



ORIGINAL INVESTIGATION

Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe)

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Abstract

For the assessment of the habitat use of bats with consideration of a complexity of environmental features a large-scale multivariate canonical correspondence analysis (CCA) was performed. Data were collected in April–September (1999–2005) using mist-netting and bat-detectors ($n = 209$ samplings) in Slovakia ($n = 160$ sites). For the habitat description, 17 environmental variables that characterised the sampling site, tree-species composition and general character of surrounding forest were selected. In study sites, altogether 93% of Slovak chiropteroфаuna species were recorded but only 16 species (2466 individuals) were recorded in more than 5% of samplings. The most common and frequent species were *Myotis mystacinus* (frequency of occurrence = 57%, species dominance = 12%) and *Myotis myotis* (44%, 10%), followed by *Barbastella barbastellus* (32%, 6%), *Plecotus auritus* (32%, 6%), *Nyctalus noctula* (31%, 9%) and *Myotis brandtii* (31%, 7%). Of the tested environmental variables used in CCA analysis, 13 had significant influence on the species' presence. On the base of gradients in ordination analysis, there were two main groups of species. In the first “true” forest bats group the tree-dwelling and gleaning species *Myotis bechsteinii*, *Myotis nattereri* and *P. auritus* dominated. Their occurrence was connected mainly with old forests of natural tree-species composition. The second group comprised species, which foraged in more open space or along the forest edge (with the farmland) and avoided closed interior (particularly *Eptesicus serotinus*, *N. noctula*, *Nyctalus leisleri*, *Pipistrellus pipistrellus*). The presence of mountain species *Eptesicus nilssonii* and *Vespertilio murinus* was associated mainly with dominance of spruce. Suggested predictive modelling of species composition in forest bat assemblages in conditions of natural forests can help in nature conservation.

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Keywords: Chiroptera; Vegetation structure; Multivariate analysis

Introduction

The presence and structure of species in forest bat assemblages are influenced by a wide complex of environmental factors. An important impact is the

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availability of suitable foraging habitats and food supply (e.g. Walsh and Mayle 1991; Walsh et al. 1995; Arlettaz 1996; Walsh and Harris 1996a,b; Brigham et al. 1997; Jung et al. 1999; Kusch et al. 2004; Zahn et al. 2005), as well as roost availability (reviewed by Lacki and Baker 2003). The range of foraging habitat used in forests is species specific and depends on the various hunting strategies of species. Strategies are governed by the type of echolocation, body morphology and main diet composition (e.g. Gaisler 1959; Norberg and Rayner 1987; Arlettaz 1996; Entwistle et al. 1996; Sierro 1999; Siemers and Schnitzler 2000). For instance, the foraging activity of forest bats is affected by tree-species composition (Rachwald 1992; Jung et al. 1999; Kalcounis et al. 1999), age (Erickson and West 1996; Crampton and Barclay 1998), structure (Brigham et al. 1997; Humes et al. 1999; Jung et al. 1999; Patriquin and Barclay 2003) or even fragmentation of stands (Crampton and Barclay 1996; Grindal and Brigham 1998). Ciechanowski (2002) and Kusch et al. (2004) presented that the occurrence of bats was also strongly influenced by the position of the observed site (e.g. on the edge of stand, watercourse or pool). Naturally, an important factor affecting the activity of bats is the seasonal changes in food supply of habitats. Local activity of insects actually changes opportunistic behaviour of some insectivorous bat species (Verboom and Spoelstra 1999; Kusch et al. 2004; Zahn et al. 2005). However, in the large-scale (tents of up to hundreds of sites) and long-term (data from more years) multivariate analysis, it is possible to assess habitat use with consideration of a complexity of environmental features. Recent studies, using mist-netting or bat-detectors, were performed in tropical or subtropical regions (Gorresen et al. 2005; Milne et al. 2005) as well in the temperate zone of North America (Ford et al. 2005) and Europe (Walsh and Harris 1996a,b; Jaberg and Guisan 2001). Those multivariate analyses indicated dependence of bat presence on a combination of several habitat features.

The study of the species requirement on the habitat quality is a basic task in biodiversity conservation. It is known that almost all European bat species exploit forest ecosystems (Zahn and Krüger-Barvels 1996; Meschede and Heller 2000). Few data exist about the bat assemblages in the forests of Slovakia (e.g. Celuch and Kaňuch 2004; Kaňuch and Krištín 2006). There is a presumption that in highly diversified indigenous ecosystems there will be higher species richness of bats, spatially differing in patterns of habitat use. The aim of this study was to examine differences in species composition in relation to the forest character and to find “true” forest species and their habitat requirement in a natural environment.

