

Bats in a Carpathian beech-oak forest (Central Europe): habitat use, foraging assemblages and activity patterns

Martin CELUCH^{1,2} and Rudolf KROPIL²

¹ Slovak Bat Conservation Society, P.O. Box 10A, 949 01 Nitra 1, Slovak Republic; e-mail: mato@netopiere.sk

² Technical University in Zvolen, Faculty of Forestry, T. G. Masaryka 24, 960 53 Zvolen, Slovak Republic; e-mail: kropil@vsld.tuzvo.sk

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A b s t r a c t. Carpathian forests represent unique and well-preserved ecosystems in relatively intensively managed forests of Europe. Habitat use, foraging assemblages and activity patterns of a bat community were investigated in semi-natural beech-oak forest by monitoring echolocation calls and mist-netting at three localities during the summers of 2003 and 2004. Six different forest habitat types were studied: oak forest, beech forest, stream, road, forest edge and open area within the forest. Bats were detected in all habitats. Sixteen species were found. Habitats were used differently by the individual species. The highest species diversity was observed in the forest interior. The first peak of flight activity was after sunset which then declined and was relatively even through the night until the second peak before sunrise, which was recorded in the forest interior, open area and on the road. The highest flight activity was recorded at the forest edge, forest stream and in open area. Recorded activity was 3× lower in the oak forest interior compared to the forest edge, but if the extent of the forests is considered, forest interior is the most important foraging habitat. Consequently future forest management should consider the needs of this endangered group of animals.

Key words: Chiroptera, detector, beech, oak, feeding sites

Introduction

Foraging grounds, together with roosts are the two main factors that enable the survival of bats (Barclay & Brigham 1996, Meschede & Heller 2000, Lacki & Baker 2003). The majority of central European bat species are partially or entirely confined to forest ecosystems (Walsh & Harris 1996, Zahn & Krüger-Barvels 1996, Meschede & Heller 2000, Russo & Jones 2003). Although understanding of suitable foraging habitats is essential for the protection of these endangered animals, knowledge of the preferred foraging grounds in forests is inadequate (Zahn & Krüger-Barvels 1996, Jung et al. 1999, Patriquin & Barclay 2003). Recently, there has been intensive development of “forest bats” research, mainly in North America and Western Europe (Barclay & Brigham 1996, Meschede & Heller 2000). Radio-telemetry and ultra-sound detectors are used to a large extent, although the relevance of data obtained by ultra-sound detectors is currently being reviewed (Jensen & Miller 1999, Scherwin et al. 2000, Gannon et al. 2003, Miller et al. 2003). There are still plenty of unanswered and controversial questions about the choice and preference of the foraging habitats of bats (Walsh & Harris 1996, Fenton 2003, Miller et al. 2003). Most acoustic studies in the forests have revealed that higher flight activity occurred at the forest edges and in open habitats. These habitats are considered as preferred (Walsh & Mayle 1991, Crampton & Barclay 1996, Grindal 1996, Kusch et al.

2004, Wolf & Bartonička 2005). Controversially, studies on individual species based on radio-telemetry show that many species use forests intensively (Sierra 1999, Albrecht et al. 2002, Bontadina et al. 2002, Kerth et al. 2002, Zahn et al. 2005) and also population density of some species probably depends on the proportion of forest in the landscape (Gleich 2002, Reiter 2004). In North America the influence of forest management is also seen as controversial (cf. Miller et al. 2003). Clearings create good foraging opportunities (Crampton & Barclay 1996, Grindal & Brigham 1999, Kusch et al. 2004) but forest management causes changes in tree species' composition, creation of unattractive monocultures, loss of roosts (Crampton & Barclay 1998, Russo et al. 2004), higher risk of predation and fragmentation (Jung et al. 1999). In Germany, attempts are being made to discover how to harmonize forest management and bat conservation (Messedede & Heller 2000).

Carpathian forests represent unique and well-preserved ecosystems in relatively intensively managed forests of Europe. Here only a few studies on foraging habitats of bat species have been undertaken. The first work was done by Vachold in the middle of the 20th century (Vachold 1960). He divided individual species by their typical foraging habitats. The first systematic acoustic studies in this area were done by Čelúch & Kaňuch (2004a,b) but these were based on limited data. Another study of bat assemblage was done in Poľana Mts (Central Slovakia) but it was aimed more on altitudinal distribution of bats and was based principally on mist-netting data (Kaňuch & Krístín 2006). There are studies from similar conditions (altitude, latitude) in Europe, but only in forests more significantly altered by man (Zahn & Krüger-Barvels 1996, Kusch et al. 2004). Habitat management for bats is constrained by limited understanding of their ecology in forests; this study is one of the first studies of forest habitat use of bats in the Carpathian Mountains.

The aim was to analyze the habitat use of bats in different forest habitats, assessment of foraging assemblages and activity patterns of bats in the broadleaved Carpathian forest.

