# Foraging and flight activity of bats in beech-oak forests (Western Carpathians)

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**Abstract**

Ceľuch M., Kaňuch P., 2004: Foraging and flight activity of bats in beech-oak forests (Western Carpathians). Folia oecol., 31 (1), p. 8–16.

Bat assemblage (14 species) was studied in beech-oak forests in south-eastern part of Kremnické vrchy Mts. (Central Slovakia) from May to September in 2002 and 2003. Mist-netting method, ultrasound bat-detectors and faecal pellets analyses were used for study of foraging and flight activity of bats. Bats were classified according to foraging strategies. Considering prey composition, 7 orders of insects and one order of arachnids were identified in examined bat droppings. The imagos of moths (Lepidoptera) were the most important component in diet of studied bat assemblage (V = 46%, F = 68%). All five basic foraging strategies were found in the studied bat assemblage. Almost the same portion took gleaning, slow hawking and fast hawking. Flight activity of bats during nights was recorded in 16% of observed 1505 minutes. Recorded bat passes were assigned to *Myotis* group (67%), and non-*Myotis* group (33%). All of seven studied habitat types were used by bats. The highest level of flight activity was recorded on small open areas and forest edges.

**Key words**

Chiroptera, assemblage, strategy, insects, hunting, diet

## Introduction

Almost all of the European bat species are dependent on the forest ecosystems, to some extent. Forest provides both basic sources for bats – food and roosts. The fidelity to the forest is different for the individual species (Kulzer 1989; Zahn, Krüger-Barvels 1996; Meschede, Heller 2000). European bat species are exclusively insectivorous (cf. Vaughan 1997), have a high energy consumption, an extremely fast metabolism and ability to look for habitats with a high concentration of prey (Fenton 1982; Beck 1995). Important portion of pest insects is nocturnal (e.g. moths from family Lymantridae, Tortricidae, Geometridae, Noctuidae, Cossidae, Coelophoridae etc.; Novák et al. 1974). Therefore, bats belong to an important insect predators, they participate on ecological

stability of forest ecosystems (Kulzer 1989; Meschede, Heller 2000).

Foraging activity of bats depends on foraging strategies of individual bat species. There are more approaches of foraging strategies classification based on the differences in echolocation calls and wing morphology, diet composition and visual observations (eg. Norberg, Rayner 1987; Beck 1995; Arlettaz 1996; Entwistle et al. 1996; Rydell et al. 1996; Siemers, Schnitzler 2000; Bontadina et al. 2002). Bats use five basic foraging strategies (Norberg, Rayner 1987): (1) Fast hawking – fast flight in pursuit of flying insects above treetops and use of loud, long-ranging echolocation calls of low frequency; (2) Slow hawking – slow flight and detecting prey at a short range; (3) Gleaning – taking roosting or non-flying prey from the ground or vegetation, use of broadband frequency modulated

calls of low intensity; (4) Trawling – picking up the prey from water surface with its tail membrane or hind legs; (5) Perch hunting or fly-catching – waiting and seeking for the prey on a branch and flight after prey detection.

The using of all the bat detectors has revolutionised the field study of flight activity and habitat selection of bats (cf. AHLÉN, BAAGOE 1999). Activity of bats in the forest environment depends on many factors (eg. BARCLAY, BRIGHAM 1996; MESCHEDE, HELLER 2000; MESCHEDE et al. 2000). Factors, which significantly influence the activity of bats are: tree species composition (RACHWALD 1992; JUNG et al. 1999; KALCOUNIS et al. 1999), age (ERICKSON, WEST 1995; CRAMPTON, BARCLAY 1996), forest structure (HUMES et al. 1999; JUNG et al. 1999), fragmentation (CRAMPTON, BARCLAY 1996). One of the most important factors is insect activity and food supply (RYDELL et al. 1996; ZAHN, KRÜGER-BARVELS 1996; VERBOOM, SPOELSTRA 1999). These factors are more complex and reflect a character of the foraging habitat. In general, activity and habitat selection of bats depends on insects availability and foraging strategies of individual bat species. There are no studies of habitat use and flight activity of individual bat species in the Western Carpathians (Central Europe) yet.

