištín 1992, Martínez 2001, Adamík et al. 2003, Laiolo et al. 2004). More objective and statistically well-founded classification of species into guilds can be achieved that is the main benefit of *a posteriori* approach. Despite the fact that these statistical methods are used, guilds still lack perspicuous, formal and testable definition; therefore it is difficult to compare the guild structure between different ecological studies (Adams 1985). The subjective factor is apparent primarily in a process of variable selection, a field data collection, and interpretation of statistical outputs as well. It can lead to biases in bird classification when comparing these two approaches. Perhaps, that is why the quantitative comparison of *a priori* and *a posteriori* approaches has not been performed.

The aim of the study was to compare two approaches commonly used for classification of birds into foraging guilds as well as third approach derived from the two previous. In addition, comparing two phenophases of a leaf period allows us to better understand the differences in the classification mechanisms of the approaches.

Material and Methods

Study areas

The study was carried out in three nature reserves which preserve remnants of natural beech-oak forests. The reserves are situated on the south-facing slopes of the “Slanské vrchy” Mts (“Kokošovská dubina” – 37.1 ha, geographical co-ordinates of the plot centre 48°57’ N/21°22’ E; “Malé Brdo” – 55.8 ha, geographical co-ordinates of the plot centre 48°48’ N/21°31’ E) and the “Čierna Hora” Mts (“Bujanov” – 88.1 ha, geographical co-ordinates of the plot centre 48°52’ N/ 21°04’ E) in the eastern part of Slovakia, geomorphologically belonging to the West Carpathians. The altitude ranges from 450 to 760 m above sea level; exposure is south-west; average slope inclination ranges from 25% to 45%. Mean annual temperature is 7–7.2°C, mean annual precipitation is 675–700 mm (K o r p e ľ 1995). The average stand age ranges from 160 to 195 years. Sessile Oak (*Quercus petraea* – 90–97%) and beech (*Fagus sylvatica* – 3–10%) compose the overstorey; beech, hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), gean (*Cerasus avium*) and hazel *(Corylus avellana*) compose the understorey.

Foraging observations

Foraging behaviour was studied during 2000–2002 (three breeding seasons) from the end of March to the middle of August. During this period, random point foraging observations of birds were recorded into the field forms with the standardized set of variables. The phenological phases before (pre-foliage period) and after (foliage period) tree foliage development were distinguished. Recording birds during the period of disproportion in foliage development of oak and beech (difference approximately two weeks) was avoided. The special attention was paid to recording birds in the random manner and avoiding repeated registration of the same individual. It was achieved by selecting different routes through the study plots. In this way the repeated records were partly eliminated. In total, 84 (38 in the pre-foliage period and 46 in the foliage period) observation sessions were conducted between 6.00 and 20.00, each lasting 2–4 hours. During each session one observer walked through the forest collecting data. After registration of foraging activity of certain species, another registration of the same species was not made within approximately 50 m radius for the smaller and 100 m radius for the larger species. The observations were performed in different times of a day. The highest number of registrations was obtained in the mornings when the bird activity and detectability was the highest.

Three different approaches for the classification of bird foraging guilds were used. The first of them (Approach 1) was the standard *a priori* classification of guilds, where we used the literary data to specify predefined guild categories and to classify species into the guilds as well. The second approach (Approach 2) was derived from the *a priori* classification. The guild categories were predefined on the basis of literary data. Two main differences set this method apart from the previous one. Firstly, the guilds separation was achieved by the real field observations. Thus, the Approach 2 includes also features of *a posteriori* classification. Secondly, the more detailed classification of birds into guilds was used. Guilds were created from species portions, not “entire” species. It enables to calculate guild densities more finely. Calculation of guild densities was the main difference between the approach 2 and the approaches 1 and 3. The third approach (Approach 3) was the standard *a posteriori* guild classification, based on quantitative measures of a large number of variables using multivariate statistical techniques.

Approach 1: Four basic foraging substrate categories were distinguished: ground (ground surface, herb layer, dead lying wood), leaves/buds (leaves, buds, twigs < 1 cm), bark (bark and wood of tree stems and branches), and air space. Three basic food categories were distinguished: vertebrates, invertebrates (mainly insects, spiders, snails and worms), plants (fruits, seeds, buds and other plant segments). Thus species were classified into a particular set of foraging guilds on the basis of their preferences to foraging substrates and basic food. Following guild categories were set (T o m i a ł o j ć et al. 1984, K r o p i l 1996a,b): IF – insectivores on leaves/buds and twigs, IG – ground insectivores, IB – bark insectivores, IA – aerial insectivores, HG – ground herbivores, HC – canopy herbivores, V – vertebratophages. Species were separated into the guilds on the basis of literature (H u d e c et al. 1983).

Approach 2: The same four categories of foraging substrates, three basic food categories as well as seven guild categories were used. During each observation session each foraging individual was classified into one of seven predefined guilds. After collecting all the data, each species was assessed by means of preference portion (from 0.0 to 1.0; total amount of portions for one species is 1.0) to each guild category. Quantity of each guild was ascertained by using the following formula:

$$GD_x = \sum p_i.d_i$$

where GD_x – density of the guild x; p_i – ith species portion in the guild x; d_i – ith species density. Thus the particular guild does not represent the list of species, but the sum of species portions belonging to this guild category.

Approach 3: Methodology formerly used in pivotal studies (H o l m e s et al. 1979, L a n d r e s & M a c M a h o n 1983) was applied with some modifications to determine *a posteriori* guilds. The initial observation method was applied to collect field foraging observations since the research was focused on separating species on the basis of their prevailing foraging strategy (H e j l et al. 1990). Foraging behaviour was characterised through the set of 28 variables belonging to four groups. The categories characterise substrate type (13 variables: bare soil, litter, dead wood, air space, herbs, shrubs, thick stem >30cm, thin stem <30 cm, thick branches > 20 cm, thin branches 2–20 cm, twigs <2 cm, buds, leaves), vertical position (four variables: height 0–1 m, 1–4 m, 4–12 m, >12 m), tree species (six variables: oak, beech, hornbeam, hazel, fir, other trees), and foraging technique (five variables: gleaning – take the food item from the substrate surface; picking – picking the food item by penetration bark slits, various interstices, soil and litter; probing – acquiring the food item by soft damage of substrate surface, primarily penetration buds, big seeds and fruits, bark surface, soft dead wood; pecking – acquiring the food item by evident substrate damage; sally – acquiring the food item by short aerial sally). Actively foraging birds were observed, with recordings on each bird from first notice to foraging substrate change. Observations were limited to two minutes. Only observations lasted over five seconds were recorded. Species with at least 20 foraging observations were included into a statistical analysis. The values in the primary data matrix represent percentages of each variable use calculated from the whole set of variables used on description of foraging behaviour. The cluster analysis of chord distances (unweighted pair-group average method – UPGMA) was used to classify species into guilds. A bootstrap cluster analysis of chord distances method (P i l l a r 1999) was applied to detect the objective guild structure within the tested assemblages. Clusters were considered to be statistically different if $P \geq 0.1$ (P i l l a r 1999). The highest number of sharp clusters was the criterion for determination of the linkage distance in guilds separating. The correspondence analysis was also used to separate bird species into the guilds and to reveal main environmental factors responsible for species segregation into the guilds. MULTIV (P i l l a r 2004) and SYN-TAX 5.10-pc (P o d a n i 1997) programs were used in statistical analyses.

Average data on species densities from three breeding seasons (L e š o 2003) were used for the guild quantification (Appendix 1). Density of birds was surveyed between 1999–2001 by using combined version of the mapping method (T o m i a ł o j ć 1980). For this purpose, three study plots of size 13.1–15.7 ha were assessed and marked out within the reserves (one study plot in each reserve). Each study plot was visited from early April to the middle of June, at least 10 times per one breeding season.

