Folia Zool. – 55(3): 273–281 (2006)

Flight activity and habitat preference of bats in a karstic area, as revealed by bat detectors

Jan ZUKAL[1,2] and Zdeněk ŘEHÁK[1]

[1] *Institute of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic; e-mail: zukal@brno.cas.cz, rehak@sci.muni.cz*

[2] *Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, 603 65 Brno, Czech Republic; e-mail: zukal@brno.cas.cz*

Received 17 February 2006; Accepted 25 August 2006

Abstract. The flight activity of bats was studied at 21 localities in the Moravian Karst (Czech Republic). From April to October, bat detectors were used to record echolocation calls of bats on line transects during the first half of the night. Nine habitats were distinguished. In total, 666 minutes of the presence of flying bats and at least 16 bat species were registered during 3387 transect minutes. *Myotis daubentonii* was the most numerous species (46.2%) The number of bat species was the highest in rocky habitats (13 species), and the lowest in agrocoenoses (3 species). The greatest intensity of flight activity of the bat community was observed over ponds (35.0 min+/h) and streams (26.6 min+/h). With respect to habitat preference, *M. mystacinus*/*brandtii*, *M. myotis*/*blythii*, *Eptesicus serotinus*, *Nyctalus noctula*, *Pipistrellus pipistrellus,* and *Plecotus auritus*/*austriacus* appear to be eurytopic and *M. daubentonii*, *M. nattereri* and *M. emarginatus* to be stenotopic species.

Key words: Moravian Karst, echolocation calls, bat community, detectoring, line transect

Introduction

During the past decade, an increased number of articles was published on the habitat preference and activity of bat communities (Walsh & Harris 1996, von Zahn & Mayer 1997, Gaisler et al. 1998). This is due to the expansion of ultrasound detector use in field research, including studies in such highly diversified landscapes as karstic regions. While the use of bat detectors has become established the standard methods of carrying out research in bat activity (Ahlén & Baagoe 1999) it has its intrinsic technical (different types of signal transformation) and ecological (whispering bat species, direction of signals etc.) constraints which could more or less influence the study results (Hayes 2000, Gannon et al. 2003). The most frequently designs used in field research include the transect method (Gaisler & Kolibáč 1992, Walsh & Harris 1996, Verboom 1998), which was adopted from ornithology, and/or the point method (Walsh & Mayle 1991, Rachwald 1992, Rydell et al. 1994).

Bats forage in various types of habitats, from forest habitats up to villages, and the spatial distribution of bat activity is mainly determined by the distribution of their prey (Rydell 1992). Habitat selection is also influenced by the ability of various bat species to exploit these habitats, depending on their structure or their accessibility (de Jong 1995, Verboom 1998, Kusch et al. 2004). Among insectivorous bats, the following five foraging strategies based on wing morphology and structure of echolocation calls (Norberg & Rayner 1987, Fenton 1990) can be identified: fast and slow aerial hawking, flycatching, trawling, and gleaning. Many bat species can use more than one foraging technique. Most central European bat species forage by aerial hawking, often with the addition of one or more other techniques (Norberg & Rayner 1987).

The bat fauna of the Moravian Karst is characterized by high density and diversity. So far, this phenomenon has only been explained by the large number of caves in this area (ca. 1200), but they are used by bats mainly as hibernacula (Zima et al. 1994). Nevertheless, there is a mosaic of various habitats under different anthropogenic impact and this fact permits the presence of a rich bat community even during the non-hibernating period.

The purpose of this study was to obtain data on the flight activity of bats during the non-hibernating period in various habitats of the karstic area under study. The landscape of the Moravian Karst is subject to management as part of the agricultural, hydrological and recreational demands of tourism. By assessing the relative importance of the particular habitats for bat distribution, it should be possible to improve the landscape management system in favour of the bats.