The purpose of this study was (1) to analyse a bat assemblage based on foraging strategies and food composition of individual bat species and (2) to assess the influence of habitat and insect activity on flight activity of bats in selected beech-oak forests.

**Material and methods**

Study area

The study area is located in south-eastern part of Kremnické vrchy Mts., Central Slovakia (48°34–40′ N, 19°00–07′ E; 300–550 m a. s. l.). It belongs to a warm climatic area with average temperature 4 °C in January (GÁBORÍK, MACKO 1981). With regard to the forest typology, the selected study area represents mainly the forest type Fageto-Quercetum and Querceto-Fagetum (sensu ZLATNÍK 1959; RANDUŠKA et al. 1986). This study was performed in beech-oak (2nd) and oak-beech (3rd) forest vegetation tire. Forests are primarily managed for timber production but the tree species composition is semi-natural. It means, that the dominant tree species correspond to the habitat conditions (sensu ZLATNÍK 1959). Fragments of coniferous forests (*Picea abies*, *Pinus silvestris* dominant) also appear in this area as unnatural stands with changed tree species composition in habitats of beech-oak forests.

To study flight activity of bats, five transects were selected. Each of them consist of the seven habitat types: (1) broad-leaved forest – mature harvested beech-oak forests stands, (2) coniferous forest – pine and spruce enclaves, (3) forest edge – between forest and meadows or clear cutting, (4) open area – meadows of minimum size of one hectare, (5) forest road – small roads inside the forest under tree crowns, (6) stream – small non-regulated streams inside the forests, (7) game mire – small water spots, mainly small pools on roads smaller than 20 m$^2$.

Field investigations and data analyses

The direct observation of foraging bats is problematic in the forest ecosystem conditions. The complicated techniques using infrared cameras or radio-telemetry make it possible to some extent (KUNZ 1988). For this purpose, the flight and foraging activity was observed with help of bat-detectors and faecal pellets analyses.

The investigation was carried out from May to September 2002–2003. To know the species composition in the study area, was used mist-netting method (KUNZ and KURTA 1988). A special, very soft-structured mist-nets were installed (Natur-Plan, Germany) on sites with high flight activity, mainly game mires, small pools and roads. These sites are very often used like water and prey source. Forest roads are also important flight corridors for bats (WALSH, HARRIS 1996; ZAHN, KRÜGER-BARVELS 1996). Netting started after the sunset and lasted until midnight. Caught individuals were immediately taken from the net. Bats were released after a species identification and collecting a sample of droppings. The main portion of the data was obtained by mist-netting (25 nights, 77 individuals). Other important data were obtained using bat-detectors (13 nights, 52 registrations) or roost control (nine roosts found). The heterodyning detector Pettersson D200 (Pettersson Elektronik AB, Uppsala, Sweden) was used and identification was made, if possible, based on call characteristics and visual observation (LIMPENS, ROSCHEN 1995). Assemblage composition was assessed, based on relative abundance (n%) of caught individuals and detector registrations.

The food composition was examined using faecal pellets analyses. Arthropod fragments in bat droppings were analysed and identified using a method similar to MCANEY et al. (1991) and WHITAKER (1988). Bats were released in 15 minutes after they were held in a textile bag. Then the droppings were collected. The fragments of the prey in the bat droppings were identified to taxon using binocular magnifying glass (25 ×). Moths were divided into two groups – imago and larva. The qualitative and quantitative structure of food composition was estimated through the volume of prey category in one dropping (V%) and frequency of occurrence in faecal pellets (F%) (cf. RYDELL, PETERSONS 1998). In total, 117 pieces of droppings were collected from 38 individuals of 10 bat species.

Classification of bats into the foraging strategies was performed based on studies dealing with morphological adaptations for foraging (NORBERG, RAYNER 1987; HORÁČEK et al. 2000), analyses of diet composition (BECK 1995; VAUGHAN 1997) and partly with the support of the material collected in the study area. Some bat species use more strategies, therefore two species (*Myotis mystacinus* and *Plecotus austriacus*) were assigned into two strategies concurrently.