Material and methods

The continental climate in Slovakia exhibits distinctive seasonal changes. Different altitudes (94–2655 m a.s.l.) have specific local climatic conditions and thereby also peculiar characteristics of the vegetation. Nationally, the long-term average temperature in January is -3.9°C and in July 17.4°C . Annual precipitation is around 740 mm. Forests cover more than 40% and the majority of them is composed of natural tree species (i.e. the main tree-species correspond to the environmental conditions). In all, the tree species represented in the Slovak forests are (given in percentage of the surface area where species are present): beech (*Fagus sylvatica*) 31%, spruce (*Picea abies*) 26%, oaks (in particular *Quercus petraea*, *Quercus robur*, *Quercus cerris*) 13%, hornbeam (*Carpinus betulus*) 6%, other broadleaved trees 10% (e.g. ash *Fraxinus excelsior*, maple *Acer* sp., elm *Ulmus* sp., lime *Tilia* sp.), pine (*Pinus sylvestris*) 7%, fir (*Abies alba*) 4% and other conifers 3% (e.g. larch *Larix decidua*, dwarf pine *Pinus mugo*). In comparison to the rest of Europe, on the altitudinal gradient (natural upper tree-line is about 1450–1700 m a.s.l.) there are eight forest vegetation levels (oak, beech-oak, oak-beech, beech, fir-beech, spruce-beech-fir, spruce and dwarf pine), often with equal portions of age classes and rich tree-species composition. Plantation management is limited; there is high natural stand restoration (60%), a high proportion of dead wood and use of pesticides only exceptionally. The primary function of around 33% of the forest area is other than economic (e.g. nature protection) and there are more than 70 primeval forest reserves. They represent unique Carpathian ecosystems (Zlatník 1959; Bublinec and Pichler 2001; Miklós and Hrnčiarová 2002; Frič and Pilná 2005). The above-mentioned information indicates the generally high species diversity.

Data were collected in April–September (1999–2005) using mist-netting and bat-detectors ($n = 209$ positive samplings) in a range of sites in Slovakia, mainly in its eastern and central parts ($48^{\circ}05'–49^{\circ}11'N$, $17^{\circ}23'–22^{\circ}32'E$; $n = 160$ sites; Fig. 1). Size (2.5 m \times 7–14 m) and number (1–2) of exposed mist-nets depended on the sampling site. Bats were captured mostly after warm days, in non-rainy weather, 3–4 h after dusk during the time of the highest activity at foraging or drinking habitats of various forest types. Captured bats were immediately removed from the mist-net, determined (according to the key Schober and Grimmberger 1998) and consequently released. Simultaneously, at the site of mist-netting, Pettersson D100 or D200 ultrasound bat-detectors were used. The use of bat detectors facilitated the identification of the few easily recognised species (i.e. *Myotis daubentonii*, species of the genus *Pipistrellus*, and *Nyctalus noctula*; by Ahlén 1990) if they were not caught in the mist-net at the site. The abundance of each detected but not mist-netted species was considered to be one individual (ind.). This method ensured correct species identification of all recorded individuals. Decreasing number of samplings at increasing altitude resulted in fewer potential opportunities for bat sampling (40% of samplings in 100–350 m a.s.l., 41% in 350–600, 11% in 600–850, 5% in 850–1100, and 3% in 1100–1350). However, such distribution approximately reflects the representation of individual altitudes in the study area. The total number mist-netted or recorded using bat-detectors was a minimum of 2540 ind. of 25 bat species. The frequency of