Methods

Study area

Beech-oak forests (*Fageto-Quercetum* and *Querceto-Fagetum*) are the most common and typical forests in Slovakia (Frič & Pilná 2005). The study area was located in the south-eastern part of Kremnické vrchy Mts, Central Slovakia (48° 34–40' N, 19° 00–07' E; 300–550 m a. s. l.) with an average annual temperature of 7–8 °C and 650–800 mm annual precipitation. Dominant tree species are oak (*Quercus petraea*), beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). Fragments of coniferous stands of spruce (*Picea abies*) and pine (*Pinus sylvestris*) also appear in this area. These are not natural stands in beech-oak forests. The forests are primarily managed for timber production but the tree species composition is semi-natural. Fourteen bat species were found in this area (Čelúch & Kaňuch 2004a,b).

Three localities were selected in the study area: locality 1 – valley above the Kováčová village, locality 2 – forests near Turová village and locality 3 – hills near city of Zvolen. Forest dominated in all localities (70.4%), followed by farmland (23.2%) and rural and water habitats (Table 1). Individual localities were 3–4 km apart.

Table 1. Habitat availability in the surrounding vicinity (diameter 1.5 km) of the three localities in the study area and material obtained by active and automatic detector recordings.

Habitat	Locality 1	Locality 2	Locality 3	Mean	ActiveDet Total min (nights)	AutoDet Nights (min)
	%					
Forested area	84.7	73.3	53.5	70.4		
Oak forest	35.7	21.5	29.6	28.9	600(28)	12(5760)
Beech forest	11.0	9.4	9.1	9.8	440(22)	–
Forest stream	3.6	4.5	1.8	3.3	270(27)	14(6720)
Forest road	8.7	15.1	7.3	10.4	260(25)	12(5760)
Forest edge	1.1	0.2	0.2	0.5	310(25)	13(6240)
Open area	1.9	1.8	2.1	1.9	270(25)	13(6240)
Other forests	22.7	20.8	3.4	15.6		
Rural area	1.9	3.1	11.4	5.5		
Farmland	12.0	23.2	34.3	23.2		
Water habitats	1.4	0.4	0.8	0.9		
Total	100	100	100	100	2150(152)	64(30720)

Six different habitat types in each locality were investigated: 1) oak forest (OF) – mature 90–100 years old forest dominated by oak (recording in forest interior – more than 50 m from the forest edge, road or water habitat), 2) beech forest (BF) – mature 70–90 years old forest dominated by beech (recording in forest interior), 3) stream (ST) – small streams within the forests (2–3 m width), 4) forest road (RO) – small roads within the forest under the tree canopy, 5) forest edge (ED) – between forest and meadows or clearing, 6) open area (OP) – meadows in the forest or glades of minimum size of one hectare. Overnight activity was recorded by automatic detectors in five habitats (beech forests were excluded due to deficiency of data for analyses). For assessment of foraging of bat assemblages, the species records from oak forests and the few records from beech forests were pooled and analysed together as forest interior. The proportion of habitat types in 1.5 km diameter in each locality was assessed from maps.

Habitat use by bats

Investigation of the foraging activity of bats was done in two ways – actively and automatically.

1) The active recording took part in three localities (Fig. 1). One sampling point was chosen in each locality for each one of the six monitored habitats ($n = 18$ points). All points were investigated eight to nine times from May until September 2004 and the order of recordings was rotated. Recording always began half an hour after sunset and lasted for approximately 3 hours. All survey nights had a temperature higher than 10 °C at sunset, with no rain or strong wind, since these conditions are optimal for bat activity. The bat activity was recorded with Pettersson D240x bat detector (Pettersson Elektronik AB, Sweden) and MiniDisc (Sony Co., Japan) for 10 minutes in each habitat. Since there is a greater dispersal of individual bats in the forest interior and stands covering the majority of the study area, the activity in oak and beech forest was recorded for 20 min to obtain a sufficient data sample. In order to record all occurring species of bats at the sampled points (with exception of *Rhinolophus* species with very weak signals), the frequency in heterodyne mode was