The foraging niche breadth was calculated to quantify the variability of foraging behaviour of bird species in two different periods of the breeding season. Use of 13 foraging substrate categories (variables 1–13) were evaluated and the foraging niche breadth was calculated for each bird species according to Levins' formula (L u d w i g & R e y n o l d s 1988):

$$B = \frac{1}{\sum_{i}^{j} (p_i)^2}$$

where *B* – foraging niche breadth, *j* – number of foraging substrates and *p* – proportion of *i*th foraging substrate use. Values of the index ranges from 1 (species uses only one foraging substrate) to *j* (species uses all foraging substrates in equal proportion).

Results

During the pre-foliage period, 1179 foraging observations of 17 bird species having at least 20 records per species were collected. Similarly, 1181 records of 20 species having at least 20 records per species were collected during the foliage period. This data was applied to classify species following the approaches 2 and 3.

A p p r o a c h 1

During the pre-foliage period, seven species belonged to the bark insectivores guild (Appendix 1). Then, the insectivores on buds and twigs consisted of five species, the ground insectivores of three species, the aerial insectivores and the ground herbivores of one species. As for the density, the insectivores on buds and twigs predominated with 15.3 pairs/10 ha (25.4%). The bark insectivores reached 13.2 pairs/10 ha (21.9%), the ground insectivores 12.5 pairs/10 ha (20.8%), the ground herbivores 11.2 pairs/10 ha (18.6%) and the aerial insectivores 8.0 pairs/10 ha (13.3%).

During the foliage period eight species were classified as the insectivores on leaves and twigs. The bark insectivores were represented by six species and the ground herbivores by four species. Two species belonged to the aerial insectivores. In this period, the insectivores on buds and twigs predominated with density 24.4 pairs/10 ha (36.1%). The ground insectivores reached density 23.7 pairs/10 ha (35.0%), the bark insectivores 10.9 pairs/10 ha (16.0%) and the aerial insectivores 8.7 pairs/10 ha (12.9%).

Approach 2

During the pre-foliage period, 15 species at least partly (from "+" to 1.0) belonged to the ground insectivores guild (Appendix 2). Then, the bark insectivores consisted of 12 species, the insectivores on buds and twigs of 11 species, the ground herbivores of eight species, the canopy herbivores of eight species, the aerial insectivores of two species, and the vertebratophages of one species. In this period, the ground insectivores reached density 19.6 pairs/10 ha (32.6%). The insectivores on buds and twigs reached 15.0 pairs/10 ha (24.9%), the bark insectivores 12.4 pairs/10 ha (20.6%), the aerial insectivores 7.2 pairs/10 ha (12.0%), the ground herbivores 4.5 pairs/10 ha (7.4%), and the canopy herbivores 1.5 pairs/10 ha (2.5%).

During the foliage period, most species (16) at least partly belonged to the ground insectivores. The insectivores on leaves and twigs were represented by 15 species, the bark insectivores by 12 species, the ground herbivores by six species, and the canopy herbivores by five species. In this period, the insectivores on buds and twigs predominated with density 33.5 pairs/10 ha (49.5%). The ground insectivores reached density 16.5 pairs/10 ha (24.3%), the bark insectivores 10.5 pairs/10 ha (15.6%), the aerial insectivores 6.9 pairs/10 ha (10.2%), and the canopy herbivores 0.3 pairs/10 ha (0.4%).

Approach 3

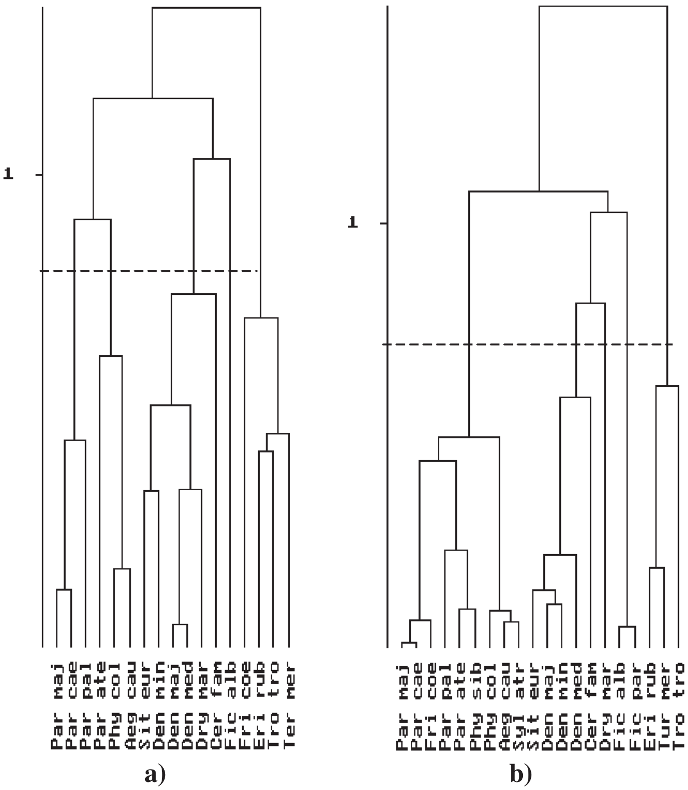
The results in the Table 1 indicate that the partitions with two, three, and five groups are not fuzzy in the pre-foliage period. According to predefined criterion, the partition with five clusters was accepted (Fig. 1a). First two groups are the most similar. They represent bird species acquiring food mostly on buds and twigs. The main difference is in foraging technique. While first three tits (great tit *Parus major,* blue tit *P. caeruleus*, and marsh tit *P. palustris*) used most frequently probing when forage on buds, second group (coal tit *Patus ater,* chiffchaff *Phylloscopus collybita,* and long-tailed tit *Aegithalus caudatus*) were typical gleaners. The third cluster represents a compact guild of the bark insectivores (nuthatch

Table 1. Bootstraped cluster analyses of chord distances (UPGMA) calculated for pre-foliage and foliage data matrices. Sharpness of classification and G probabilities were estimated by 10 000 iterations. Sharp partitions are given in bold.

Number of clusters	Pre-foliage data matrix		Foliage data matrix	
	Average of sample atribute (G*)	P(GNull≤G*)	Average of sample atribute (G*)	P(GNull≤G*)
2	**0.95022**	**0.1892**	**0.96909**	**0.4514**
3	**0.92582**	**0.1126**	**0.93126**	**0.1587**
4	0.93037	0.0925	**0.96124**	**0.2962**
5	**0.93952**	**0.1209**	**0.94801**	**0.1906**
6	0.93271	0.064	0.92525	0.0751
7	0.92727	0.0467	0.91366	0.0421
8	0.91981	0.0268	0.92786	0.0349
9	0.91297	0.0159	0.94415	0.0544
10	0.91223	0.0072	0.93882	0.0247

Sitta europaea, lesser spotted woodpecker *Dendrocopos minor*, great spotted woodpecker *D. major*, middle spotted woodpecker *D. medius*, black woodpecker *Dryocopus martius*, and treecreeper *Certhia familiaris*). Collared flycatcher *Ficedula albicollis* is an aerial insectivore and the fifth cluster represents the insectivores on the ground surface (chaffinch *Fringilla coelebs*, robin *Erithacus rubecula*, wren *Troglodytes troglodytes*, and blackbird *Turdus merula*).