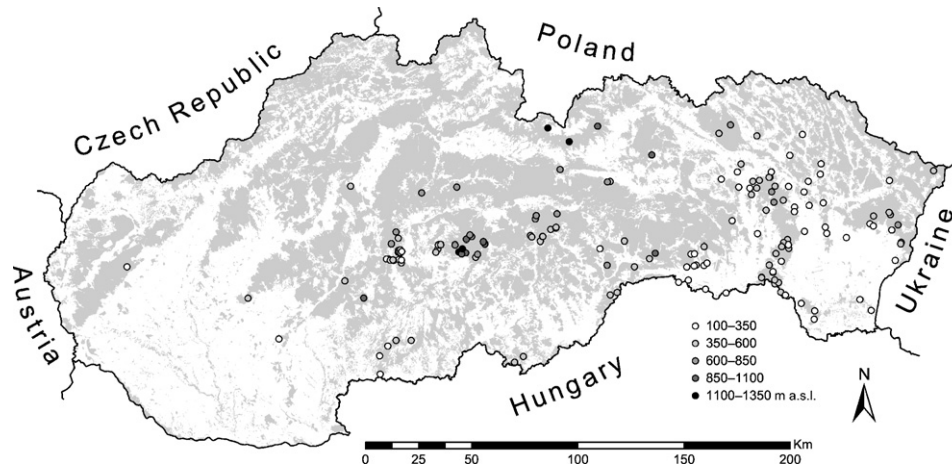


Fig. 1. Study sites in Slovakia ($n = 160$ sites). Explanations: circles – sites with graduated colour of the altitude, grey area – forests.

occurrence and species dominance as well as altitudinal distribution of species was evaluated. Species with a frequency of occurrence of more than 20% were considered common.

For the habitat description, environmental variables that characterised the sampling site, tree-species composition and general character of surrounding forest were selected (Table 1). Data samples were taken from forest brooks (mostly at a backwater or ford), game mires or other small water pools (diameter less than 10 m), forest roads (often with puddle) and larger water pools, reservoirs at the streams or ponds (width more than 10 m). In addition to the forest interior (in this study it was considered a site more than 100 m from the forest edge), samples were also taken at the forest edges. Three types of ecotones were distinguished: forest/farmland, forest/clear-cutting and forest/settlement. Farmland included meadows, fields and pastures (open sites without trees in general), clear-cuttings represented harvested stands, possibly with immature trees (up to 20 years) and areas of forest buildings (cottages) were considered as settlements. Data about the character of the forest surrounding the sampling site (tree-species composition, naturalness, age and heterogeneity of stands) were obtained from the stands of the area within a radius of 500 m (i.e. 78.5 ha) using GIS map documents (Slovak National Forest Database) in the software ArcView GIS 3.2 (ESRI, Inc.). Heterogeneity was determined by the mean of Simpson's indices of diversity (Simpson 1949) of tree-species and age composition of the surrounding forest. Total age of forest presented mean weighted by area of individual stands. Naturalness of forests was the percentage of natural tree-species composition, by the method used in the programme NATURA 2000 (Schwarz et al. 2005). The majority of sampling sites were located in generally older (80–100 years), heterogeneous habitats of natural tree-species composition with favourable conservation status (Table 1).

The environmental impact on the use of foraging habitats of bats was investigated with the help of gradient analysis in the software CANOCO for Windows 4.5 (Ter Braak and Šmilauer 2002). Since the influence of altitude (the interpretation of which was not the object of the ordination) on the species occurrence was expected, it was used as a co-variable (Ter Braak and Šmilauer 1998). In the analysis of the relation

Table 1. Tested environmental variables ($n = 17$) and their percentage in all samplings ($n = 209$)

Tested environmental variables	%
Game mire, small pool (< 10 m)	28
Larger pool (> 10 m)	20
Brook	30
Forest road	22
Forest interior	61
Ecotone forest/farmland	27
Ecotone forest/clear-cutting	7
Ecotone forest/settlement	5
Beech	29
Oak	31
Hornbeam	14
Other broadleaved trees	7
Spruce	11
Other conifers	8
Heterogeneity (mean of Simpson's indices of diversity of tree-species composition and age)	
< 0.25	6
0.25–0.5	32
0.5–0.75	61
> 0.75	1
Total age (weighted mean)	
< 40 years	1
40–60 years	8
60–80 years	34
80–100 years	36
100–120 years	14
> 120 years	7
Naturalness (natural tree-species composition)	
< 40% (no important habitat)	9
40–70% (unfavourable conservation status)	27
> 70% (favourable conservation status)	64

between bats and habitats, the species registration only was used (because the abundance varied strongly according to the proximity of potential roosts, flight corridors, etc.). Species recorded more frequently than in 5% of samplings were applied exclusively. Altogether, 861 species registrations were analysed (4.5% of them were obtained by the bat-detector). To emphasise the species' affinity to habitat, in the statistical matrix, different weights according to reproduction status were assigned to the species in the sampling (only males – weight 1, some females or young – 2). This theoretical scaling followed the presumption that individuals indicating reproduction at the site (females or young) should confirm higher species affinity to the habitat. In species recorded only by bat-detector at the site, the lower weight was automatically assigned. Considering non-parametric species data distribution, the presence of species was compared with the intensity of environmental variables using simple comparative analysis – Kendall τ rank correlation (Zar 1999) in the software STATISTICA for Windows 6.0 (StatSoft, Inc.).