Material and Methods

The flight activity of bats was studied in 21 localities in all parts of the Moravian Karst area (Central Moravia, Czech Republic) (Table 1). The size of this karstic area is 85 km^2. Nine habitat types were distinguished for the comparison of bat activity: fields (fi), meadows (m), linear landscape elements (l), villages (v), rocks (r), forests (fo), edges of forest (e), streams (s), and ponds (p).

Bat detectors (Pettersson Elektronik, D100 and D980) were used to record echolocation calls of bats on the line transects. The transects were mostly carried out during the first half of the night from April to October of 1992–1994. The number of minutes during which a particular species or two sibling species was registered, related to 1 hour of transect (min+/h), was used as the measure of bat activity (McAney & Fairley 1988).

Table 1. Summary of monitoring activity in particular habitats.

Habitats	Number of monitoring minutes (min)	Number of positive minutes (min+)	Dominance of positive minutes (%)
rocks	615	79	11,9
forests	515	52	7,8
linear landscape elements	484	38	5,7
streams	470	206	30,9
edges of forest	382	39	5,9
villages	359	67	10,1
ponds	238	163	24,5
fields	176	8	1,2
meadows	148	14	2,1
Sum	3387	666	100,0

With regard to the difficult determination of some of the bat species in the field, the transects were conducted simultaneously by two researchers using two detectors. Where appropriate, we made records for comparison with reference records (Ahlén 1987). Foraging behaviour was also included in the process of species identification when we tried to catch flying bats in the beam of a halogen lamp.

In order to group bat species that use similar foraging habitats, we performed a cluster analysis using the complete linkage method (Euclidean distance) (Zar 1984). The same type of clustering (complete linkage) was also applied to the matrix of Renkonen's index of dominance similarity (dominance of particular bat species) to compare the habitat types under study. In order to provide a comprehensive account of bat species-habitat association (bat species recorded for over 10 min+ in the total sample of 11 hours), the data on total bat activity in various habitats were subjected to canonical correspondence analysis.

Results

In total, 666 minutes of bat activity were registered by bat detectors during 3387 transect minutes (68 monitoring nights). At least 16 bat species were recorded, viz., *Rhinolophus hipposideros* (Rh), *Myotis mystacinus/brandtii* (Ms), *M. emarginatus* (Me), *M. nattereri* (Mn), *M. bechsteinii* (Mb), *M. myotis/blythii* (Mm), *M. daubentonii* (Md), *Vespertilio murinus* (Vm), *Eptesicus nilssonii* (En), *E. serotinus* (Es), *Nyctalus leisleri* (Nl), *N. noctula* (Nn), *Pipistrellus pipistrellus* (Pp), *P. nathusii* (Pn), *Barbastella barbastellus* (Bb), *Plecotus auritus/austriacus* (Pa). In field work, the two species of *Pipistrellus* i.e. *P. pipistrellus* and *P. pygmaeus* were not distinguished but later analyses revealed the presence of both species in the area under study, with the absolute predominance of *P. pipistrellus*.

The greatest intensity of flight activity of bats was observed over ponds (41.1 min+/h) and streams (26.3 min+/h) (Fig. 1). The interior of villages was another important habitat showing high flight activity of flying bats, above all, near streetlamps (11.2 min+/h). However, agrocoenoses lacking patches of trees or shrubs were poorly used by bats (2.7 min+/h).

The greatest intensity of flight activity was recorded in *M. daubentonii* (52.1 min+/h), especially at watersides (Fig. 2). Further species with relatively high activity included *Pipistrellus pipistrellus* (13.3 min+/h) and *Eptesicus serotinus* (11.6 min+/h), which are able to exploit a wider variety of habitats as foraging sites. On the other hand, *E. nilssonii* and *Vespertilio murinus* represent very rare faunistic records of these bat species in the area.

Cluster analysis divided habitat types into four groups (Fig. 3). The first group consists of water habitats, showing the specific structure of the bat community which was dominated by *M. daubentonii*. Fields, being highly influenced anthropogenic habitat types, are used by bats only for sporadic passes. Like the villages, this habitat is specific and separated. However the villages are providing roosts and foraging sites for synanthropic bat species. Cluttered and semi-cluttered habitats with similar bat communities (mainly forest-dwelling species) formed the last group.