The same number of guilds was accepted in the foliage period (sharp partitions with two, three, four, and five groups, Fig. 1b). The most species belonged to the first cluster which can be considered as a guild of insectivores on leaves and twigs (great tit, blue tit, chaffinch, marsh tit, coal tit, wood warbler *Phylloscopus sibilatrix*, chiffchaff, long-tailed tit, and blackcap *Sylvia atricapilla*). The guild of bark insectivores split up into two groups. The first of them consists of five species (nuthatch, great spotted woodpecker, lesser spotted woodpecker, middle spotted woodpecker, and treecreeper), the only black woodpecker represents a separate cluster. In comparison to other bark insectivores, black woodpecker used more frequently dead wood, lower parts of stem, and it never used horizontal branches and leaves. Red-breasted flycatcher *Ficedula parva* joined collared flycatcher in the guild of aerial insectivores.



a) b)

Fig. 1. Classification of bird species based on foraging preferences from bootstraped cluster analysis in the pre-foliage period (a) and in the foliage period (b). Broken arrow – boundary linkage distance for guild separation with sharp clusters. Bird species codes: Aeg cau - *Aegithalos caudatus*, Cer fam - *Certhia familiaris*, Den maj - *Dendrocopos major*, Den med - *Dendrocopos medius*, Den min - *Dendrocopos minor*, Dry mar - *Dryocopus martius*, Eri rub - *Erithacus rubecula*, Fic alb - *Ficedula albicollis*, Fri coe - *Fringilla coelebs*, Fic par - *Ficedula parva*, Par ate - *Parus ater*, Par cae - *Parus caeruleus*, Par maj - *Parus major*, Par pal - *Parus palustris*, Phy col - *Phylloscopus collybita*, Phy sib - *Phylloscopus sibilatrix*, Syl atr - *Sylvia atricapilla*, Sit eur - *Sitta europaea*, Tur mer - *Turdus merula*, Tro tro - *Troglodytes troglodytes*.

First three factors of correspondence analysis explained together 62.58 % of total variability in the pre-foliage period (Appendix 3a). Since first two factors had a very similar meaning, correlating mainly with the foraging substrate “air space” and the foraging technique “sally”, the factors I and III were selected to display species partition in two-dimensional space (third factor correlated mainly with the substrate “shrubs”, the tree species “hazel”, and the foraging technique “pecking”). Ordination of the 17 species, using 27 foraging variables,

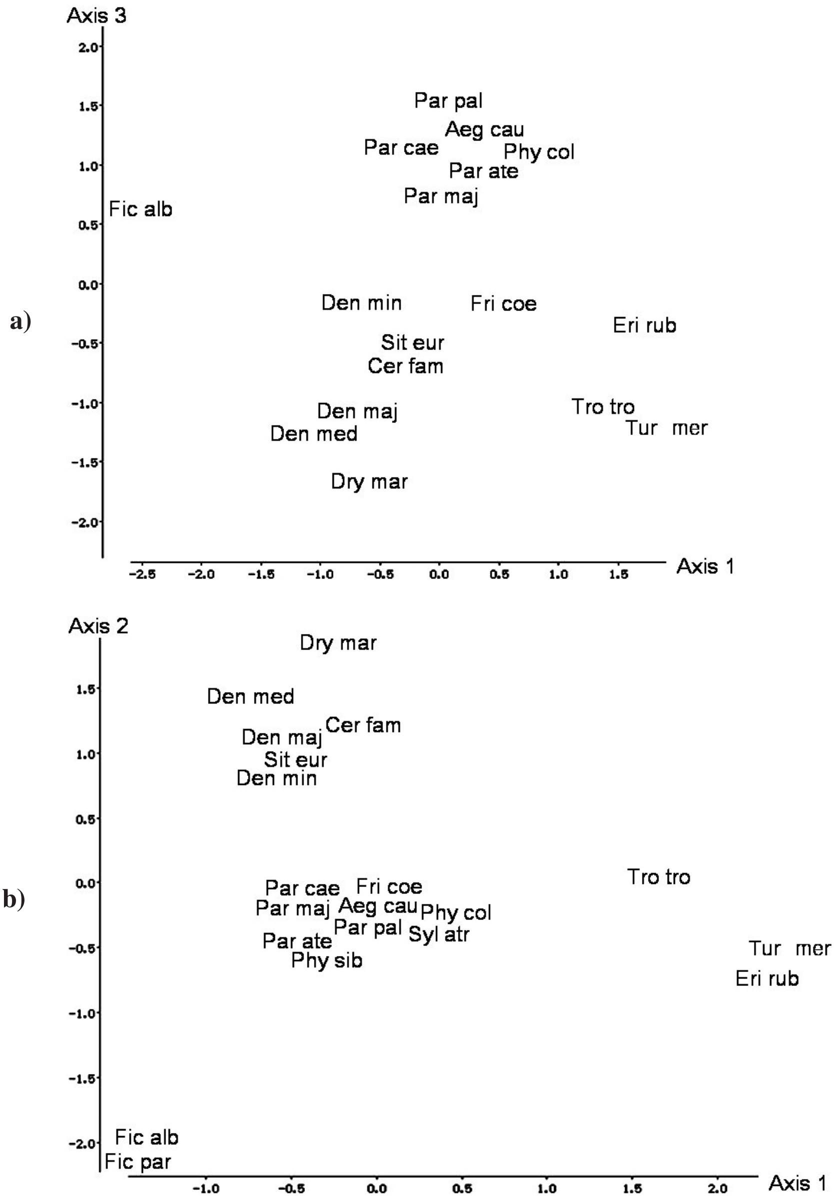


Fig. 2. Ordination of 17–20 bird species according to their foraging strategies using correspondence analysis; a) pre-foliage period; b) foliage period; abbreviations as in Fig. 1. Vertebratophages are omitted due to insignificant values (small portion only in the Approach 2).

indicated four distinct groups of species discernible on axes I and III (Fig. 2a). These groups may roughly be labelled as foragers on buds and twigs (the same six species as in first two clusters on the Fig. 1a), bark foragers (the same six species as in the third cluster on the Fig. 1a), aerial insectivore (collared flycatcher), and insectivores on the ground surface (the fifth cluster on the Fig. 1a), though chaffinch was located closer to bark insectivores.

In the foliage period, first three factors explained together 64.23 % of the total variability (Appendix 3b). First factor is related to foraging activities in lower layer and separated species mainly according to their affinity with the variables “bare soil”, “litter”, “height 0–1 m”, and “fir”. The second and third factors correlated mainly with foraging substrate “air space” and foraging technique “sally”. Ordination of the 20 species, using 26 foraging variables (variable “other tree species” was excluded from the analysis owing to zero values in this period) yielded four distinct groups of species discernible on axes I and II (Fig. 2b). First two factors effectively separated bird species into clear groups. The groups may be labelled as insectivores on leaves and twigs (the same nine species as in the first cluster from the Fig. 1b), insectivores on the ground surface (the same three species as in the fifth cluster from the Fig. 1b), aerial insectivores (collared flycatcher and red-breasted flycatcher), and bark insectivores (second and third clusters from the Fig. 1b).

Summing up, before leaves sprouting, the insectivores on the ground surface constituted 23.7 pairs/10 ha, followed by the insectivores on buds and twigs with overall density 17.6 pairs/10 ha (probers 14.5 and gleaners 3,4 pairs/10 ha), the bark insectivores 10.9 pairs/10 ha, and the aerial insectivores 8.0 pairs/10 ha. In the foliage period, the insectivores on leaves

Table 2. Foraging niche breadth of bird species occurred in both the pre-foliage and the foliage periods included in guild analysis. Guild codes are explained in the chapter 2.2.