Results

Forest bat assemblages

In study sites of the forested range of Slovakia, altogether 93% species of Slovak chiropterofauna were recorded using the methods presented. But only 16 species (2466 ind.) were recorded in more than 5% of samplings (Fig. 2). Other recorded species were *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros*, *Myotis blythii*, *Myotis alcathoe*, *Myotis dasycneme*, *Nyctalus lasiopterus*, *Pipistrellus pygmaeus*, *Pipistrellus nathusii* and *Miniopterus schreibersii*. The most common and frequent species there were *Myotis mystacinus* (frequency of occurrence = 57%, species dominance = 12%) and *Myotis myotis* (44%, 10%). Frequent species were also *B. barbastellus* (32%, 6%), *P. auritus* (32%, 6%), *N. noctula* (31%, 9%) and *M. brandtii* (31%, 7%), as well as *M. bechsteini*, *Pipistrellus pipistrellus*, *M. daubentonii*,

M. nattereri, *N. leisleri* and *E. serotinus* (Fig. 2). In spite of no proportional distribution of sampling elevations, which affected possible objective altitudinal analysis, some species occurred more often in higher or lower altitudes. Altitudinal generalists appeared to be mainly *M. mystacinus* and *Myotis brandtii*. Similarly, in almost all altitudes (also over 1100 m a.s.l.) *M. bechsteini*, *M. nattereri*, *B. barbastellus*, *P. auritus* and *M. myotis* occurred. Species *N. leisleri* and *N. noctula* were only exceptionally found in the highest elevations (just one case at 1220 and 1130 m a.s.l., respectively). The group of sub-mountainous species at altitudes not higher than 560 m a.s.l. included *Plecotus austriacus* and *Myotis emarginatus*, or *E. serotinus* and *P. pipistrellus* (not higher than 800 m a.s.l.), eventually also *M. daubentonii*. By contrast, the “true” mountain species were assumed to be *Eptesicus nilssonii* and *Vespertilio murinus* only. Their mean occurrences at the vertical gradient took the highest value and were not found lower than 300 m a.s.l. (Fig. 3).

Habitat use by species

Multivariate analysis of data from various types of natural forests showed the presence of species in relation to several factors of forest environment. In total, 13 of the 17 tested environmental variables used in CCA (Table 1), had significant influence (Monte-Carlo permutation test, $p < 0.05$) on the species' presence. Only the position of sampling sites at the ecotone forest/clear-cutting, share of hornbeam and other broad-leaved trees, and the age and tree-species heterogeneity of forests did not have an important influence on the presence of bat species. Thereafter, the rest of factors explained up to 88% of data variability. On the base of gradients in ordination analysis, it was possible to divide the species into two main groups (Fig. 4). The first was the group of forest bats, dominated by tree-dwelling

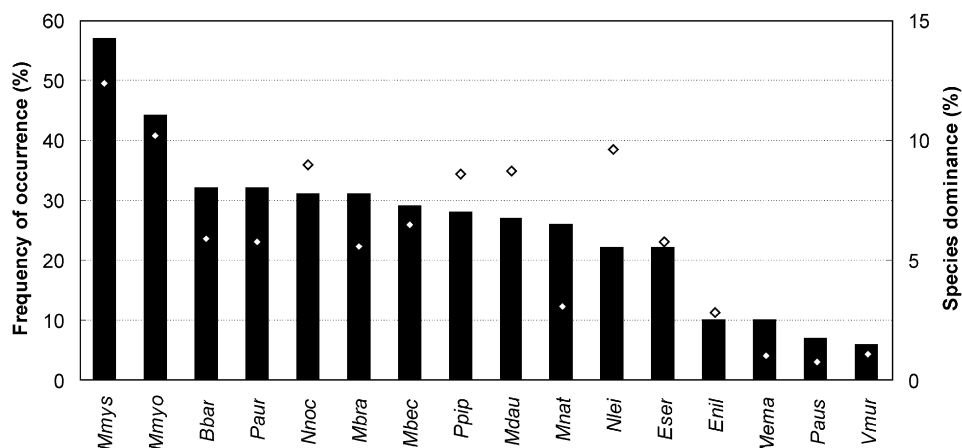


Fig. 2. Frequency of occurrence (black columns) and species dominance (white diamonds) of recorded bats with a frequency of occurrence more than 5% (total $n = 2540$ ind.). Species abbreviations see in Table 2.