Comparisons of the flight activity of nine common bat species or species pairs (over 1% of total sample) in particular habitats separated into three clusters (Fig. 4). *E. serotinus* differs from other bat species in its greatest ability to exploit man-made environments (e.g. villages). Further two clusters comprise groups of bat species. *M. emarginatus*, *M. mystacinus/brandtii*, *M. myotis/blythii* and *Plecotus auritus/austriacus* forage in cluttered and semi-cluttered habitats. Finally, *M. daubentonii*, *M. nattereri*, *Nyctalus noctula* and *P. pipistrellus* show high levels of flight activity at watersides.

The habitat preference of nine common species or species pairs (over 10 min+ in the total sample) was assessed by canonical analysis (Fig. 5). The total level of flight activity in particular habitats was used for this analysis. The highest preference of a single habitat type is apparent for the following species: *M. daubentonii* (watersides, i.e. streams and ponds), *M. mystacinus/brandtii* (forest), *E. serotinus* (villages) and *N. noctula* (open habitats, i.e. fields). *M. myotis/blythii* shows relatively close affinity to narrow meadow belts and linear

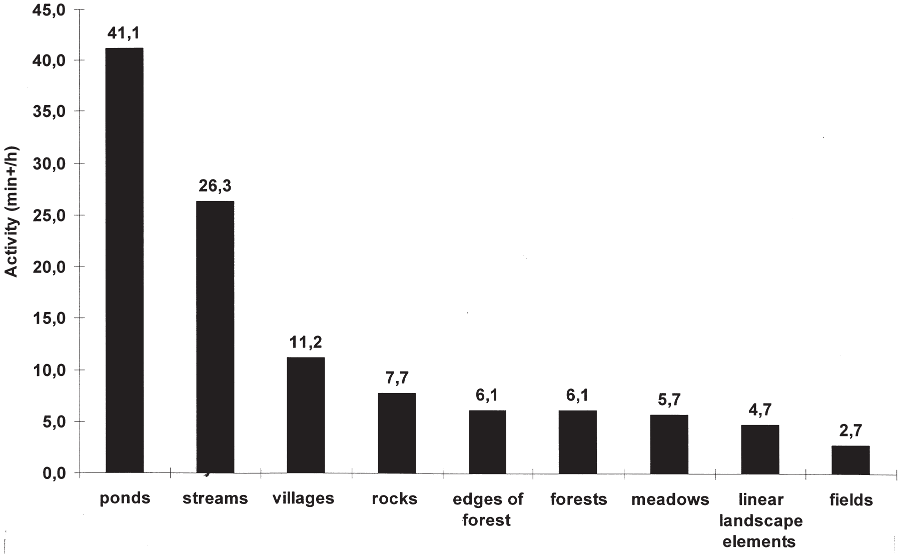

Fig. 1. Total intensity of bat flight activity (all species) in particular habitat types.