Foraging guild	Species	Foraging niche breadth			
		Pre-foliage period	Foliage period	Difference absolute	Difference percentic
IF	*Parus major*	4.12	1.54	2.58	+62.5
	Parus caeruleus	1.54	1.15	0.39	+25.2
	Parus palustris	3.06	2.35	0.70	+23.0
	Parus ater	2.99	1.00	1.99	+66.6
	Phylloscopus collybita	2.46	1.83	0.63	+25.7
	Aegithalos caudatus	2.61	2.55	0.06	+2.2
	Fringilla coelebs	3.74	2.80	0.94	+25.2
IB	*Dendrocopos major*	3.82	4.54	-0.72	-18.9
	Dendrocopos medius	1.86	2.20	-0.34	-18.3
	Dendrocopos minor	2.90	5.05	-2.15	-74.0
	Dryocopus martius	1.96	2.11	-0.15	-7.7
	Certhia familiaris	1.06	1.04	0.03	+2.5
	Sitta europaea	3.29	3.24	0.05	+1.6
IG	*Troglodytes troglodytes*	2.84	2.66	0.18	+6.4
	Turdus merula	1.45	1.51	-0.07	-4.7
	Erithacus rubecula	2.09	1.97	0.11	+5.4
IA	*Ficedula albicollis*	1.32	1.58	-0.25	-19.1

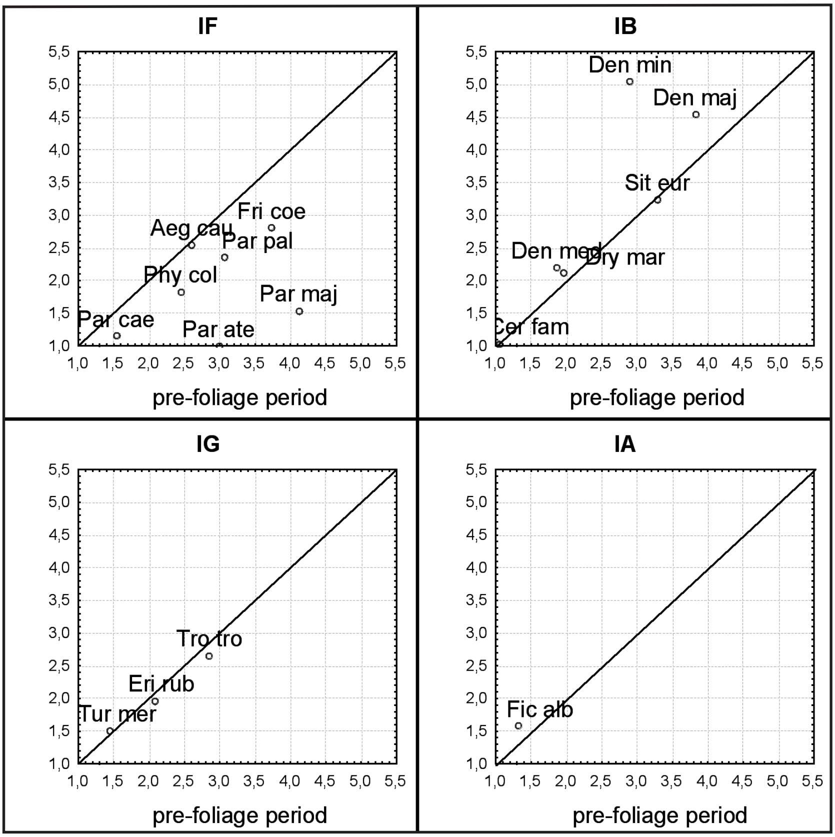


Fig. 3. Foraging niche breadth of bird species belonging to the most abundant foraging guilds occurred in both the pre-foliage and the foliage periods. The diagonal means equal niche breadth. Guild codes are explained in the chapter 2.2, bird species codes are explained in the Fig. 1.

and twigs predominated, constituting 35.6 pairs/10 ha. Then the insectivores on the ground surface constituted 12.5 pairs/10 ha, all bark insectivores 10.9 pairs/10 ha, and aerial insectivores 8.7 pairs/10 ha.

All members of the first guild (insectivores on buds/leaves and twigs) narrowed their foraging niches during the foliage period (mean decrease 32.9%, Table 2, Fig. 3). On the other hand, four woodpecker species used more variable foraging strategies during the foliage period (mean increase 29.7%). The similar pattern was observed in collared flycatcher's foraging strategy. The others changed their preferences just negligibly.

Comparison

Since the number of guild types obtained by three procedures is not identical, only four common guild types were considered as comparable. For the purpose of this comparison, first two clusters on the Fig. 1a were considered as one guild representing insectivores on buds and twigs. The same was made with bark insectivores on the Fig. 1b (second and third clusters). Densities of four guilds calculated using all methods are compared on the Fig. 4. Extrapolating from the Fig. 4a (pre-foliage period), the highest differences in guild density occurs in the insectivores on ground surface. The relative difference between minimal

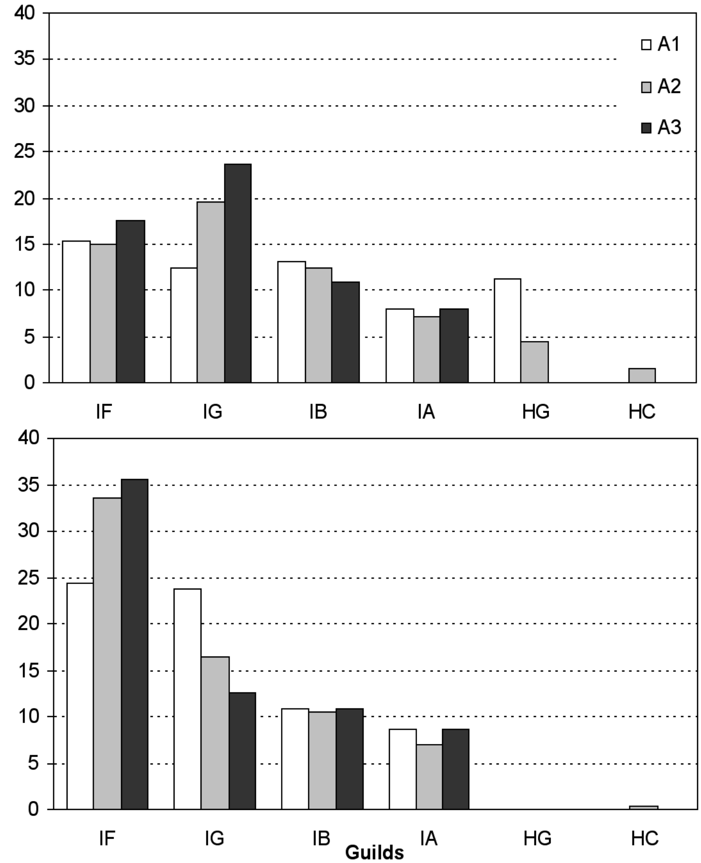


Fig. 4. Quantitative comparison of guild densities obtained by using three methods in the pre-foliage period (a) and in the foliage period (b). Guild codes are explained in the chapter 2.2.

(Approach 1) and maximal (Approach 3) density comprises 89.6% (considering the Approach 1 as 100%). The difference results from the fact, that during the pre-foliage period, some species (e. g. abundant chaffinch) belonged also to two herbivorous guilds classified only by the approaches 1 and 2, which deprived the four common guilds of some density share. Bark insectivores varied within 17.5%, reaching the highest density by the Approach 1. The density of the insectivores on buds and twigs was the highest using the Approach 3. The difference between the minimal (Approach 2) and the maximal values was 15.0%. Differences in the fourth guild did not exceed 10.0%, being the minimal by using the Approach 2.

Different classification of chaffinch caused notable variance in the first two guilds during the foliage period (Fig. 4b). It was considered as a ground insectivore according to the literature (Approach 1). However, approaches 2 and 3 classified the species mostly as a foliage insectivore. Thus, the density of foliage insectivores obtained by using the Approach 1 seems to be lower by 37.3–45.9% in comparison to other two methods. On the contrary, the density of ground insectivores was higher by 30.5–47.3% by using the Approach 1. Densities in the guild of bark insectivores are very similar (difference between minimal and maximal values was 3.1%). Aerial insectivores were identically classified by the approaches

1 and 3. Density of the guild was lower by 20.8% using the Approach 2. The difference resulted from the fact, that two flycatchers belonging to this guild used also gleaning from leaves in considerable portion (20–30%). Between-guilds differences are generally higher in the foliage period.

Discussion

Four-five guilds derived from the results of *a posteriori* classification are similar to the first four guild types defined by the approaches 1–2. The most species represented the insectivores on buds/leaves and twigs. This guild also appears in other studies being often called the "foliage gleaners" (Karr 1976, Holmes et al. 1979, Landres & MacMahon 1980, 1983, Holmes & Recher 1986, Krištín 1992, Adamík et al. 2003, Shirley 2004), the "leaf foragers" (Laiolo et al. 2003), the "crown insectivores" (Kropil 1996a), the "foliage insectivores" (Cody 1983, Kropil 1996b), or the "foliage-foraging insectivores" (Canterbury et al. 2000). During the pre-foliage period, cluster analysis revealed two groups of foragers on buds and twigs – probers and gleaners. Three tits belonging to the first group used their bills to penetrate into the buds. After foliage sprouting, those species used mainly gleaning technique and composed the most numerous guild of foliage gleaners.