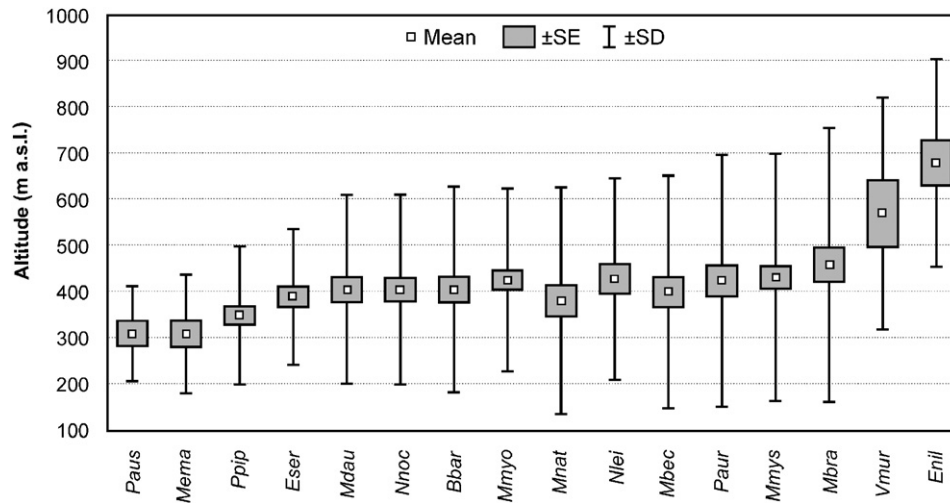


Fig. 3. Altitudinal distribution of recorded bats. Explanations: \pm SE – standard error, \pm SD – standard deviation. Species abbreviations see in Table 2.

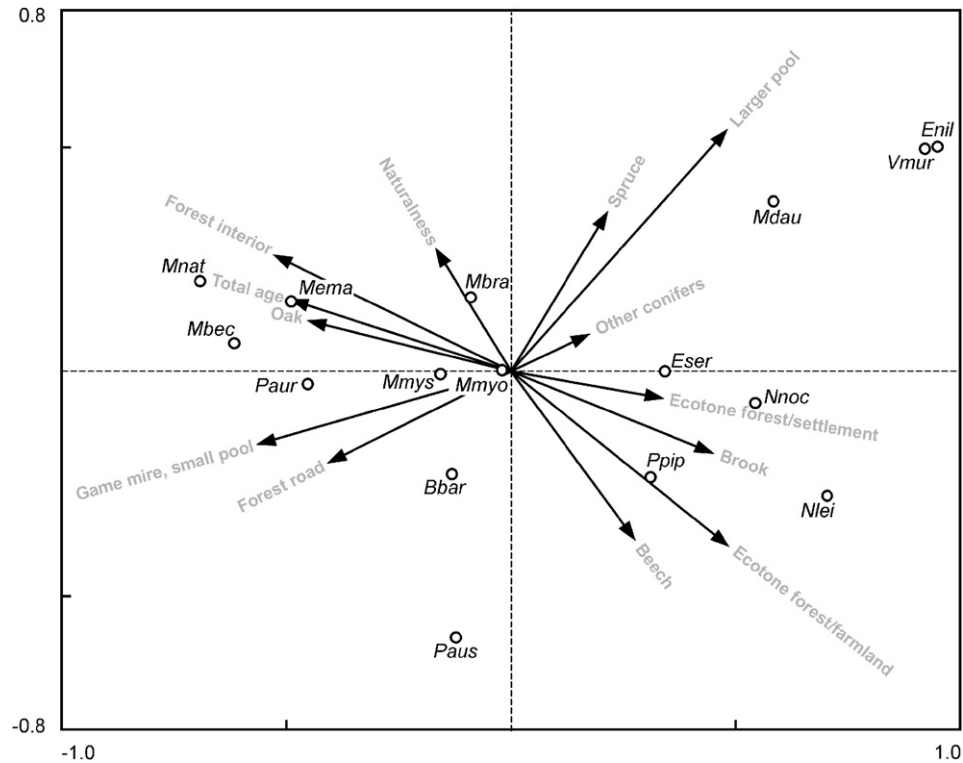


Fig. 4. Relating presence of bats to environmental factors (canonical correspondence analysis). Species abbreviations see in Table 2.