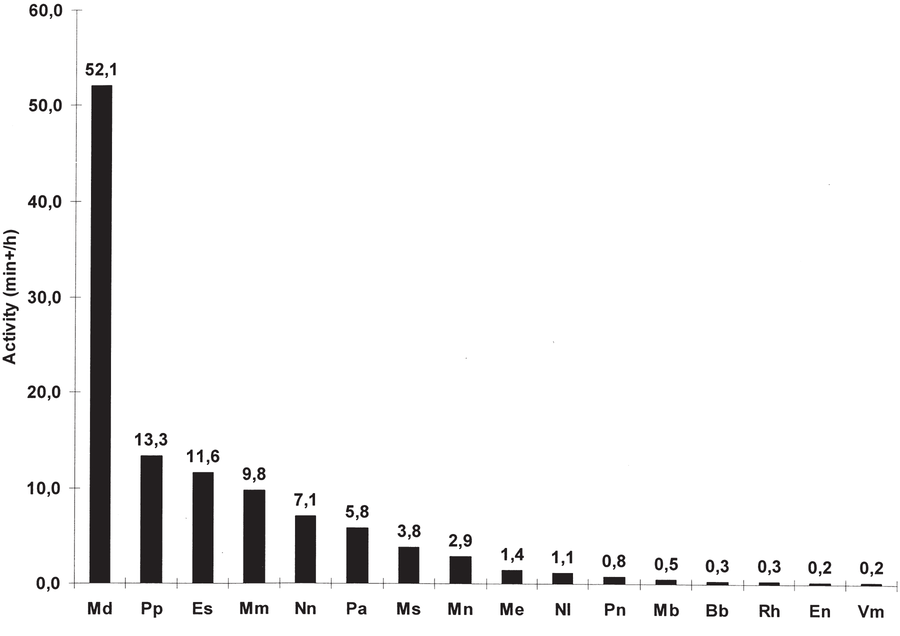

Fig. 2. Total intensity of the flight activity of particular bat species in the area under study. For abbreviation of bat species see chapter Results.

landscape elements. These two habitats may be considered semi-cluttered spaces for flying bats. Four species (*M. emarginatus, P. auritus/austriacus*, *M. nattereri,* and *P. pipistrellus*) show no strong habitat preference. Nevertheless, each of these bat species shows somewhat different requirements for foraging habitat.

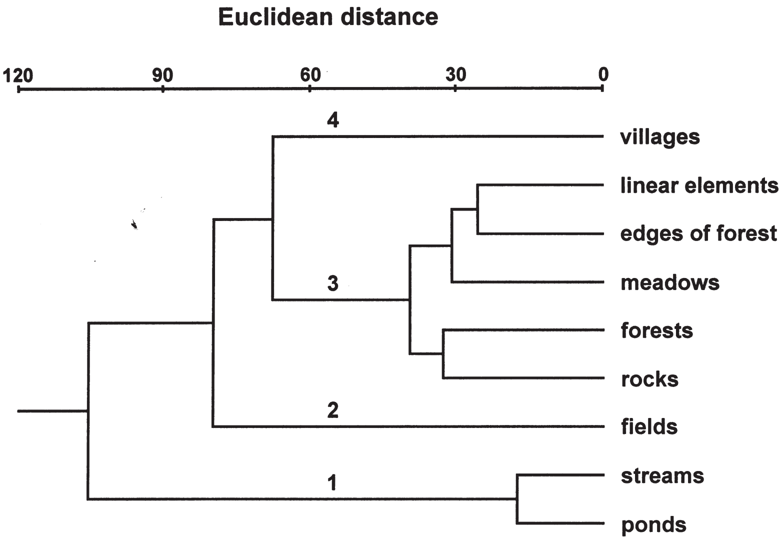

Fig. 3. Comparison of habitat types according to the dominance of particular bat species (cluster analysis – complete linkage).