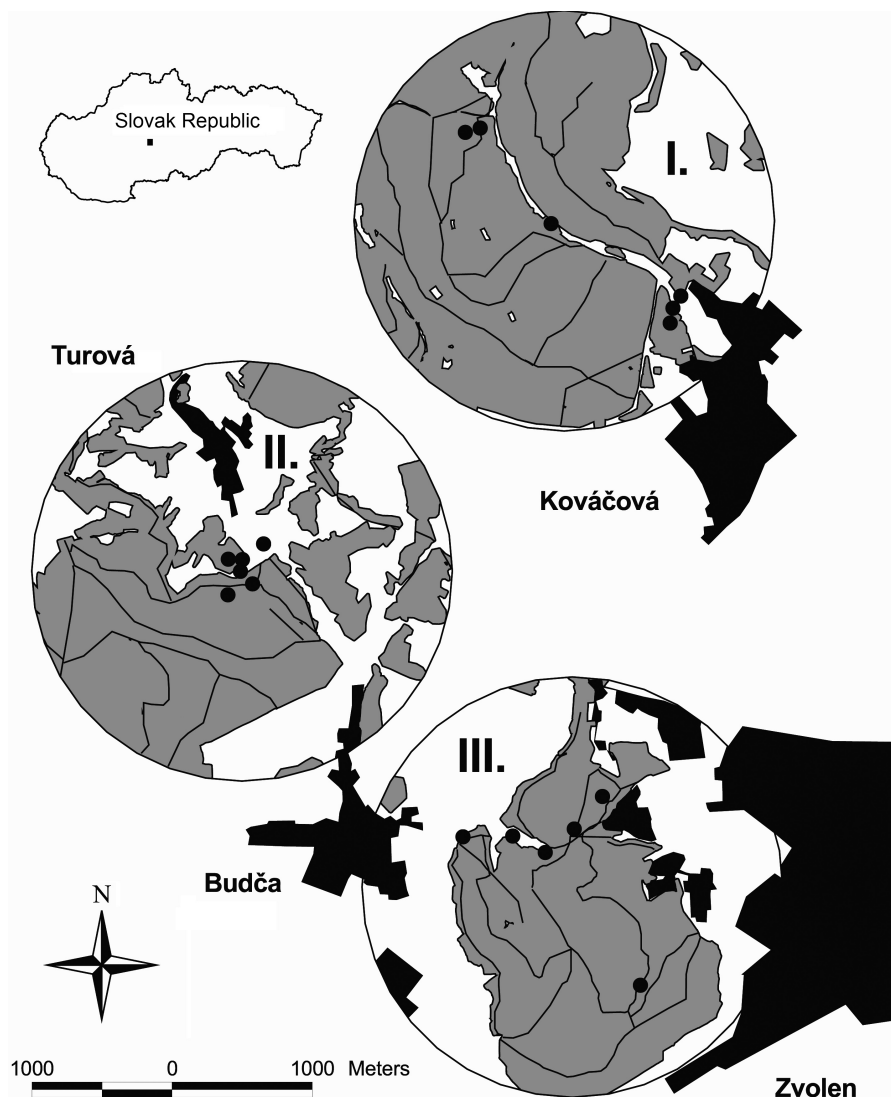


Fig. 1. Habitat composition in the three study areas and the position of the sampling points (black dots) showing the proportion of forest (grey), agricultural (white) and rural (black) habitats in each of the 1.5 km diameter areas: I. – Kováčová, II. – Turová, III. – Zvolen.

changed constantly between 20–60 kHz. Habitat use of bats was finally interpreted as a percentage of time intervals of one minute where bat ultrasonic calls were recorded from total time on the sampling point in the habitat and also in bat passes per minute (BP/min, for better comparison with other studies). Bat pass was defined as a call sequence of duration greater than 10 ms and consisting of ≥ 2 individual calls (Thomas 1988). Simultaneously the “feeding buzzes” which are typical for foraging bats were recorded. The rate of final buzzes indicates foraging activity (Vaughan et al. 1996).

The recordings were analysed by SonoBat 1.42 software (SonoBat, California), and where possible, the bats were identified by the characteristics of echolocation calls (Limpens &

Roschen 1995, Ahlén & Baagøe 1999). Along with characteristics of echolocation calls, morphological features (size, colour, flight) helped with the identification in the field. Species records were used for the assessment of foraging assemblages in individual habitats. Species identification according to characteristics of echolocation call was not always possible in forest conditions; therefore, the echolocation calls were divided into two species groups – *Myotis* group and non-*Myotis* group. Species of genus *Myotis* and also other species with strong frequency-modulated signals were included in the *Myotis* group. The other species occurring in the study area (*Nyctalus* sp., *Eptesicus* sp. and *Pipistrellus* sp.) have typical quasi-constant frequency parts of their signals. *R. hipposideros* emits very quiet signals and was recorded by mist-netting only. Because the distribution of the data departed from normality (records with zero activity were most numerous), distribution-free, nonparametric tests were used (Kruskal-Wallis H-test and Mann-Whitney U-test). Insect and bat activity were recorded simultaneously. In a period of one minute the number of flying insects was counted in the beam (up to 10 m) of a strong pocket torch. A light circle was drawn with the torch around the observer in a horizontal plane and in a semicircle vertically at each observation point. Activity was assigned into one of five classes according to the number of insects counted: 0 = 0 observed insects, 1 = one to five, 2 = six to ten, 3 = eleven to fifteen, 4 = more than fifteen insects.

2) For the automatic recording three heterodyne broad-band detector systems LAAR TDM 7 (BVL von LAAR, Germany) were used. The detectors recorded activity during 64 nights in total. In years 2003–2004 there were 12 to 14 recordings done in each habitat type from May till August. Detectors were placed on the ground and the microphone was attached to the tree trunk at the height of 1.5 m, pointing horizontally. For recording in more cluttered habitats more open places were chosen so that the records could be comparable with the other habitats. Recorded echolocation calls were analysed and divided into two species groups – *Myotis* group and non-*Myotis* group.

Foraging bat assemblages

All acoustic records identified to species were used for the assessment of foraging bat assemblages in the individual habitats. Species records from supplementary mist-nettings were added to these. Species records from oak forests were pooled with the few records from beech forests and analysed together as forest interior. The majority of the mist-netting was done in the forest interior where accurate identification based on echolocation is seldom possible. The supplementary mist-nettings were performed during 23 nights (forest interior – 11 nights, forest edge – 2, open area – 3, stream – 3, road – 4) during 2–3 hours after sunset using very fine-structured mist-nets (Natur-Plan, Germany).

Relative species dominance was assessed based on species records (each species was recorded in the habitat only once in one night, $n = 34\text{--}65$ nights per habitat) Shannon's diversity index (H') was used for species diversity assessment.