species *M. bechsteinii*, *M. nattereri* and *P. auritus*. These are gleaning species with slow skilful flight within vegetation and strongly frequency modulated echolocation calls used for foraging or drinking from small water pools inside the stands (often only puddles on the roads or game-mires). The occurrence of these species was connected mainly with old forests of natural tree-species composition. Such conditions bats probably found in particular in forests with a predominance of oaks (Table 2). In this type of forest another gleaning species,

M. emarginatus also occurred. In nearly every stand without any difference in quality, *M. mystacinus* was present. The species typically flew along corridors of forest roads. In the contrast to *M. mystacinus*, the presence of its congeneric species *M. brandtii* did not significantly correlate with just natural tree-species composition (Table 2).

The second main group comprised species which foraged in more open space or along the forest edge and avoided closed interior (particularly *E. serotinus*,

Table 2. Comparison of species occurrence with the intensity of environmental factors (significant in CCA analysis) by Kendall τ rank correlation

Environmental variables	Mmyo	Mbec	Mnat	Mema	Mmys	Mbra	Mdau	Vmur	Eser	Enil	Ppip	Nnoc	Nlei	Paur	Paus	Bbar
Game mire, small pool	0.111	0.241	0.289	0.122	-0.118	0.030	-0.302	-0.152	-0.058	-0.204	-0.005	-0.142	-0.166	0.262	0.005	0.066
Larger pool	0.143	-0.143	-0.109	0.001	-0.006	0.134	0.371	0.133	0.238	0.237	0.145	0.265	0.150	-0.063	-0.133	-0.100
Brook	-0.117	-0.180	-0.214	-0.073	0.002	-0.076	0.164	0.151	-0.029	0.150	0.065	0.082	0.159	-0.207	0.076	0.034
Forest road	-0.129	0.077	0.029	-0.051	0.131	-0.079	-0.214	-0.131	-0.137	-0.175	-0.207	-0.194	-0.142	0.007	0.039	-0.012
Forest interior	-0.013	0.162	0.060	0.030	0.167	0.111	-0.149	-0.096	-0.124	-0.213	-0.138	-0.286	-0.317	0.046	-0.098	-0.025
Ecotone forest/farmland	0.059	-0.177	-0.184	-0.020	-0.121	-0.130	0.148	0.034	0.121	0.116	0.092	0.261	0.245	-0.101	0.136	0.120
Ecotone forest/settlement	-0.041	-0.106	-0.035	-0.076	-0.053	-0.028	0.121	0.124	0.127	0.131	0.065	0.172	0.252	0.016	-0.063	-0.101
Beech	0.084	-0.039	-0.156	-0.053	-0.099	0.049	0.020	0.001	0.137	0.044	0.193	0.076	0.140	-0.098	-0.081	0.040
Oak	-0.010	0.177	0.196	0.114	0.051	-0.025	-0.104	-0.127	-0.006	-0.315	-0.023	-0.081	-0.126	0.199	0.081	0.073
Spruce	-0.114	-0.245	-0.224	-0.156	-0.159	-0.094	0.057	0.150	-0.101	0.339	-0.198	0.010	0.027	-0.280	-0.158	-0.117
Other conifers	-0.133	-0.094	-0.024	-0.088	-0.091	-0.111	-0.096	0.001	-0.057	0.168	-0.063	0.037	0.017	-0.151	-0.049	-0.111
Total age	-0.136	0.108	0.109	0.019	-0.045	-0.069	-0.131	-0.109	-0.103	-0.094	-0.194	-0.224	-0.203	0.001	-0.128	-0.061
Naturalness	0.070	0.138	0.034	-0.014	-0.052	0.079	-0.095	0.026	0.111	-0.049	-0.006	-0.036	0.011	0.112	-0.038	0.034

Bold marked positive correlations are significant at $p < 0.05$.

Species abbreviations: Mmyo, *M. myotis*; Mbec, *M. bechsteinii*; Mnat, *M. nattereri*; Mema, *M. emarginatus*; Mmys, *M. mystacinus*; Mbra, *M. brandtii*; Mdau, *M. daubentonii*; Vmur, *V. murinus*; Eser, *E. serotinus*; Enil, *E. nilssonii*; Ppip, *P. pipistrellus*; Nnoc, *N. noctula*; Nlei, *N. leisleri*; Paur, *P. auritus*; Paus, *P. austriacus*; Bbar, *B. barbastellus*.