To determine relative levels of bat flight and foraging activity among habitat types, the heterodyne bat-detector Pettersson D200 was used. Each night (13 nights from 1th July to 1st September 2003) one selected transect was monitored for 150 minutes after sunset. When detecting in open area or in the forest interior, the distance of 50 m from the forest edge was important. In each habitat, the active minutes (at least one bat pass / minute) and number of bat passes was registered. Activity in each habitat was calculated as the number of bat passes per minute. In total, 1505 minutes of monitoring were obtained. Species identification in forest conditions based on echolocation calls is difficult – in most cases, the bat pass was registered only with few calls, without any chance to see the bat. Therefore, registered bats were divided only into groups based on call characteristics – *Myotis* group a non-*Myotis* group. A typical feature for the first group is strong frequency-modulated call. Non-*Myotis* group contains a part of the call with relatively constant frequency. The typical species of this group are *Nyctalus noctula*, *Nyctalus leisleri*, *Eptesicus serotinus* and *Pipistrellus pipistrellus*. Other species were assigned to *Myotis* group. Feeding buzzes (call signal characteristic for the closing part of attack on its prey) were also registered.

Flight activity of insect was studied in each visited habitat, based on counting of flying individuals in the beam of a strong torchlight. In 15 seconds, the torchlight was turned around in a horizontal circle and the insects flying closer than 10 meters were counted (cf. ZAHN, KRÜGER-BARVELS 1996). Activity was assigned to classes: 1 = 0–4 insects, 2 = 5–9, 3 = 10–14, 4 = 15–19, 5 = 20 and more.

The statistic software Statistica for Windows 5.1 (StatSoft, Inc.) was used for data analysis. When comparing bat and insect activity in different habitat types, Kruskal-Wallis oneway ANOVA combined with Kruskal-Wallis Multiple-Comparison Z-Value Test at $p = 0.05$ level were used.

## Results

Species composition

Altogether fourteen bat species were recorded in the study area (Table 1). The most abundant mist-netted species were *Myotis daubentonii* and *E. serotinus*. The species *Myotis bechsteinii*, *M. myotis*, *M. mystacinus* and *P. auritus* were also dominant (> 5 %). There were big, between-night differences in netting success and species composition. More than one quarter of nights were negative and on the other hand in the most successful night (20th June, game mire) 28 individuals of eight species were captured.

Most detector registrations belong to species *N. noctula*, followed by *E. serotinus*, *Barbastella barbastellus*, *N. leisleri* and *P. pipistrellus*. Another three species (*Myotis nattereri, M. myotis, M. daubentonii*) were detected and identified only if observing conditions were sufficient (visual observation, more detections). It was not possible to identify other species in the forest conditions.

In the study area, eight potential roosts in churches were controlled. This type of habitat represents a typical summer roost for more species. No maternity roost was found, only sporadically some individuals of *M. mystacinus* and *Plecotus austriacus* were found. Four tree roosts were found occasionally, three were used by *N. noctula*, and one by *M. daubentonii*. One individual of *R. hipposideros* was found in a 12 m long mine.

Prey composition and foraging bat assemblage

One order of arachnids (Araneida) and 7 orders of insects (Homoptera, Heteroptera, Neuroptera, Coleoptera, Hymenoptera, Lepidoptera and Diptera, Table 2) were identified in examined bat droppings. In total, the moths imagoes (Lepidoptera) were the most important component in diet of studied bat assemblage ($V = 46\%$, $F = 68\%$). Other important diet components were beetles (Coleoptera) $V = 23\%$, $F = 43\%$ and dipterans (Diptera) $V = 11\%$, $F = 50\%$. The frequency of dipterous insects was relatively high, however volume dominance was low. Underestimation of volume dominance could be caused by easier digestion of soft fly's bodies. The moths took up to 100% in frequency of diet components (found in droppings) of *M. nattereri*, *M. emarginatus*, *M. mystacinus*, *N. noctula*, *P. auritus* and *B. barbastellus*. Similarly, the moths had an important portion of volume dominance in diet composition of several species (*P. auritus* = 96%, *M. nattereri* = 68%, *M. mystacinus* = 65%). Just in *B. barbastellus* the moths had 100% of volume dominance (n = 3). Consuming of moth females (presence of eggs) and larvae was recorded. Especially, the larvae of geometrid moth *Lycia hirtaria* took up to 28% of diet volume dominance in *M. bechsteinii*. Another important diet component were beetles (*M. myotis* = 76% and *E. serotinus* = 58%). In *M. myotis* it was mainly beetles from Carabidae family and in *M. bechsteinii* and *E. serotinus* it was beetles from *Curculio* genus.