Overnight activity patterns

Recordings from automatic systems were used for assessment of overnight activity patterns. TDM 7 D has an integrated timer – every 15 minutes the timer emits a sound signal. Overnight records could be then divided into intervals. Since the length of night changes during the season, the bat activity was interpreted only in four one-hour intervals after sunset

and four hours before sunrise. The period around midnight represented only a few minutes (maximum half-hour) and was excluded from the interpretation.

Results

Sixteen species were found in the study area: lesser horseshoe bat *Rhinolophus hipposideros* (Bechstein, 1800), greater mouse-eared bat *Myotis myotis* (Borkhausen, 1797), Bechstein's bat *Myotis bechsteinii* (Kuhl, 1817), Natterer's bat *Myotis nattereri* (Kuhl, 1817), Geoffroy's bat *Myotis emarginatus* (Geoffroy, 1806), whiskered bat *Myotis mystacinus* (Kuhl, 1817), Daubenton's bat *Myotis daubentonii* (Kuhl, 1817), serotine *Eptesicus serotinus* (Schreber, 1774), northern bat *Eptesicus nilssonii* (Keyserling et Blasius, 1839), common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), soprano pipistrelle *Pipistrellus pygmaeus* (Leach, 1825), Nathusius' pipistrelle *Pipistrellus nathusii* (Keyserling et Blasius, 1839), noctule *Nyctalus noctula* (Schreber, 1774), Leisler's bat *Nyctalus leisleri* (Kuhl, 1817), common long-eared bat *Plecotus auritus* (Linnaeus, 1758) and barbastelle *Barbastella barbastellus* (Schreber, 1774). With the exception of *P. pygmaeus*, *P. pipistrellus* and *P. nathusii*, all species were also confirmed by mist-netting.

Habitat use by bats

The bats were detected by active recording in all habitats (Fig. 2). There were 658 bat passes recorded in all habitats during 2150 minutes of monitoring. The average activity was 0.4 BP/min and active minutes comprised 22% of total time. One half of the recorded passes were species from the non-*Myotis* group, which is typical for more open habitats. As much as 87.7% of these passes were recorded in open areas and at the forest edges, where they dominated significantly (Table 2). A small proportion of non-*Myotis* group bat passes was also found in other habitats. In contrast, signals characteristic of the *Myotis* group were predominantly in oak and beech forest, streams and roads – the more enclosed and cluttered habitats. The activity in many habitats varied significantly within the individual nights (from 0 to 100% active minutes).

The flight activity showed significant differences (Kruskal–Wallis H-test, $H = 25.788$, d.f. = 5, $p = 0.0001$, $n = 163$) among individual habitat types. The highest flight activity

Table 2. Overview of recorded data in particular forest habitats. *M-g* – bat passes of species belonging to *Myotis* group, *nM-g* – non-*Myotis* group.

Habitat	Active recording							Automatic recording					
	Bat passes			Bat passes/min			Relative activity (%)	Bat passes			BP/night		
	M-g	nM-g	FB	Mean	±	SE		M-g	nM-g	FB	Mean	±	SE
Oak forest	80	18	5	0.16	±	0.03	12.8 ± 2.1	27	2	0	2.4	±	1.3
Beech forest	25	3	1	0.06	±	0.02	5.2 ± 1.5	–	–	–			
Forest stream	133	16	9	0.48	±	0.11	31.3 ± 5.9	80	1	1	6.2	±	2.4
Forest road	50	4	2	0.20	±	0.06	15.6 ± 3.6	167	2	3	13.0	±	4.8
Forest edge	31	194	10	0.83	±	0.25	37.0 ± 6.7	245	429	16	49.1	±	13.8
Open area	5	99	3	0.40	±	0.08	29.2 ± 5.4	100	330	25	35.8	±	14.5
Total	324	334	30					619	764	45			

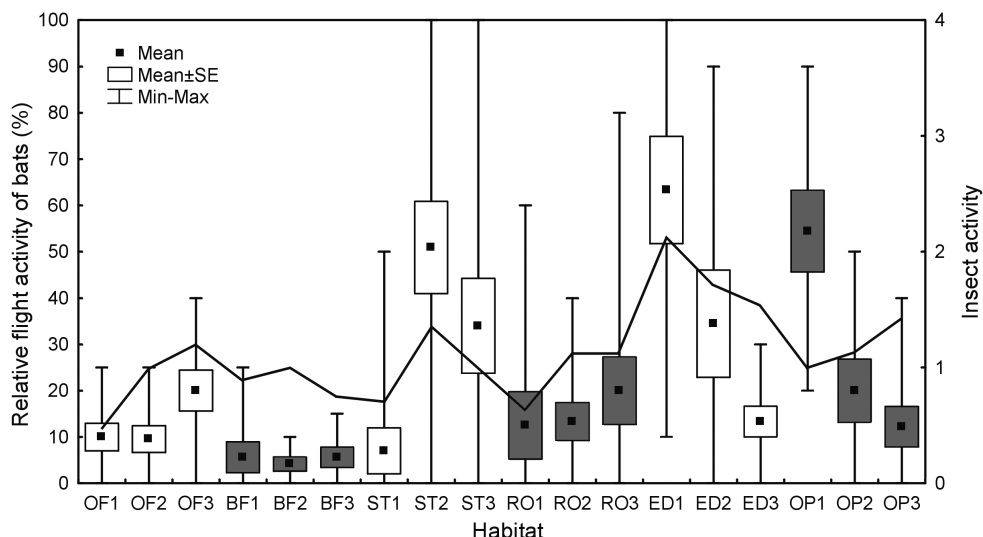


Fig. 2. Relative flight activity of bats in active minutes (presence in % of time) in six habitats (OF – oak forest, BF – beech forest, ST – stream, RO – road, ED – forest edge, OP – open area) on the localities 1–3. Data based on active recording. The right Y-axis represents the mean insect activity (line).