N. noctula, *N. leisleri*, *P. pipistrellus*). The group included tree-dwelling species, which potentially had roosts inside the forests but after the evening emergence they forage outside the forest interior (e.g. *Nyctalus* sp.) or almost exclusively over water surface (*M. daubentonii*). Fast or slow hawking species in open space reached the food or water at larger accessible water pools in the forests or in the vicinity of open farmland, where they also forage (e.g. *E. serotinus*, *N. noctula*, *N. leisleri*, *P. pipistrellus*). Eventually, they appeared in forest connected to some settlement where potential artificial roosts could be found (*E. serotinus*, *E. nilssonii*, *V. murinus*, *P. pipistrellus*). Inside closed stands, species used sufficiently broad brooks as flying corridors or drank at them where accessible (broadened fords with open canopy) (e.g. *E. nilssonii*, *V. murinus*, *N. leisleri*). In this group, mountain species *E. nilssonii* and *V. murinus* were conspicuous outliers. Their presence was associated with dominance of spruce or the existence of other coniferous trees (Fig. 4).

Discussion

High species richness found in the natural forests of Slovakia confirms the exceptionality of this environment. The comparison of bat species composition with other temperate forests in Europe is not easy since there are insufficient similar large-scale studies. Furthermore, the situation is complicated by the use of different methods or not having natural forest character (e.g. Walsh and Mayle 1991; Walsh et al. 1995; Walsh and Harris 1996a,b; Jaberg and Guisan 2001; Rachwald et al. 2001; Ciechanowski 2002; Kusch et al. 2004). However, we can conclude that diversified conditions reflect more various species composition. The high frequency of *M. mystacinus* and *M. myotis* and altitudinal distribution of other species correspond with the results found along a selected mountain gradient (350–1350 m a.s.l.) in Slovakia (Kaňuch and Kristín 2006). Similarly, in other natural forest conditions in Europe, the most abundant species of lower altitudes was *M. myotis* and in contrast, *M. mystacinus* dominated with *M. brandtii* at higher altitudes (over 850 m a.s.l. in Bavarian Alps; Holzhaider and Zahn 2001). In our results, dominance was not figured to be the important indicator. It shows more the sensitivity of individual species to applied methods of data collection. Thus, for instance *M. daubentonii* (foraging over water surface) and species of the genus *Nyctalus* (lower manoeuvrability) were mist-netted quite abundantly. Rare findings of species *M. alcaethoe* and *N. lasiopterus* in the area of Slovakia, which were included in this study, are commented on elsewhere (Benda et al. 2003; Matis et al. 2003; Uhrin et al. 2006).

We found clear differences in species composition related to the forest character in natural conditions.

Species-specific use of habitats can be interpreted only with regard to the complex of features (cf. Jaberg and Guisan 2001; Kusch et al. 2004; Ford et al. 2005; Gorresen et al. 2005; Milne et al. 2005). Dependency on tree-species composition or on overall forest character also referred to other studies using different methods – radio-telemetry or bat-detecting only (e.g. Rachwald 1992; Erickson and West 1996; Crampton and Barclay 1998; Jung et al. 1999; Kalcounis et al. 1999). It should be mentioned that the sampling site also influences the success of mist-netting (cf. Ciechanowski 2002). From a methodological point of view the same portion of individual environmental variables in sampling would be required; but this was not possible in the presented scale. Not all selected environmental variables were factors influencing the presence of bats. Subjective selection of them was under the pressure of possibilities to obtain data documents in the large-scale analysis. Narrow clear-cuttings (i.e. up to 50 m, which mostly originated from timber harvesting) probably does not have as great an influence on the occurrence of bats foraging in the forest interior as the completely open surrounding, e.g. farmland (Jung et al. 1999). But excessive reduction of the canopy closure can reduce the forest suitability for these species, as can be found in artificial timber plantations. Missing influence of forest heterogeneity on habitat use by bats could be a consequence of the very large scale of the applied method.