In the studied bat assemblage, all five foraging strategies were observed or assigned to individual species. Species *N. noctula* and *N. leisleri* were observed using the strategy "fast hawking". Foraging strategy "slow hawking" was typically observed by *E. serotinus* and *B. barbastellus*, also *P. pipistrellus* was assigned to this strategy and partly *M. mystacinus* and *P. austriacus*. "Gleaning" from the ground or vegetation is typical for species of *Myotis* genus – *Myotis emarginatus*, *M. myotis*, *M. bechsteinii*, *M. nattereri*, also for *P. auritus*, and partly for *M. mystacinus* and *P. austriacus*. Species *M. daubentonii* used mostly "trawling" from water surfaces. The last foraging strategy called "perch hunting" or "fly-catching" is typical for *R. hipposideros*. This species was registered just once, therefore this strategy was not included in further analyses. Based on literature and field observations, attempt to classify the foraging strategy composition of the bat assemblage was performed (Fig. 1).

Table 1. All bat species records in the study area. Data obtained by netting (number of caught individuals / %) batdetectoring (number of records / %) and control of roosts (number of roosts / %) are presented.

| Species | Netting n / % | Detectoring n / % | Roosts n / % | All records N / % |
|---|---|---|---|---|
| *Nyctalus noctula* (Schreber, 1774) | 3/4 | 28/53 | 3/34 | 34/26 |
| *Eptesicus serotinus* (Schreber, 1774) | 14/18 | 10/19 | | 24/17 |
| *Myotis daubentonii* (Kuhl, 1817) | 14/18 | 2/4 | 1/11 | 17/12 |
| *Myotis myotis* (Borkhausen, 1797) | 12/16 | 3/6 | | 15/11 |
| *Myotis bechsteinii* (Kuhl, 1817) | 13/17 | | | 13/9 |
| *Myotis mystacinus* (Kuhl, 1817) | 9/12 | | 2/22 | 11/8 |
| *Barbastella barbastellus* (Schreber, 1774) | 3/4 | 5/10 | | 8/6 |
| *Plecotus auritus* (Linnaeus, 1758) | 5/6 | | | 5/4 |
| *Myotis nattereri* (Kuhl, 1817) | 2/3 | 1/2 | | 3/2 |
| *Rhinolophus hipposideros* (Bechstein, 1800) | 1/1 | | 1/11 | 2/1 |
| *Nyctalus leisleri* (Kuhl, 1817) | | 2/4 | | 2/1 |
| *Plecotus austriacus* (Fischer,1829) | | | 2/22 | 2/1 |
| *Myotis emarginatus* (Geoffroy, 1806) | 1/1 | | | 1/1 |
| *Pipistrellus pipistrellus* (Schreber, 1774) | | 1/2 | | 1/1 |

Table 2. Food composition (volume dominance % / frequency of occurrence %) in the beech-oak forest bat assemblage (N = 38 bat individuals / n = 117 pellets)