Species preferring tree bark and wood foraging substrates created the second most numerous guild. This guild corresponds to the category of bark insectivores predefined in the approaches 1–2. It has commonly been called the "bark foragers" (Krištín 1992, Adamík et al. 2003, Laiolo et al. 2004), the "bark-foraging insectivores" (Canterbury et al. 2000), the "bark insectivores" (Kropil 1996a,b), or the "bark gleaners" (Karr 1976, Shirley 2004). Some authors discriminated between the "bark gleaners" (Karr 1976, Landres & MacMahon 1980, 1983, Holmes & Recher 1986) and mostly woodpeckers termed as "bark drillers" (Karr 1976), "bark probers" (Landres & MacMahon 1980, 1983) and "loose–bark prisers" (Holmes & Recher 1986). Laiolo et al. (2003) separated the "bark-distal foragers" (branch-twig foragers) from the "bark-proximal foragers" (stem foragers).

Various terms have been applied for the guild of aerial insectivores, being also called the "salliers" (Karr 1976), "air salliers" (Landres & MacMahon 1980, 1983), "sallying flycatchers" (Cody 1983), the "airspace foragers" (Adamík et al. 2003), the "aerial foragers" (Shirley 2004), the "aerial hawkers" (Holmes & Recher 1986), the "air insectivores" (Kropil 1996a,b), or the "aerial-foraging insectivores" (Canterbury et al. 2000). Bailey et al. (2004) discriminated between the "aerial insect pursuers" (i.e., swallow or swift), and the "insect hawkers" (i.e., flycatchers).

Mainly insectivorous species searching for food in the lower strata represent the "ground insectivores", being also termed by another authors the "ground salliers" (Landres & MacMahon 1980, 1983), the "ground gleaners" (Karr 1976, Lindsay et al. 2002, Laiolo et al. 2003, Shirley 2004), the "ground insectivores" (Kropil 1996a,b, Laiolo et al. 2004), or the "ground-foraging insectivores" (Canterbury et al. 2000). Holmes & Recher (1986) discriminated between the "ground gleaners/probers" and the "ground pouncers".

Comparison of three different methods for the guilds classification revealed some obscurities. The differences between separate approaches spring from three sources. Firstly, densities of common four guilds were impoverished by shares of herbivores in approaches 1 and 2, considerably in the pre-foliage period. Secondly, calculation of guild densities in the Approach 2 provides more detailed partitioning, thus naturally provides different (in most cases moderate) values. Thirdly, classification based on real observations takes into consideration also local and seasonal factors, which sometimes leads to discrepancies with results obtained from literature. During the pre-foliage period the density of insectivores on buds and twigs was higher by using the Approach 3. Contrary to the Approach 2, some generalists (four tits) were entirely included into the guild of insectivores on buds and twigs, although they exploited also another substrates (ground surface and tree bark) in considerable portion. The approaches 1 and 3 differed in the classification of chaffinch and marsh tit. First mentioned species was considered to be a ground herbivore, the second species as a bark insectivore in the Approach 1. Chaffinch belonged to the ground insectivores and marsh tit to the insectivores on buds and twigs in the Approach 3.

During the foliage period, differences arose in the density of foliage insectivores as well as ground insectivores. The difference emerges mainly from the classification of chaffinch. According to the literary data used for the *a priori* classification, the species was classified as a ground insectivore. Our observations showed that after the foliage sprouting, the leaves were the most preferred foraging substrate (more than 50% of all registrations). If the species was classified as a foliage insectivore in the Approach 1, the results would be absolutely consistent with the densities obtained by using the Approach 3. The insectivores on leaves and twigs were enriched in the Approach 2 by some share of another species partially collecting food from the leaves. The most frequently, the Approach 2 provided moderate densities of separate guilds.

The guilds are tightly related to foraging niches. All members of the first guild (insectivores on buds/leaves and twigs) exhibited wider foraging niche breadth during the pre-foliage period. It relates to the lack of abundant and easy accessible foraging sources in this period. Those species exhibited as generalists during this period. Four tit species as well as chaffinch compensated the lack of insect on leaves by gleaning branch bark and ground surface. After leaves sprouting, they shifted foraging sites towards foliage gleaning. The same noticed L a i o l o et al. (2004) in a native oak forest when comparing bird foraging behaviour in the winter and breeding periods. Two woodpecker species (great spotted woodpecker and lesser spotted woodpecker) exhibited as generalists after the foliage development. They considerably expanded their foraging niche towards foliage gleaning. The share of leaves comprised 10–20% of their total substrate use during this period. Dominance of generalists (especially dense species) led to the more even distribution of foraging guilds before leaves development. Three methods differed especially in the classification of foraging generalists.

The *a priori* classification is considered as a subjective method for guild determination. Besides subjective setting of guild categories, it does not take into consideration local factors. After a little modification, the method enables to quantify also fractional preference of each foraging substrate. The main objective of *a posteriori* approach is to ascertain species resource exploitation function within the ecosystem on the basis of dominant foraging strategy and preferred resources. It is difficult to quantify the real structure of each foraging guild created by using this method. It is not possible to determine species portions belonging to separate guilds. Birds are classified into foraging guilds on the basis of dominant foraging strategies, but the species foraging niches are usually wider. Although *a posteriori* classification is considered to be more objective method, it also brings some inconsistencies.

The subjective elements occur in variables design as well as in the results interpretation. Classification analysis (often cluster analysis) may give also fuzzy groups, because it always reveals groups, even if the data set does not have a clear group structure (P i l l a r 1999). Furthermore, a specific guild membership of a bird is valid only on the specific linkage distance. There is no general criterion to specify cut-off distance for grouping guilds. For this purpose many clustering algorithms have been proposed (P o d a n i 1994). P i l l a r (1999) offers a general method, based on bootstrap resampling, which was used in our study.

The Approach 2 might be more appropriate method for the quantitative comparisons of different bird communities from the guild aspect, in which the proportionality of foraging substrates use is taken into consideration. We suppose the Approach 2 can be considered to be some modification of *a priori* way, better than "a coarse" *a posteriori*. The guild categories were defined on the basis of a literary data before the factual study. The species classification into the predefined guild categories was performed on the basis of the real field observations, which is a little rare in *a priori* method, although some authors made that (C o d y 1983, K r o p i l 1996a,b; partially T o m i a ł o j ć et al. 1984). W i e n s (1989) described the *a priori* method as a species categorization into predefined very general guild categories on the basis of one's own observations, published information, or previous guild classifications of other authors. Since the main difference between *a priori* and *a posteriori* approaches is grounded in way to define guilds (in *a posteriori* guilds are created after a numerical resp. statistical analysis), we suppose the Approach 2 has more *a priori* features. The method is primarily focused on the analyses of resource exploitation in ecosystems on community or assemblage levels. This effect can be quantified on the basis of proportional exploitation of foraging resources by each species. Provided we know amount of consumed biomass (K a r r 1971), we can estimate predation pressure on animal community in a certain habitat. We are not sure if the guilds created by the Approach 2 are really guilds defined by R o o t (1967). The result of the Approach 2 is not a list of particular species creating guilds, but just a model of general guild structure. A species is usually a member of several foraging guilds. The most numerous guild is not always the guild of the highest density. Unlike *a posteriori* approach, the Approach 2 does not respect a foraging strategy that ignores R o o t ' s (1967) "similar way of exploitation of the same resources". Thus, it inclines to the J a k s i c ' s concept (1981), who considers resource type exploitation patterns regardless of exploitation tactics to be principal and the most important for the guild membership. Although Root originally defined a guild without regard to taxonomy, most authors restricted guild on the taxonomic class or order levels (H a i r s t o n 1981, J a k s i c 1981, H a w k i n s & M a c M a h o n 1989, W i e n s 1989). Some authors used term the "functional group" (S i m b e r l o f f & D a y a n 1991) as a synonym. The guild and functional group are not always considered as equivalent terms (W i e n s 1989). B l o n d e l (2003) supposed that these two concepts bear different meanings: "The guild concept refers primarily to the mechanisms of resource sharing by species in a competitive context, whereas the functional groups concept is concerned with how a resource or any other ecological component is processed by different species to provide a specific ecosystem service or function."