was at the forest edge (average 37.0% of active minutes from total minutes), forest stream (31.3%) and in open areas close to the forest (29.2%). Recorded activity was 3× lower in the oak forest (12.8%) and 7× lower inside the beech forest (5.2%) compared to the forest edge.

The highest bat activity at the forest edges was caused by swarms of cockchafer *Melolontha melolontha* (Linnaeus 1758) in locality 1 (ED1), where the average flight activity was very high (63.3%). The flight activity of insects was highest here of all the sampled habitats also (Fig. 2). This site significantly differed from the other sites along the forest edge ($H = 10.089$, d.f. = 2, $p < 0.05$). Approximately 10 min after sunset, large numbers of *Nyctalus* sp. and *E. serotinus* were intensively feeding on the swarming cockchafer. Often it was impossible to distinguish individual passes or number of individuals due to the continuous activity. Extremely high flight activity was recorded here on June 14, 2004 – 4.3 BP/min, July 27, 2004 – 4.7 BP/min. Flying cockchafer probably also caused an increase in the average activity in the neighbouring open area (54.4% active minutes), which significantly differed from the other open areas ($H = 11.902$, d.f. = 2, $p < 0.05$).

In total there were 30 bat passes with feeding buzzes recorded, which comprises only 4.6% of all passes. They were recorded in all habitats but mainly at forest edges; therefore it is assumed that all habitats were used as foraging grounds.

Automatic recording systems gave results comparable with active recordings of bat activity. Bats were recorded in all habitats and significant differences were found in habitat use. A total of 1383 bat passes were recorded; 55.2% non-*Myotis* group and 44.8% *Myotis* group. Almost all bat passes from the non-*Myotis* group were recorded at the forest edges and open areas (99.3%). The highest number of passes was recorded at the forest edge (49.1 BP per night on average). The last two nights of recordings (July 19 and 27, 2004) added significantly to this number, when there were 191 and 121 BP recorded. High activity was also recorded in the open area (35.8 BP per night), with one extreme night (July 27, 2004) when 177 BP were recorded. Lower activity was recorded on the road (13 BP per night), over

the stream (6.2 BP per night); the lowest was in the oak forest (2.4 BP per night). Signals of non-*Myotis* group were significantly predominant at the forest edge (63.6%) and in the open area (76.7%), although they were also recorded in small numbers in other habitats. The automatic systems recorded 45 passes with feeding buzzes (3.3% of all BP); most of them at the forest edges and in open areas.

The insect activity (Fig. 2) showed significant differences ($H = 15.509$, d.f. = 5, $p = 0.0084$, $n = 163$) in the individual habitat types. Significant correlation between insect activity and bat activity was found in 18 sampled habitats ($r = 0.60$, $p < 0.05$). The highest insect activity was recorded at the forest edges.

Foraging bat assemblages

Although the data were relatively limited, the habitats were used differently by the individual species. There were 230 species records obtained; 23% mist-netting and 77% bat detector.

There were 14 species ($n = 51$) recorded in the forest interior, where, in comparison with other habitats, dominance of individual species was best balanced (Fig. 3). The most frequently recorded were *M. mystacinus* (21.6%) and *M. myotis* (19.6%). *N. noctula* (34.2%), *E. serotinus* (22.4%), *B. barbastellus* (14.5%) and *N. leisleri* (10.5%) dominated substantially at the forest edge. *M. mystacinus* also used the forest edge relatively frequently (9.3%). There were only three obvious dominants typical for the open habitats found in the open areas – *N. noctula* (42.6%), *N. leisleri* (23.4%) and *E. serotinus* (19.1%). Forest streams (10 species) and roads (9 species) had very similar composition of species. *M. mystacinus*, *M. myotis*, *B. barbastellus* and *P. auritus* were recorded most frequently in these habitats. Forest interior had the highest species diversity ($H' = 2.35$). Relatively high species diversity was also found over the streams and roads ($H' = 1.99$ and 1.91). The lowest species diversity was characteristic for the forest borders and open areas ($H' = 1.82$ and 1.50 , respectively).

Overnight activity patterns

The flight activity was recorded in each of the monitored habitats and in each part of the night, even though the number of bat passes fluctuated significantly (Fig. 4). There were also frequent periods during some of the nights without any passes at all. Three nights with extremely high number of bat passes were excluded from the overall evaluation, since these would have suppressed the typical activity patterns in these habitats. Extreme levels of flight activity were recorded at the forest edge in locality 1 (July 19, 2004 – 191 passes, July 27, 2004 – 121 passes) and in the neighbouring open area (July 27, 2004 – 177 passes). These were the nights when insect swarming took place (at an edge or an open area).