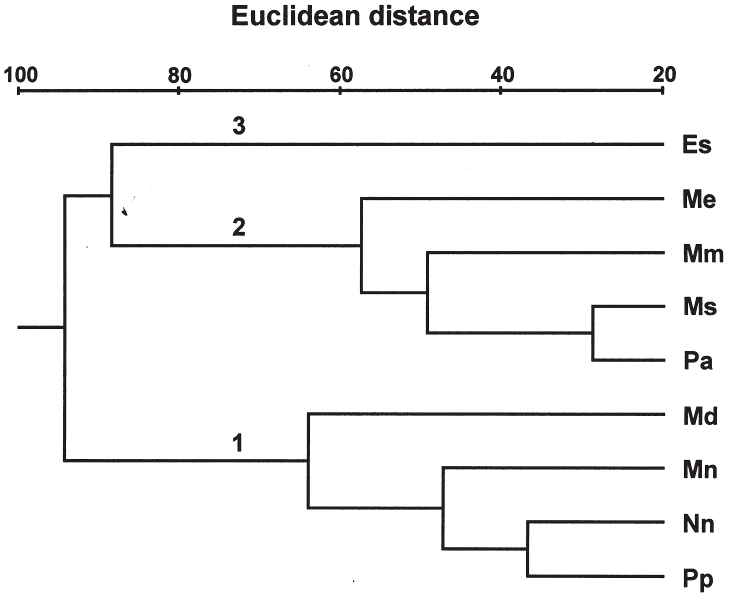

Fig. 4. Comparison of the nine common bat species or pair of species according to the distribution (in %) of their total flight activity in the particular habitats (cluster analysis – complete linkage). For abbreviation of bat species see chapter Results.

Discussion

The use of bat detectors, like any other research method, has its internal constraints. A major problem in bat community research is posed by correct species determination of echolocating bats (Walsh & Harris 1996, Gannon et al. 2003). It is influenced by many different

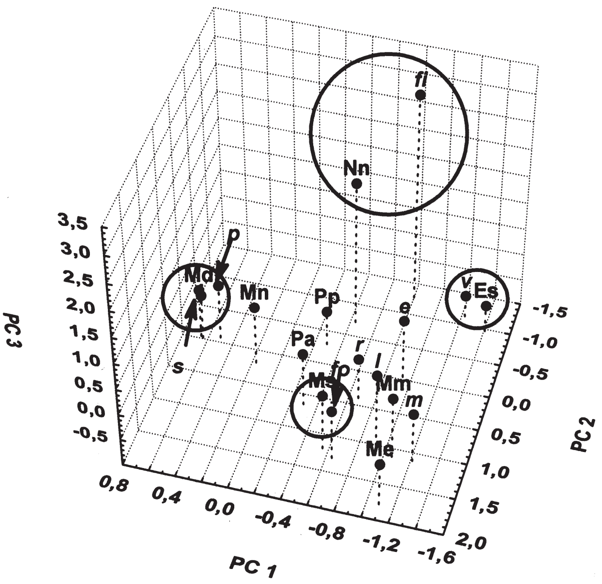

Fig. 5. Habitat preference of nine common species or couple of species according to the total flight activity (results of canonical analysis). For abbreviation of bat species see chapter Results.

factors, such as the duration of bat calls, presence of "whispering bat species", and experience of the researcher. Nevertheless, bat-detectors, mist nets and harp traps are the only useful research methods for study of the activity of whole bat communities, and detectors are the most widespread method used at present. The authors tried to minimize the impact of technical and ecological constraints on the results of study in various ways, e.g. by using the same types of bat detectors, grouping species with similar echolocation calls, using reference records, as well as long-term experience in using bat-detectors in the field. A less complicated situation is found in investigating the flight activity of only one bat species (Rachwald 1992, Catto et al. 1996, Robinson & Stebbings 1997) and/or the activity of a group of selected and readily distinguishable species (von Zahn & Maier 1997, Gaisler et al. 1998, Bartonička & Zukal 2003, Kusch et al. 2004).

Bats forage in various habitat types. Nevertheless, their preference for particular habitats depends on the presence of suitable food resources. The foraging activity of bats is affected by the distribution of prey not by the type of the habitat used (Brigham et al. 1992, Racey & Swift 1985, Warren et al. 2000, Kusch et al. 2004). Roosting requirements (number and distance of potential shelters) may also influence habitat utilization (Geggie & Fenton 1985). Many bat species forage only in the surroundings of their shelters. However, a habitat offering abundant food has no useful roosts in its vicinity the bats will seldom utilize it. On the contrary, if bats have the possibility of selecting from a large number of roosts they will choose those the closest to the food resources (Rydell 1989, Kusch et al. 2004). Bats prefer mainly diversified habitats and, on the contrary, their density is significantly lower in open landscape and/or inside dense forests (McAney & Fairley 1988, Kusch et al. 2004).