Based on our results, the applicability needs encourage using also modified *a priori* method (Approach 2) in connection to the applied disciplines, although *a priori* approach is considered to be less objective than *a posteriori* classification. We also recommend using the more detailed calculation modification of *a priori* method for the quantitative comparisons of guild structure of different bird assemblages. In this way, the proportionality of foraging substrate, diet, and strategy variables utilization is considered. Observations carried out in several control samples of a habitat type would allow us to test and confirm an accuracy and a generality of a species classification into guild types more precisely.

A c k n o w l e d g e m e n t s

The study was founded by the Faculty of Forestry, Technical University in Zvolen and the Slovak Science Grant Agency, project numbers 1/1327/04 and 1/4383/07. We thank to Martin K o r ň a n for statistical analyses, critical remarks and linguistic assistance. We thank also two anonymous referees for valuable comments.

LITERATURE

Adamík P. & Korňan M. 2004: Foraging ecology of two bark foraging passerine birds in an old-growth temperate forest. *Ornis Fennica 81: 13–22*.

Adamík P., Korňan M. & Vojtek J. 2003: The effect of habitat structure on guild patterns and the foraging strategies of insectivorous birds in forests. *Biologia, Bratislava 58: 275–286*.

Adams J. 1985: The definition and interpretation of guild structure in ecological communities. *J. Anim. Ecol. 54: 43–59*.

Alatalo R.V., Gustafsson L., Linden M. & Lundberg A. 1985: Interspecific competition and niche shifts in tits and the gold-crest: an experiment. *J. Anim. Ecol. 54: 77–984*.

Bailey S.A., Horner-Devine M.C., Luck G., Moore L.A., Carney K.M., Anderson S., Betrus C. & Fleishman E. 2004: Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. *Ecography 27: 207–217*.

Blondel J. 2003: Guilds or functional groups: does it matter? *Oikos 100: 223–231*.

Brandl R., Krištín A. & Leisler B. 1994: Dietary niche breadth in a local community of passerine birds: an analysis using phylogenetic contrasts. *Oecologia 98: 109–116*.

Canterbury G.E., Martin T.E., Petit D.R., Petit L.J. & Brandford D.F. 2000: Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conserv. Biol. 14: 544–558*.

Cody M.L. 1983: Bird diversity and density in south African forest. *Oecologia 59: 201–215*.

Dolby A.S. & Grubb T.C. 1999: Effect of winter weather on horizontal vertical use of isolated forest fragments by bark-foraging birds. *Condor 101: 408–412*.

Emlen J.T. 1972: Size and structure of a wintering avian community in southern Texas. *Ecology: 53: 317–329*.

Forsman J.T., Seppänen J.T. & Mönkkönen M. 2002: Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society London, Series B 269: 1619–1623*.

Gustafsson L. 1988: Foraging behaviour of individual coal tits, *Parus ater*, in relation to their age, sex and morphology. *Anim. Behav. 36: 969–704*.

Hairston N.G. 1981: An experimental test of a guild: salamander competition. *Ecology 62: 65–72*.

Hawkins, C.P. & MacMahon J.A. 1989: Guilds: the multiple meanings of a concept. *Annu. Rev. Entomol. 34: 423–451*.

Hejl S., Verner J. & Bell G. W. 1990: Sequential versus initial observations in studies of avian foraging. *Stud. Avian Biol. 13: 166–173*.

Hino T., Unno A. & Nakano S. 2002: Prey distribution and foraging preference for tits. *Ornithol. Sci. 1: 81–87*.

Holmes R.T., R.E. Bonney J.R. & Pacala S.W. 1979: Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology 60: 512–520*.

Holmes R. T. & Recher H. F. 1986: Search tactics of insectivorous birds foraging in an Australian eucalypt forest. *The Auk 103: 515–530*.

Hudec K. (et al.) 1983: Fauna ČSSR, Birds III/1, 2. *Academia, Praha (in Czech with German summary)*.

Jaksic F.M. 1981: Abuse and misuse of the term “guild” in ecological studies. *Oikos 37: 397–400*.

Jedlicka J.A., Greenberg R., Perfecto I., Philpott S.M. & Dietsch T.V. 2006: Seasonal shift in the foraging niche in a tropical avian resident: resource competition at work? *J. Trop. Ecol. 22: 385–395*.

Johnson N.K. 1975: Controls of number of bird species on montane islands in the Great Basin. *Evolution 29: 545–567*.

Johnson M.D. & Sherry T.W. 2001: Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *J. Anim. Ecol. 70: 546–560.*

Karr J.R. 1971: Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr. 41: 207–233.*

Karr J.R. 1976: Within- and between-habitat avian diversity in African and Neotropical lowland habitats. *Ecol. Monogr. 46: 457–481.*

Korpeľ Š. 1995: Die Urwälder der Westkarpaten. *Gustav Fischer Verlag, Stuttgart, Jena, New York.*

Krebs Ch.J. 1989: Ecological methodology. *Harper & Row, New York.*

Krištín A. 1992: Trophische Beziehungen zwischen Singvögeln und Wirbellosen im Eichen-Buchenwald zur Brutzeit. *Ornitol. Beob. 89: 157–169.*

Kropil R. 1996a: The breeding bird community of the West Carpathians fir-spruce-beech primeval forest (The Dobroč nature reserve). *Biologia, Bratislava 51: 585–598.*

Kropil R. 1996b: Structure of the breeding bird assemblage of the fir-beech primeval forest in the West Carpathians (Badín nature reserve). *Folia Zool. 45: 311–324.*

Kropil R. 1998: Breeding bird community of primeval and natural forests in the west Carpathians. *Ostrich 69: 294.*

Kropil R. 2004: Central European natural forest bird communities and guilds: Case study in West Carpathians fragmented forest landscape. In: Sano M., Miyamoto A. & Sugimura K. (eds), Landscape Ecology 2004: Conservation and management of fragmented Forest Landscapes. *Forestry and Forest Products Research Institute, Tsukuba & United Nations University, Tokyo: 44.*

Kullberg C. & Ekman J. 2000: Does predation maintain tit community diversity? *Oikos 89: 41–45.*

Laiolo P. 2002: Effects of habitat structure, floral composition and diversity on a forest bird community in north-western Italy. *Folia Zool. 51: 121–128.*

Laiolo P., Caprio E. & Rolando A. 2003: Effects of logging and non-native tree proliferation on the birds overwintering in the upland forests of north-western Italy. *Forest Ecol. Manage. 179: 441–454.*

Laiolo P., Caprio E. & Rolando A. 2004: Can forest management have season-dependent effects on bird diversity? *Biodivers. Conserv. 13: 1925–1941.*

Landres P.B. & MacMahon A. 1980: Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. *Auk 97: 351–365.*

Landres P.B. & MacMahon A. 1983: Community organization of arboreal birds in some oak woodlands of western North America. *Ecol. Monogr. 53: 183–208.*

Lešo P. 2003: Structure and ecological relationships of oak forests breeding bird assemblages in selected nature reserves of Slovakia. *PhD-thesis, Faculty of Forestry, Technical University in Zvolen, Slovakia (in Slovak with English summary).*

Lindsday A.R., Gillum S.S. & Meyer M.W. 2002: Influence of lakeshore development on breeding bird communities in a mixed northern forest. *Biol. Conserv. 107: 1–11.*