Bimodal activity was observed in the oak forest, open areas and roads. The first peak was during the first hour after sunset and the second just before sunrise. The activity dropped in the middle of night. The highest activity was recorded during the first hour after sunset in almost all habitats, with exception of forest roads. Here, the highest activity was one hour before sunrise (21.0% from the overall activity). Slightly lower activity on the road was during the first two hours after sunset (19.1% and 19.1%). The most significant peak was recorded one hour after sunset at the forest edge (43.7%), in oak forest (42.9%) and in open areas (42.7%). On the road and over the stream activity was also recorded one hour after sunrise (2.9% or 3.4%, not displayed in Fig. 4).

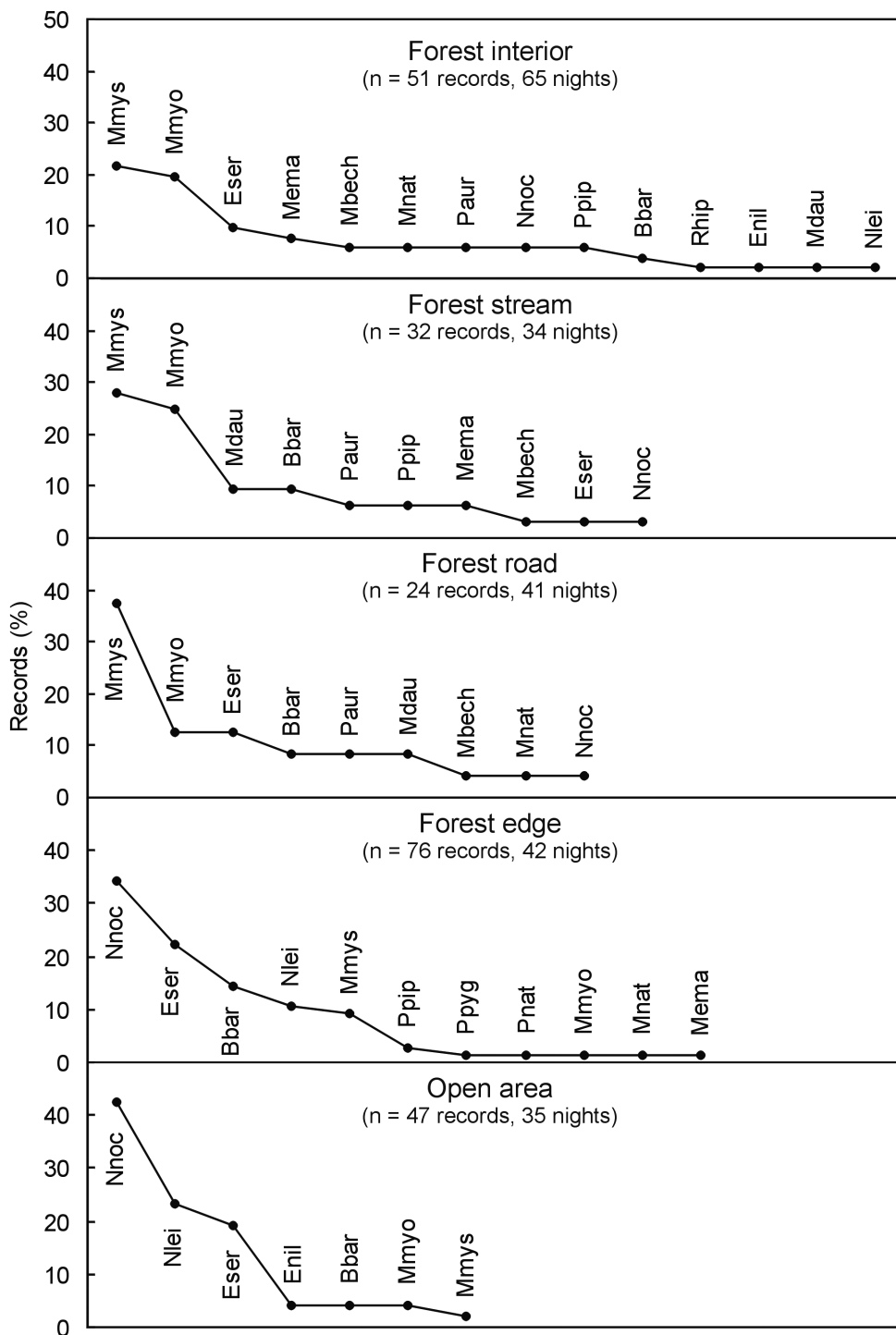


Fig. 3. Relative species dominance of bats in five habitat types. Structures of assemblages are based on all acoustic and mist-netting species records (abbreviations of species scientific names on X-axis, e.g. *M. myotis* = Mmyo).