A preference for foraging in a single habitat type is very rare in insectivorous bats, as in general they use more habitat types, depending on actual food supply (Brigham et al. 1992), and they move between them during the night (Verboom & Spoelstra 1999).

The most important foraging areas include all types of water bodies, from small streams and ponds to larger rivers, canals and lakes, as confirmed by our results. Their attractiveness is due to the great biomass of insects swarming over the water surface. From this point of view, stagnant water bodies are preferred to running ones (Frenckell & Barclay 1987, Mackey & Barclay 1989). Riparian vegetation is also important, mainly where watercourses run through open landscape (Rydell et al. 1994, Zahn & Maier 1997). In open agricultural landscape, patches of woods and linear elements (e.g. windbreaks) are also highly important as reservoirs of insects. Similar habitat types are only suitable where the bats can obtain enough food in agrocoenoses (Gaisler & Kolibáč 1992). In the opposite, this type of habitats was utilised by bats minimally in variable area of the Moravian Karst. Lowland deciduous and mixed forests are preferred among forest habitats. In such forests, open forest edges and clearings are favourite foraging areas of bats (Mayle 1990, Limpens & Bongers 1991, Walsh & Mayle 1991, Rachwald 1992). The extent to which bats make use of man-made structures is expressed in their habitat preference. A number of bat species forage in villages mainly in the vicinity of streetlamps where a high density of insects was registered (cf. Furlonger et al. 1987, Rydell 1992).

Different bat species can utilize different foraging strategies, which also indirectly influences the selection of foraging habitats. There is a clear relationship between a bat functional design, i.e. flight morphology and structure of echolocation calls, and its commuting and foraging behaviour including the structure of used habitats (Fenton 1990, Verboom 1998). Wing morphology confers mechanical and energetical constraints on flight speed and manoeuvrability (Norberg & Rayner 1987). Echolocation signals have evolved to optimize foraging efficiency of various bat species in particular habitats.

M. daubentonii shows a strong association with watersides and its activity is extremely high there. It is a typical trawler, gaffing prey from the water surface or aerially hawking insects over the smooth water surface (Warren et al. 2000). Turbulent rapid streams are used rather more for commuting flights than for foraging, as this species often forages in groups and creates group foraging territories. *M. daubentonii* has a considerable overlap in the structure of calls with *M. nattereri* and there might be some misidentifications. Nevertheless, *M. nattereri* was detected mainly foraging higher over the water surface in the vicinity of the riparian vegetation (deJong 1995). Its activity would also be underestimated due to silent calls and/or if the calls had a poor signal to noise ratio when the calls of *M. nattereri* are masked by the loud signals of *M. daubentonii* foraging groups.

M. mystacinus/brandtii were the species most frequent recorded in forests, as in Sweden where *M. brandtii* used the coniferous forest more than expected and the deciduous woodland in proportion to its area (de Jong 1995). Generally, flight activity in forests is very low. *M. mystacinus/brandtii* also forage in the vicinity of water courses (von Zahn & Maier 1997) and they may be underestimated here, as with *M. nattereri*. The presence of both species i.e. *M. mystacinus* and *M. brandtii* in the region under study was documented by netting (Řehák et al. 1994). Together with *M. mystacinus/brandtii*, individuals of the genus *Plecotus* were often recorded in the forests. Most probably, these were to *P. auritus*, which prefers forest habitats (de Jong 1995) whereas records from gardens within villages probably pertain to the sibling species *P. austriacus* (Bauerová 1982). Similarly as in other pairs of sibling species, their echolocation calls cannot be differentiated in the field.

A relatively low activity was registered for *M. emarginatus*, a species foraging in cluttered and semi-cluttered habitats. This species behaved as a typical gleaner using edges of forests with a well-developed shrub layer adjacent to vertical rock walls surrounded by shrubs. In these habitats, *M. emarginatus* will probably glean small arthropods, especially spiders (Bauerová 1986).