| Bat species | Araneida | Homop. | Heterop. | Neurop. | Coleop. | Hymenop. | Lepidop. | Lepidop. (larvae) | Dip. | N/n |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Prey category | | | | | |
| *M. myotis* | | | | | 76/93 | 13/40 | | 8/27 | 3/20 | 6/15 |
| *M. bechsteinii* | 5/31 | | 1/3 | 1/3 | 6/26 | 2/11 | 49/60 | 28/40 | 9/49 | 10/35 |
| *M. nattereri* | 2/17 | | | | 5/50 | 8/17 | 68/100 | | 17/100 | 1/6 |
| *M. emarginatus* | | | | | | | 30/100 | 40/100 | 30/100 | 1/1 |
| *M. mystacinus* | | | | 16/43 | | | 65/100 | | 19/64 | 5/14 |
| *M. daubentonii* | | | | | | | | | 100/100 | 1/1 |
| *E. serotinus* | | 1/5 | 3/19 | 3/24 | 58/95 | 5/19 | 19/62 | | 11/67 | 6/21 |
| *N. noctula* | | | 25/56 | | 4/33 | | 54/100 | | 17/67 | 2/9 |
| *P. auritus* | | | | | 1/11 | | 96/100 | 1/11 | 2/22 | 3/9 |
| *B. barbastellus* | | | | | | | 100/100 | | | 3/6 |

The ratio of individual strategies was relatively equalled. The same portion took gleaning, slow hawking and fast hawking. Individual groups of bats (*Myotis* group, non-*Myotis* group) were registered not equally in all strategies by detectoring and netting. Fast hawking species were registered often by detectors and gleaners almost exclusively by mist-netting (Fig. 2).
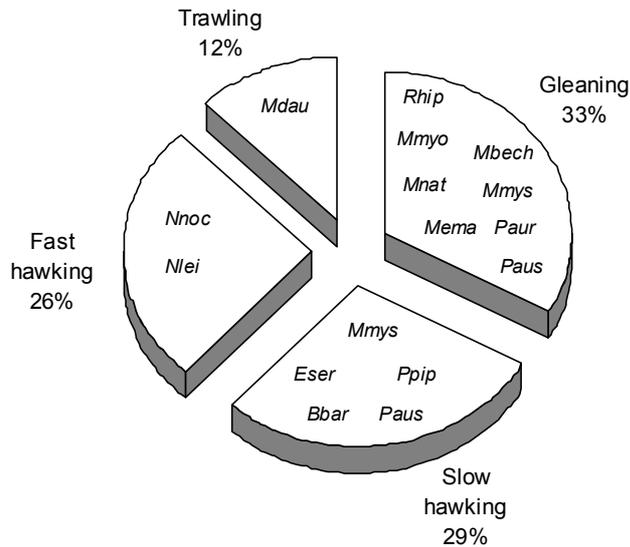


Fig. 1. Hypothetical structure of bat assemblage based on the foraging strategies in the selected beech-oak forests (n = 138). Abbreviations: Bbar = *Barbastella barbastellus*, Eser = *Eptesicus serotinus*, Mbech = *Myotis bechsteinii*, Mdau = *Myotis daubentonii*, Mema = *Myotis emarginatus*, Mmyo = *Myotis myotis*, Mmys = *Myotis mystacinus*, Mnat = *Myotis nattereri*, Nlei = *Nyctalus leislerii*, Nnoc = *Nyctalus noctula*, Paur = *Plecotus auritus*, Paus = *Plecotus austriacus*, Ppip = *Pipistrellus pipistrellus*



Fig. 2. The typical hunting space (hatches) of selected foraging strategies (A = gleaning, B = slow hawking, C = trawling, D = fast hawking) and relationship of such bat groups to recording in the field (by bat-detectoring – black percentage in the circle, by mist netting – white)

Flight activity

Of 1505 total assessed minutes, 16% were positive. In positive minutes 249 bat passes and 16 "feding buzzes" were recorded. Bat passes were assigned to *Myotis* group (67%), and non-*Myotis* group (33%). All of studied habitats were used by bats.