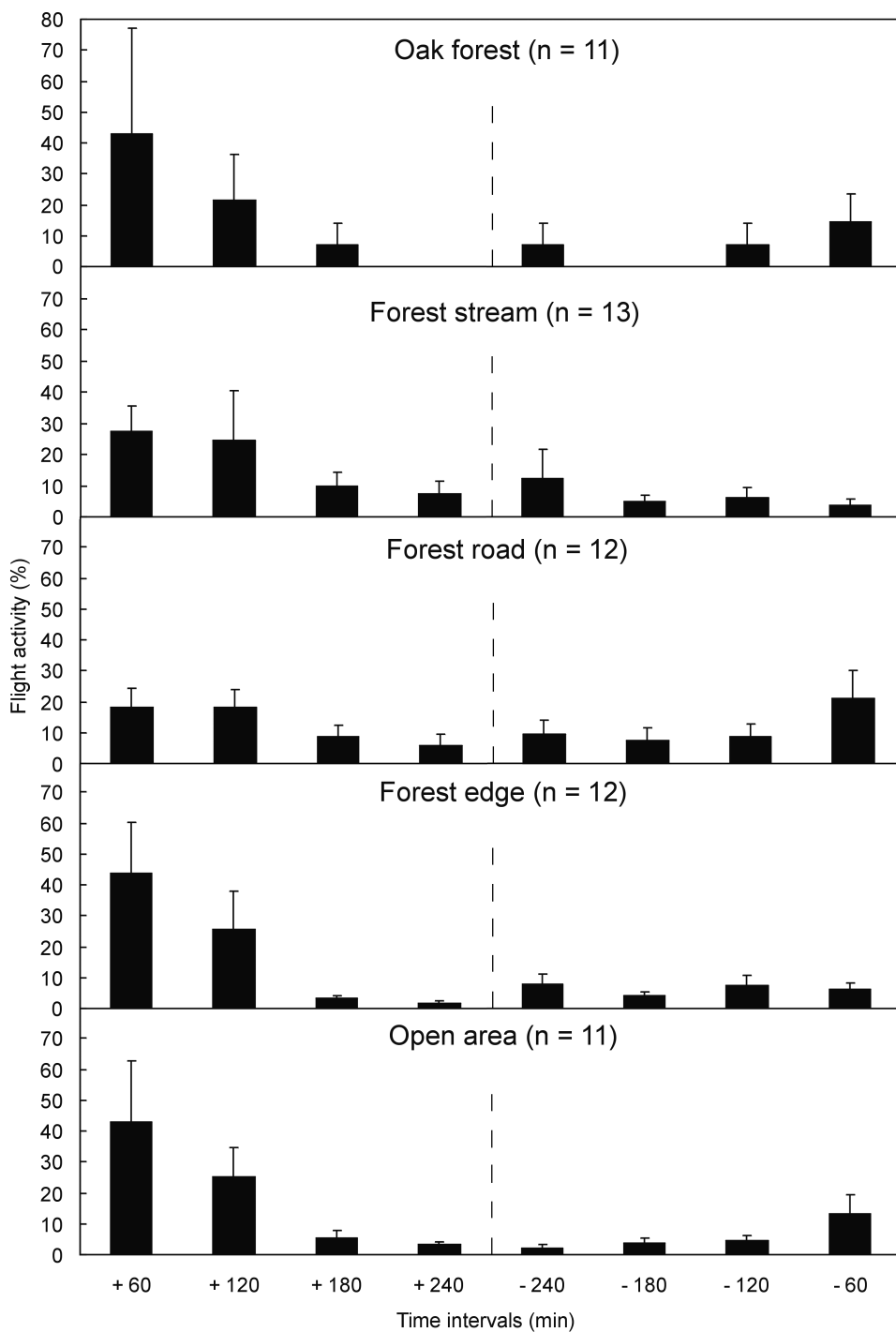


Fig. 4. Relative overnight flight activity patterns of bats (mean \pm SE flight activity in each 60 min time interval in % from all bat passes) in the habitats in first 4 hours after sunset (+60 min = first hour to +240 min = fourth hour) and last 4 hours before sunrise (–60 min to –240 min).

Discussion

Habitat use by bats

The foraging activity of bats in broadleaved forests around Zvolen was higher in 2004 in comparison with 2003 (Čeľuch & Kaňuch 2004a). This was obvious mainly at the forest edge. It was caused by swarming of the cockchafers in locality 1 in 2004. Due to this, the overall proportion of non-*Myotis* group bat passes was higher as well (50.8% in 2004 compared with 33% in 2003). However, the average activity was comparable in all habitats – highest at the forest edges, in open areas and over streams.

The highest activity in similar conditions of German forests (altitude, latitude, bat species composition) was found over streams (Zahn & Krüger-Barvels 1996). Mixed forests had the second highest activity and forest edges had the third highest activity.

Kusch et al. (2004) in Germany, as well as Vaughan et al. (1997) in Great Britain, assessed lakes in forests as preferred habitats and the *Pipistrellus* species had the highest activity. However, these were mainly pine plantations (Germany) or fragmented forests (Great Britain). Since water surfaces in our study area were scarce, they were not systematically surveyed. Higher activity of *P. pipistrellus* was recorded only during several observations on the fishpond near locality 1. This species is probably more common close to water surfaces or in the forests more significantly changed by the activity of man.