The species included in the *M. myotis/blythii* pair differ significantly in habitat preference and thus also in different prey selection – terrestrial (e.g. carabid beetles) vs. grass-dwelling (mostly bush crickets) (Arlettaz et al. 1997). Higher activity registered over the meadows should indicate the presence of *M. blythii* in the Moravian Karst. However, in the present study such sites were mostly narrow meadow belts surrounded by woods. In addition, only search calls were recorded there, and thus these bats may have been commuting specimens of *M. myotis*. During the past three years, telemetry has revealed that even *M. myotis* will forage in the open habitats of the Moravian Karst, including fields (Pokorný, Berková & Zukal, unpublished data). In addition, *M. blythii* is a very rare species in the area under study, recorded sporadically in the caves during hibernation and/or at cave entrances during autumn migrations (Řehák et al. 1994).

E. serotinus is able to exploit a wide range of habitats foraging mainly over streetlamps, in gardens as well as over ponds (Catto et al. 1996). As a typical semisynantropic species, *E. serotinus* differs from other bat species recorded in the Moravian Karst by the highest ability to exploit man-made environment (Verboom 1998). Only *N. noctula* is able to forage in similar habitats. Nevertheless, this species regularly used open habitats and was recorded flying very high over fields. At twilight, *N. noctula* often preys on swarming insects over the ponds but, later on, it appears in villages, catching prey in the vicinity of streetlamps (Rachwald 1992). This movement is influenced by the dwindling abundance of insects due to the falling ambient temperature in the natural habitats.

P. pipistrellus seems to be highly adaptive in foraging habitat preference in comparison with other bat species showing similar foraging strategies (Warren et al. 2000). *P. pipistrellus* forages both over water bodies and in riparian vegetation and, together with *E. serotinus* and *N. noctula*, use the parts of villages illuminated by streetlamps (Rydell 1992). Nevertheless, their activity is very low in very dense as well as in entirely open habitats (von Zahn & Maier 1997, Verboom & Spoelstra 1999).

Ackowledgement

The authors wish to thank Martin Pokorný for his help in field work. The technical support for the study was provided by grant No. MSM 0021622416.

LITERATURE

Ahlén I. 1987: European bat sounds transformed by ultrasound detectors – 25 species flying in natural habitats. *Tape. Univ. Agr. Sci. Uppsala.*

Ahlén I. & Baagoe H.J. 1999: Use of ultrasound detectors for bat studies in Europe: experiences from field identification, surveys, and monitoring, *Acta Chiropterologica 1: 137–150.*

Arlettaz R., Perrin N. & Hausser J. 1997: Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol. 66: 897–911.*

Bartonička T. & Zukal J. 2003: Flight activity and habitat use of four bat species in a small town revealed by bat detectors. *Folia Zool. 52: 155–166.*

Bauerová Z. 1982: Contribution to the trophic ecology of the grey long-eared bat, *Plecotus austriacus*. *Folia Zool. 31: 113–122.*

Bauerová Z. 1986: Contribution to the trophic bionomics of *Myotis emarginatus*. *Folia Zool. 35: 305–310.*

Brigham R.M., Aldridge H.D.J.N. & Mackey R.L. 1992: Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. *J. Mammal. 73: 640–645.*

Catto C.M.C., Hutson A.M., Racey P.A. & Stephenson P.J. 1996: Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool., London 238: 623–633.*

Fenton M.B. 1990: The foraging behaviour and ecology of animal-eating bats. *Can. J. Zool. 68: 411–422.*

von Frenckell B. & Barclay R.M.R. 1987: Bat activity over calm and turbulent water. *Can. J. Zool. 65: 219–222.*

Furlonger C.L., Dewar H.J. & Fenton M.B. 1987: Habitat use by foraging insectivorous bats. *Can. J. Zool. 65: 284–288.*

Gaisler J. & Kolibáč J. 1992: Summer occurrence of bats in agrocoenoses. *Folia Zool. 41: 19–27.*