The highest level of activity (number of bat passes per minute) was recorded in open areas. Extreme values of activity were also typical for this habitat type (0.8 bat passes/minute). A relatively high level of flight activity was recorded on forest edges and forest streams (Fig. 3). Coniferous and broad-leaved forests had the lowest number of detections. No bat passes typical for non-*Myotis* group were in broad-leaved or coniferous forests. They were recorded often in the open area (61%) and on the forest edge (43%). The comparison of the number of bat passes per minute between all habitats made by Kruskal-Wallis *H*-test showed significant differences ($H = 33.61$, d. f. = 6, $p < 0.001$). Significant differences were found between the open area and coniferous forest (Z-Value Test, $z = 3.59$, $p < 0.05$), stream and coniferous forest (Z-Value Test, $z = 3.61$, $p < 0.05$). High activity was detected on the forest edge, but differences were significant only in relation to activity in broad-leaved forest (Z-Value Test, $z = 3.36$, $p < 0.05$) and coniferous forest (Z-Value Test, $z = 5.03$, $p < 0.05$). "Feeding buzzes" were recorded in open area and forest edge in very small numbers, in broad-leaved forest were recorded just once.

The flight activity of bats differed significantly in relation to flight activity of insects (Kruskal-Wallis *H* test, $H = 44.77$, d.f. = 4, $p < 0.001$). With increasing flight activity of insects, the flight activity of bats increased as well ($R = 0.34$; $p < 0.001$; n = 297).

**Discussion**

Proportional use of different investigation methods (mist-netting, bat-detectoring, roost controls) is necessary for study of bat assemblages and can provide an elementary view on the bat species composition in study area. Some species are easily recorded by mist-netting and another species with help of bat detectors (GAISLER 1973; MURRAY et al. 1999). Individual species are distinctive in their ecology, therefore it is important to take this fact into consideration. *M. daubentonii* hunts typically on the open water surfaces. Foraging of this species was recorded exclusively at one locality – Kováčovský rybník pond. It was probably a group of animals from a 1.5 km distant tree-hollow roost. It was confirmed by netting of nine individuals on a forest road between the roost tree and the pond. Similarly, the use of bat detectors can overestimate species with loud echolocation calls. It is possible to detect a *N. noctula* on 150 meters in contrast to *M. bechsteinii*, which could be usually detected only at 3–5 meters (OBRIST 1995).

Food composition of bats in the study area did not differ significantly from findings of other authors in European countries (GREGOR, BAUEROVÁ 1987; BECK 1995; VAUGHAN 1997). Foraging strategies of individual bat species (cf. NORBERG, RAYNER 1987) and seasonal food accessibility probably determined the prey type and composition.

Importance of different forest habitats for bats is still not clear. Our results correspond with another authors. Forest interior (broad-leaved or coniferous forests) had a low level of flight activity and the highest level of activity was typical for forest openings and edges. Some of the authors concluded, that bats
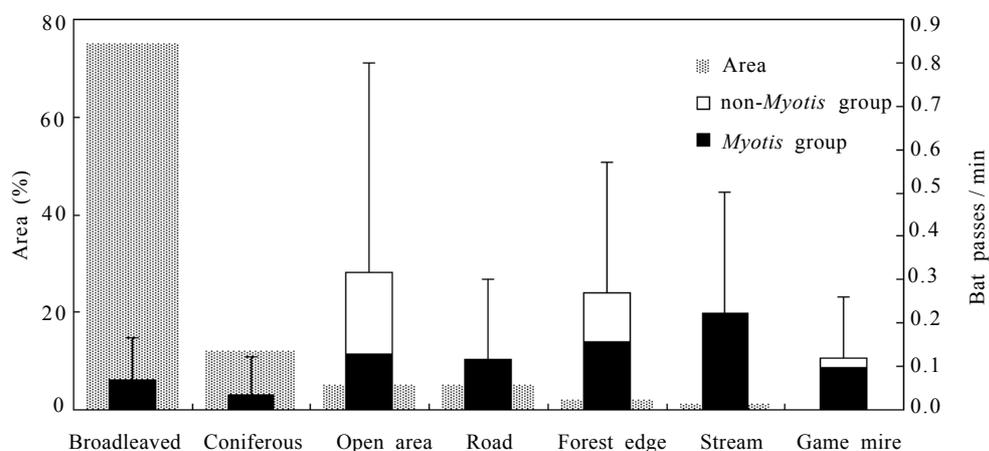