Ludwig J.A. & Reynolds J.F. 1988: Statistical ecology: a primer on methods and computing. *A Wiley – Interscience publication. New York, Chichester, Brisbane, Toronto, Singapore.*

MacArthur R.H. 1958: Population ecology of some warblers of northeastern coniferous forests. *Ecology 39: 599–619.*

MacArthur R.H., MacArthur J.W. & Preer J. 1962: On bird species diversity. II. Prediction of bird census from habitat measurement. *Am. Nat. 96: 167–174.*

Martínez del Rio P.C. 2001: The abundance of four bird guilds and their use of plants in a Mexican dry forest-oak woodland gradient in two contrasting seasons. *Huitzil 2: 3–14.*

Mönkkönen M., Forsman J.T. & Helle P. 1996: Mixed-species foraging aggregations and heterospecific attraction in boreal bird communities. *Oikos 77: 127–136.*

Odum E.P. 1945: The concept of the biome as applied to the distribution of North American birds. *Wilson Bull. 57: 191–210.*

Pearson D.L. 1975: The relation of foliage complexity to ecological diversity of three Amazonian bird communities. *Condor 77: 453–466.*

Pearson D.L. 1977: A pantropical comparison of bird community structure on six lowland forest sites. *Condor 79: 232–244.*

Pillar V.D. 1999: How sharp are classifications? *Ecology 80: 2508–2516.*

Pillar V.D. 2004: MULTIV. Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling. User's Guide v. 2.3.9. *Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil.*

Podani J. 1994: Multivariate data analysis in ecology and systematics. *SPB Academic Publishing, Hague, Netherlands.*

Podani J. 1997: SYN-TAX 5.10-pc. Supplement to User's Manual. *Scientia Publishing, Budapest*.
Robinson S.K. & Holmes R.T. 1982: Foraging behaviour of forest birds: The relationships among search tactics, diet, and habitat structure. *Ecology 63: 1918–1931*.
Root R.B. 1967: The niche exploitation pattern of the blue-grey gnatcatcher. *Ecol. Monogr. 37: 317–350*.
Shirley S. 2004: The influence of habitat diversity and structure on bird use of riparian buffer strips in coastal forests of British Columbia, Canada. *Can. J. For. Res. 34: 1499–1510*.
Simberloff D. & Dayan T. 1991: The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst. 22: 115–143*.
Suhonen J., Alatalo R.V., Carlson A. & Höglund J. 1992: Food resource distribution and the organization of the Parus guild in a spruce forest. *Ornis Scand. 23: 467–474*.
Suhonen J. & Kuitunen M. 1991: Intersexual foraging niche differentiation within the breeding pair in the Common Treecreeper *Certhia familiaris*. *Ornis Scand. 22: 313–318*.
Thomson R.L., Forsman J.T. & Mönkkönen M. 2003: Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. *Oecologia 134: 431–438*.
Tomiałojć L. 1980: The combined version of the mapping method. In: Oelke H. (ed.), *Proceedings of the VI. International Conference Bird census work, Göttingen: 92–104*.
Tomiałojć L., Wesolowski T. & Walankiewicz W. 1984: Breeding bird community of a primeval forest (Bialowieza National Park, Poland). *Acta Ornithol. 20: 241–310*.
Whelan Ch.J. 2001: Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology 82: 219–231*.
Wiens J.A. 1989: The ecology of bird communities. Vols I, II. *Cambridge Univ. Press, Cambridge*.

Appendix 1. *A priori* classification of species into the predefined foraging guilds on the basis of literature (Approach 1). The number before the slash represents the pre-foliage period; number behind the slash represents the foliage period. Second column represents mean densities of 20 bird species from all study plots in 1999-2002 used for guild quantification. Bird species codes are explained in the Fig. 1, guild codes are explained in the chapter 2.2.

Species	Mean density (breeding pairs/10 ha)	Guild category						
		IF	IG	IB	IA	HG	HC	V
Aeg cau	1.4	1/1	0/0	0/0	0/0	0/0	0/0	0/0
Cer fam	2.3	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Den maj	2.7	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Den med	1.3	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Den min	0.7	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Dry mar	0.1	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Eri rub	7.1	0/0	1/1	0/0	0/0	0/0	0/0	0/0
Fic alb	8.0	0/0	0/0	0/0	1/1	0/0	0/0	0/0
Fic par	0.7	-/0	-/0	-/0	-/0	-/1	-/0	-/0
Fri coe	11.2	0/0	0/1	0/0	0/0	1/0	0/0	0/0
Par ate	0.3	1/1	0/0	0/0	0/0	0/0	0/0	0/0
Par cae	6.6	1/1	0/0	0/0	0/0	0/0	0/0	0/0
Par maj	5.6	1/1	0/0	0/0	0/0	0/0	0/0	0/0
Par pal	2.3	0/1	0/0	1/0	0/0	0/0	0/0	0/0
Phy col	1.4	1/1	0/0	0/0	0/0	0/0	0/0	0/0
Phy sib	4.7	-/1	-/0	-/0	-/0	-/0	-/0	-/0
Sit eur	3.8	0/0	0/0	1/1	0/0	0/0	0/0	0/0
Syl atr	2.1	-/1	-/0	-/0	-/0	-/0	-/0	-/0
Tro tro	2.6	0/0	1/1	0/0	0/0	0/0	0/0	0/0
Tur mer	2.8	0/0	1/1	0/0	0/0	0/0	0/0	0/0

Appendix 2. Proportional classification of species into the predefined foraging guilds on the basis of own observations (Approach 2). Portions under 0.1 are marked by "+". Missing species in the pre-foliage period are marked by "-".Bird species codes are explained in the Fig. 1, guild codes are explained in the chapter 2.2.

Species	Guild category						
	IF	IG	IB	IA	HG	HC	V
Aeg cau	1.0/1.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Cer fam	0.0/0.0	0.0/0.0	1.0/1.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Den maj	0.0/0.1	0.1/0.1	0.6/0.8	0.0/0.0	0.2/+	0.1/+	+/0.0
Den med	+/0.0	+/+	1.0/1.0	0.0/0.0	0.0/0.0	+/+	0.0/0.0
Den min	+/0.2	+/0.0	0.8/0.8	0.0/0.0	0.1/0.0	0.1/0.0	0.0/0.0
Dry mar	0.0/0.0	0.2/0.3	0.8/0.7	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Eri rub	+/+	1/1.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Fic alb	0.0/0.2	+/+	0.1/+	0.9/0.8	0.0/0.0	0.0/0.0	0.0/0.0
Fic par	-/0.3	-/0.0	-/0.0	-/0.7	-/0.0	-/0.0	-/0.0
Fri coe	0.1/0.6	0.5/0.3	0.2/0.1	+/0.0	0.2/+	+/+	0.0/0.0
Par ate	0.7/1.0	0.2/+	0.1/+	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Par cae	0.9/1.0	0/+	0.1/+	0.0/0.0	+/0.0	+/0.0	0.0/0.0
Par maj	0.6/1.0	0.1/+	0.2/+	0.0/0.0	0.1/+	+/0.0	0.0/0.0
Par pal	0.8/0.9	0.1/0.1	0.1/+	0.0/0.0	+/+	+/0.0	0.0/0.0
Phy col	0.8/1.0	0.2/+	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Phy sib	-/1.0	-/+	-/0.0	-/0.0	-/0.0	-/0.0	-/0.0
Sit eur	+/0.1	0.1/0.1	0.4/0.8	0.0/0.0	0.2/+	0.3/+	0.0/0.0
Syl atr	-/1.0	-/+	-/0.0	-/0.0	-/0.0	-/0.0	-/0.0
Tro tro	0.0/0.0	1.0/1.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Tur mer	0.0/0.0	0.9/0.9	0.0/0.0	0.0/0.0	0.1/+	0.0/0.1	0.0/0.0

Appendix 3a. Table of factor loadings for variables calculated from pre-foliage data matrix.