Gaisler J., Zukal J., Řehák Z. & Homolka M. 1998: Habitat preference and flight activity of bats in a city. *J. Zool., London 244: 439–445.*

Gannon W. L., Sherwin R. E. & Haymond S. 2003: On the Importance of Articulating Assumptions When Conducting Acoustic Studies of Habitat Use by Bats. *Wildlife Society Bulletin 31: 45–61.*

Geggie J. F. & Fenton M. B. 1985: A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool. 63: 263–267.*

Hayes J.P. 2000: Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica 2: 225–236.*

deJong J. 1995: Habitat use and species richness of bats in a patchy landscape. *Acta Theriol. 40: 237–248.*

Jüdes U. 1989: Erfassung von Fledermäusen im Freiland Mittels Ultraschall-detektor. *Myotis 27: 27–40.*

Kusch J., Weber C., Idelberger S. & Koob T. 2004: Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zool. 53: 113–128.*

Limpens H. J. G. A. & Bongers W. 1991: Bats in Dutch forest. *Myotis 29: 129–136.*

Mackey R.L. & Barclay R.M.R. 1989: The influence of physical clutter and noise on the activity of bats over water. *Can. J. Zool. 67: 1167–1170.*

Mayle B.A. 1990: A biological basis for bat conservation in British woodlands – a review. *Mammal Review 20: 159–195.*

McAnney M.C. & Fairley J.S. 1988: Habitat preference and overnight and seasonal variation in the foraging activity of lesser horseshoe bats. *Acta Theriol. 33: 393–402.*

Norberg U.M. & Rayner J.M. 1987: Ecological morphology and flight in bats: wing adaptation, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B 316: 335–427.*

Racey P.A. & Swift S.M. 1985: Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. *J. Anim. Ecol. 54: 205–215.*

Rachwald A. 1992: Habitat preference and activity of the noctule bat *Nyctalus noctula* in the Bialowieza Primeval Forest. *Acta Theriol. 37: 413–422.*

Robinson M.F. & Stebbings R.E. 1997: Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *J. Zool., Lond. 243: 117–136.*

Rydell J. 1989: Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. *Oecologia 80: 562–565.*

Rydell J. 1992: Exploitation of insects around street lamps by bats in Sweden. *Functional Ecology 6: 705–744.*

Rydell J., Bushby A., Cosgrove C. & Racey P.A. 1994: Habitat use by bats along rivers in North East Scotland. *Folia Zool. 43: 417–424.*

Řehák Z., Zukal J. & Kovařík M. 1994: Long- and short-term changes in the bat community of the Kateřinská cave (Moravian Karst) – a fundamental assessment. *Folia Zool. 43: 425–436.*

Verboom B. 1998: The use of edge habitats by commuting and foraging bats. *Dissertation Thesis, DLO Institute for Forestry and Nature Research (IBN-DLO), Wageningen, 121 pp.*

Verboom B. & Spoelstra K. 1999: Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Can. J. Zool. 77: 1393–1401.*

Walsh A.L. & Harris S. 1996: Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology 33: 508–518.*

Walsh A.L. & Mayle B.A. 1991: Bat activity in different habitat in a mixed lowland woodland. *Myotis 24: 97–104.*

Warren R.D., Waters D.A., Altringham J.D. & Bullock D.J. 2000: The distribution of Daubenton's bats (*Myotis dabentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. *Biological Conservation 92: 85–91.*

von Zahn A. & Maier S. 1997: Jagdaktivität von Fledermausen an Bächen und Teichen. *Z. Säugetierkd. 62: 1–11.*

Zar J. H. 1984: Biostatistical analysis. *Simon and Schuster, Englewood Cliffs, New Jersey, USA.*

Zima J., Kovařík M., Gaisler J., Řehák Z. & Zukal J. 1994: Dynamics of the number of bats hibernating in the Moravian karst in 1983 to 1992. *Folia Zool. 43: 109–119.*