Fig. 3. Flight activity of bats in seven investigated habitat types (mean, +SD; proportion in percentage of *Myotis* group – black and non-*Myotis* group – white, 1505 minutes) and area of the habitat types (grey)

prefer hunting in these habitats and they are crucial for bats. They supposed that low clutter and therefore, easily accessible prey is the reason for this preference (CRAMPTON, BARCLAY 1996; KRUSIC, NEEFUS 1996). We assume that interpretation of bat detector data is not so simple in these conditions. Studied habitats often have very unequal proportion in the study area and the function of habitats is also different. High activity in open areas and forest edge is caused by limited area of these habitats and bats do not spent much time in these habitats. On the other hand, there was recorded minimal activity in the forest. But these results must be handled carefully. The forest takes up a majority of the area and that is the cause of a big dispersion of individuals (Fig. 3). Studies combining radio-telemetry and bat detectors brought a controversial results (CRAM-PTON, BARCLAY 1998). Very low level of activity was detected in the forest interior, but the radio-telemetry data showed that bats did not leave the forests. Streams and small water pools are also a water source. Therefore, their presence could be crucial for bats, regardless to their negligible small surface.

There are other factors which have negative influences on the registered level of activity. The forests are mostly very cluttered habitats. Hunting in such habitat demands the use of high frequency calls, which are attenuated more in atmosphere (OBRIST 1995; PATRIQUIN et al. 2003). In more open areas, bats use low frequency calls within a long range. These frequencies are recorded at a farther distance by bat detectors. This fact can overestimate more open habitats, like cuttings or forest edges. In other respects, the crown layer of the forest could also be an important foraging area (HAYES, GRUVER 2000). The bat detectors in this study were placed 1.5 m above the ground, so the crown layer was not surveyed at all.

## Conclusions

Using different methods the wide spectrum of bat species was recorded in beech-oak forests in the Central Slovakia. Bats use forest ecosystems for hunting completely, in all dimensions – they hunt insects on the ground, on the trunks, in the crowns and also in free space above the forest and clearings. The dominant prey taken by bats were Lepidoptera, Coleoptera and Diptera. The flight activity of bats positively correlated with flight activity of insects, which confirms the opportunistic foraging strategy of bats. The highest level of flight activity of bats was recorded in open areas (meadows, clearings) and on the forest edges. But interpretation of these results must be handled carefully, because of very different size of individual habitats. We suggest that forest interior is an important foraging habitat for bats. It is not possible to assess importance of habitats or habitat preference based only on results from bat detectors. Higher activity need not mean the preference. There is a need for more studies or experiments in the future to know the real habitat preference of bats in forest ecosystems.

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# Lovná a letová aktivita netopierov v bukovo-dubových lesoch (Západné Karpaty)

## Súhrn

Kombináciou viacerých metód bolo v bukovo-dubových lesoch na skúmanom území zaznamenané pomerne široké druhové spektrum netopierov (14 druhov). Najvýznamnejší podiel v potrave tvorili Lepidoptera, Coleoptera a Diptera. Rozbor potravy a priame pozorovania ukázali, že netopiere využívali skúmané lesné ekosystémy ako zdroj potravy komplexne – od povrchu pôdy, cez korunovú vrstvu až po voľný priestor nad korunami stromov. Bola zistená pozitívna závislosť letovej aktivity netopierov od letovej aktivity hmyzu, čo potvrdzuje oportunistický spôsob lovu – vyhľadávanie lokálne bohatých zdrojov potravy. Najvyššia aktivita bola zistená na otvorených plochách v porastoch (čistinky, lúky) a na okrajoch porastov. Interpretáciu týchto výsledkov ako habitatovej preferencie je však potrebné robiť citlivo, vzhľadom na odlišný plošný podiel jednotlivých habitatov. Je pravdepodobne zjednodušené usudzovať o význame či preferencii habitatov len na základe hodnotenia aktivity získanej pomocou detektorov. Predpokladáme naopak, že interiér lesa je významným lovným habitatom netopierov. Pre poznanie skutočných habitatových preferencií netopierov v lesoch budú v budúcnosti potrebné porovnávacie štúdie vo viacerých územiach príp. modelových podmienkach.