	Eigenvalues	0.536	0.428	0.344	0.215	0.126	0.119	0.109	0.077	0.058	0.0277
	Eigenvalues as %	25.66	20.48	16.44	10.27	6.01	5.67	5.21	3.66	2.79	1.33
	Cummulative %	25.66	46.14	62.58	72.86	78.87	84.54	89.75	93.41	96.19	97.53
No.	List of variables	Factor 1	Factor 2	Factor 3	Factor4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10
1.	Bare soil	1.513	1.483	-1.068	0.256	0.641	-0.879	0.777	-1.726	-0.228	0.381
2.	Litter	1.444	1.036	-0.561	1.043	-0.566	0.206	-0.108	1.127	0.190	-0.016
3.	Dead wood	0.081	-0.261	-1.939	-0.828	2.014	0.056	3.274	-1.891	-0.006	0.897
4.	Air space	-3.290	4.363	1.082	-0.406	0.187	0.160	0.696	0.156	0.033	0.513
5.	Herbs	0.612	-0.471	1.907	-1.844	-2.132	0.006	1.727	0.080	-1.796	0.939
6.	Shrubs	0.597	-0.511	2.067	-2.218	-1.478	0.606	1.309	0.622	-1.794	-1.306
7.	Thick stem >30cm	-0.797	-0.735	-1.429	-0.722	-0.628	0.801	-1.896	-0.316	0.981	1.019
8.	Thin stem <30 cm	-0.681	-0.916	-0.780	1.076	-0.345	-1.360	0.164	1.055	1.313	-2.708
9.	Thick branches > 20 cm	-0.482	-0.758	-0.444	1.255	-0.114	-1.128	-1.079	0.230	-2.420	-0.037
10.	Thin branches 2-20 cm	-0.521	-0.828	-0.264	1.583	-0.685	-2.184	-0.579	-0.298	-4.638	0.642
11.	Twigs <2 cm	0.329	-0.517	1.581	-0.005	1.466	1.177	-0.435	0.919	-1.067	-1.503
12.	Buds	0.157	-0.740	1.866	0.906	0.763	0.249	0.616	-0.266	2.471	-1.134
13.	0-1 m	1.325	0.968	-0.731	0.362	0.117	-0.006	0.534	-0.536	-0.115	0.213
14.	1-4 m	-0.080	-0.749	0.124	-1.839	-0.884	1.287	0.255	-0.452	0.522	1.027
15.	4-12 m	-1.027	0.154	-0.360	-0.196	-0.285	0.088	-0.843	0.449	-0.512	-0.036
16.	>12 m	-0.419	-0.450	0.680	0.919	0.471	-0.443	0.124	0.238	0.015	-0.736
17.	Oak	-0.679	-0.234	-0.250	0.176	-0.255	-0.151	-0.336	-0.398	0.206	-0.676
18.	Beech	0.162	-0.649	1.182	0.550	2.676	1.532	-0.332	1.966	-0.802	2.526
19.	Hornbeam	0.097	-0.706	1.367	-0.232	-0.419	0.159	0.391	-0.238	0.052	-4.972
20.	Hazel	0.510	-0.620	2.121	-1.779	-1.911	0.329	1.882	0.308	-1.387	1.599
21.	Fir	0.514	-0.381	1.682	1.968	7.724	4.097	-2.923	4.621	-0.420	5.946
22.	Other trees	1.626	0.882	0.390	-2.248	0.053	-3.824	-1.219	2.281	1.559	0.601
23.	Gleaning	0.777	0.241	0.196	-0.433	0.535	0.479	-0.835	-0.769	-0.414	-0.559
24.	Picking	1.820	1.586	-1.495	3.351	-4.810	4.261	1.019	3.682	0.685	-0.583
25.	Probing	-0.233	-0.850	0.824	1.380	-1.218	-1.119	0.684	-0.803	0.671	1.967
26.	Pecking	-0.951	-1.137	-2.051	-0.605	0.664	-0.378	1.784	2.152	0.045	-.871
27.	Sally	-3.301	4.374	1.086	-0.412	0.186	0.162	0.702	0.166	0.044	0.533

Appendix 3b. Table of factor loadings for variables calculated from foliage data matrix.

	Eigenvalues	0.582	0.414	0.376	0.210	0.195	0.123	0.086	0.074	0.029	0.0159
	Eigenvalues as %	27.24	19.38	17.61	9.83	9.12	5.75	4.01	3.47	1.37	0.74
	Cummulative %	27.24	46.61	64.23	74.06	83.18	88.93	92.94	96.41	97.78	98.53
No.	List of variables	Factor 1	Factor 2	Factor 3	Factor4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Factor 10
1.	Bare soil	2.107	-0.511	0.681	0.798	-1.774	0.032	2.439	1.389	-2.852	2.680
2.	Litter	2.702	-0.732	1.085	-0.773	-0.282	-0.087	-1.210	-0.427	0.778	0.261
3.	Dead wood	0.478	1.551	1.306	3.432	-1.241	-0.556	1.776	1.012	1.733	1.841
4.	Air space	-1.806	-3.220	2.557	0.605	0.613	0.571	0.339	0.209	0.062	-0.190
5.	Herbs	1.185	-0.649	-0.507	-0.121	-1.041	0.138	-1.143	-0.807	-4.287	-9.647
6.	Shrubs	0.314	-0.369	-1.770	0.842	2.209	2.383	0.131	0.681	0.307	1.638
7.	Thick stem >30cm	-0.500	1.902	1.116	-1.048	1.441	-1.078	0.860	0.653	-2.037	-0.888
8.	Thin stem <30 cm	-0.542	1.968	1.038	1.090	-0.963	1.318	-2.208	-0.287	4.133	-4.456
9.	Thick branches > 20 cm	-0.651	1.461	0.701	-1.728	-1.168	1.700	-0.581	1.834	-0.095	0.860
10.	Thin branches 2-20 cm	-0.674	1.150	0.518	-1.797	-1.809	2.390	-0.536	1.622	3.813	-3.004
11.	Twigs <2 cm	-0.359	0.384	-0.845	-0.545	-0.851	1.682	0.454	-0.853	3.236	-4.949
12.	Buds	-0.339	-0.515	-1.274	0.021	-0.573	-1.024	-0.306	-0.975	-0.132	0.923
13.	0-1 m	2.096	-0.269	0.877	0.678	-0.732	-0.199	1.056	0.569	0.311	0.393
14.	1-4 m	-0.108	0.692	-0.357	0.995	2.156	0.384	0.428	-0.225	0.223	-1.112
15.	4-12 m	-0.620	-0.182	-0.157	-0.199	0.233	-0.885	-0.602	1.279	-0.581	0.378
16.	>12 m	-0.568	-0.016	-0.167	-0.571	-0.939	0.618	0.111	-1.082	0.312	0.233
17.	Oak	-0.577	0.352	0.294	-0.258	-0.128	0.118	0.212	-0.842	-0.254	-0.080
18.	Beech	-0.454	-0.702	-1.239	0.422	-0.214	-2.271	-1.816	2.276	1.346	-1.359
19.	Hornbeam	-0.189	-0.304	-1.663	0.124	0.194	-1.183	-1.198	2.257	0.708	0.499
20.	Hazel	0.081	-0.328	-2.013	1.047	2.160	2.448	0.470	0.974	0.267	-0.066
21.	Fir	2.499	-0.813	0.605	-0.860	0.797	0.888	-2.668	-0.603	-1.157	-0.326
23.	Gleaning	0.331	-0.133	-0.742	0.053	-0.343	-0.041	0.580	0.025	-0.309	-0.291
24.	Picking	1.088	0.672	1.217	-2.806	3.158	-2.543	1.340	-0.983	3.732	1.326
25.	Probing	-0.696	1.647	0.728	-1.878	-1.212	1.952	-0.943	2.777	-0.173	2.439
26.	Pecking	-0.468	2.454	1.531	3.303	0.115	-0.162	-3.184	-1.444	-0.027	0.000
27.	Sally	-1.797	-3.216	2.499	0.613	0.596	0.420	0.195	0.356	0.154	0.029