In a natural forest environment we can designate some “true” forest species (species that predominantly forage and roost in forests). Specific habitat requirements were found only in gleaner species (*M. bechsteinii*, *M. nattereri* and *P. auritus*) with relatively small home range (Entwistle et al. 1996; Siemers and Schnitzler 2000) for old, natural even oak forests. Their concentration there can be explained by roost-site supply. Comparison of woodpecker populations in forest conditions in Slovakia indicated a noticeable decrease in species richness as well as the population density towards the spruce forests (Krištín 2002). In contrast, no special habitat requirements but very frequent occurrence in all spectra of studied forest habitats classify *M. mystacinus* (possibly *M. brandtii*) as “true” forest species there. Dominance in occurrence of *E. nilssonii* in spruce forests corroborates that also in conditions of central Europe it is a species adapted mainly for hemiboreal coniferous forest (De Jong 1994). In fact, a theoretical relationship of beech forests with slow or fast hawking species in open space *E. serotinus*, *P. pipistrellus* and *N. leisleri* (Fig. 4, Table 2) confirms their large space dispersion during foraging, where the beech is the most common tree in Slovakia. Moreover, typical Carpathian beech forests are more open stands in comparison to the other forest types investigated, and thus they can also be more accessible for open space species. Interestingly, Rachwald (1992) found in *N. noctula* generally very low activity directly over forest stands. Species of that group

can forage over a relatively larger distance in contrast to species of the first group. We assume that their presence will be probably not connected with the certain tree-species composition or forest age. With some species it was not possible to identify the characteristics of habitats used, probably as a consequence of their very narrow dietary niche (*M. myotis* – big carabids, *B. barbastellus* – moths) which can have a greater influence on selection of foraging habitat (Arlettaz 1996; Sierro 1999; Zahn et al. 2005). It is known that in the majority of other, more opportunistic hunters, a positive correlation with total food supply or biomass was not found. On the contrary, habitat use by bats depended more on the spatial structure of vegetation (Kusch et al. 2004; Milne et al. 2005). The method used did not focus on some additional aspects such as differences in habitat use following seasonal or migratory behaviour of species. These should be considered but we assume that their potential influence was suppressed thanks to extensive material.

Classic species census of forest bats is complicated by the difficulty of field observations. The presented large-scale analysis could suggest possible predictive modelling of species composition in forest bat assemblages in conditions of natural forests of central Europe. This can serve as an effective tool in nature conservation (Jaberg and Guisan 2001).

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Zusammenfassung

Beziehungen zwischen Fledermäusen und Habitatparametern in naturnahen Wäldern der Slowakei (Mitteleuropa)

Untersuchungen zur Habitatnutzung von Fledermäusen unter Berücksichtigung der Habitatfaktoren wurden mithilfe der multidimensionalen kanonischen Korrespondenzanalyse (CCA) durchgeführt. Die Datenerhebungen

erfolgten jeweils zwischen April–September in den Jahren 1999–2005. Dazu wurden an 160 Orten in der Slowakei Fangnetze gestellt und Detektoraufzeichnungen durchgeführt (insgesamt 209 Datensätze). Für die Habitatbeschreibung fanden 17 Habitatparameter Verwendung, die den Fangort, das Baumartenspektrum und allgemeine Parameter der angrenzenden Wälder charakterisierten. Insgesamt wurden in den Untersuchungsflächen 93% der in der Slowakei vorkommenden Fledermausarten registriert. Am individuenreichsten und häufigsten fanden die Verfasser *Myotis mystacinus* (Frequenz = 57%, Dominanz = 12%) und *M. myotis* (44%, 10%), gefolgt von *B. barbastellus* (32%, 6%), *P. auritus* (32%, 6%), *N. noctula* (31%, 9%) und *M. brandtii* (31%, 7%). Insgesamt 13 der 17 Habitatparameter (nach CCA) waren signifikant bezüglich der Artenpräsenz. Aufgrund des Gradienten in der Ordinationsanalyse wurden zwei Hauptgruppen gefunden. In der ersten “echten” Waldfledermausgruppe dominierten die Baumbewohner und Arten, die ihre Nahrung von Bäumen absammelten (*Myotis bechsteinii*, *M. nattereri* und *Plecotus auritus*). Das Vorkommen dieser Arten steht im direkten Zusammenhang mit dem Vorhandensein alter Wälder und einem natürlichen Baumartenspektrum. Die zweite Gruppe charakterisiert jene Arten, die ihre Nahrung mehr in offener Landschaft oder am Waldrand jagen, vorwiegend *Eptesicus serotinus*, *Nyctalus noctula*, *N. leisleri* und *Pipistrellus pipistrellus*. Das Vorkommen von Gebirgsarten wie *Eptesicus nilssonii* und *Vespertilio murinus* korrelierte mit der Dominanz der Fichte. Das vorgeschlagene prognostische Modellieren des Artenspektrums von Waldfledermausgesellschaften in naturnahen Wäldern stellt eine hilfreiche Unterstützung für artenschutzrelevante Belange dar.

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