There is often higher activity recorded in more open habitats (forest edges and meadows), and therefore the usual conclusion is that these offer better foraging opportunities for bats than more cluttered habitats (Walsh & Mayle 1991, Walsh & Harris 1996). According to observations in our study area, the forest edges are habitats with lower bat species diversity ($H' = 1.82$) compared to forest interior ($H' = 2.35$) and they are dominated by open space species such as *Nyctalus* sp. and *Eptesicus* sp. These species have high intensity calls, and during investigation were recorded at distances of up to 50–150 m. The typical species for forest interior are those with relatively weak signals (Waters & Jones 1995, Schnitzler & Kalko 2001) and therefore they are underestimated in acoustic studies (Walsh & Mayle 1991, Zahn & Krüger-Barvels 1996, Broders et al. 2003). Besides, there is also high activity in the canopy, which is not recorded during ground surveys (Hayes & Gruber 2000). This was confirmed also in the Carpathian broadleaved forests (Čeľuch & Kaňuch 2004b). Similarly, Zahn & Krüger-Barvels (1996) found relatively small levels of activity in forests of southeast Germany, but they also pointed out the large extent of the forests. When they considered the extent of the area (calculated theoretically), the foraging activity was seven times higher than on the most intensively used pond. Forests in Slovakia are the most extensive habitat covering 41% so, if the extent of the forests is considered, then forests are the most important foraging habitats for bats.

Foraging bat assemblages

The number of species recorded in the study area is comparable with results from studies in similar conditions (Kaňuch & Krištín 2006); even in significantly altered forests of Germany (Zahn & Krüger-Barvels 1996, Kusch et al. 2004). The species composition was also similar. In most of the studies, *P. pipistrellus* was one of the most often recorded species (Vaughan et al. 1997, Roche & Eliot 2000, Kusch et al. 2004).

However, this species was recorded only seven times in our study area and the most frequent species were *N. noctula* together with *M. mystacinus* and *E. serotinus*.

We found that at least 14 species also use the forest interior. The remaining two species (*P. pygmaeus* and *P. nathusii*) were recorded only once at the forest edge, but it is expected that they use the forest interior as well (Jarzembowski et al. 1998, Bartonička & Řehák 2004). The most frequently recorded here were *M. mystacinus*, *M. myotis* and *E. serotinus*, which reflects their adaptation for flight in cluttered habitats (Norberg & Rayner 1987, Schnitzler & Kalko 2001, Fenton & Bogdanowicz 2002). This agrees with a study from Poľana Mts (Central Slovakia), based on mist-netting data, where these three species were also the most frequently caught (Kaňuch & Krištín 2006). However, Kusch et al. (2004) found the preference of *Myotis* species was for open areas, which was probably caused by the fact that they assessed foraging *M. daubentonii* on lakes together with other *Myotis* species. This species has significantly different foraging strategy – trawling from the water surface – and it prefers the open spaces (Kalko & Schnitzler 1989). The most frequently recorded species on the forest stream was *M. mystacinus* (28.1% of all records), but most of the records were only acoustic (84%). This species has a similar call design to other *Myotis* species (Russo & Jones 2002, Obrist et al. 2004), so misinterpretation could occur. Zahn & Krüger-Barvels (1996) also mentioned *Myotis* species mainly on streams.

Open areas and forest edges are relatively open habitats and this is reflected by the species composition. The most frequent species here were members of the genus *Nyctalus* and *Eptesicus*. On the contrary, Kusch et al. (2004) did not find any preference of *Nyctalus* sp. for open areas. But they pooled data from species with different foraging strategies (e.g. *Nyctalus* sp. vs. *Myotis myotis*). The differences in the habitat use and the overall number of recorded bats are influenced by the constraints of the methods used. However, it can be concluded from the differences in habitat use that bats do not use the forest habitats randomly but according to their adaptations (Norberg & Rayner 1987, Whitaker 2004).

Overnight activity patterns

Observed bimodal type of activity is typical for the majority of insectivorous bats (Erkert 1982) although activity is also influenced by many factors and varies during the season (Adam et al. 1994, Shiel & Fairley 1998, Hayes & Gruver 2000). *N. noctula*, *N. leisleri* and *E. serotinus*, species with common bimodal activity, dominate the forest edges and open areas (Stutz & Haffner 1986, Kronwitter 1988, Shiel & Fairley 1998, Rachwald 1992). Differing activity of *N. noctula* was observed at three periods during the night. Several tens of individuals were recorded after sunset and before sunrise but with only a few bat passes around midnight (Stutz & Haffner 1986); this species has relatively short foraging periods (Kronwitter 1988). Shiel & Fairley (1998) found the activity peak for *N. leisleri* in the first third of the night, when the airborne insects are most abundant, and was independent of temperature.

The activity in the habitats depends also on their function. Forest edges, roads or streams could be also used as flight corridors connecting roosts and foraging areas (Limpens & Kaptayn 1991, Verboom & Huitema 1997). The activity observed on the road and stream one hour after sunrise suggests the connecting function of these habitats. These are covered by the tree canopy and therefore enable safe return (lower risk of predation) to the roosts even after sunrise.

These results have implications for forest management. Flight activity was recorded in each of the monitored habitats and in each part of the night. The number of species recorded in the area comprises 57% of all bat species in Slovakia (28 species). The highest species diversity was observed in the forest interior. Consequently future forest management should consider the needs of this endangered group of animals. Forests in Slovakia are the most extensive habitat, and if the extent of the forests was considered, then forests are the most important foraging habitats for bats.

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