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CONSTRAINTS IN ROOST-SITE SELECTION BY TREE-DWELLING BECHSTEIN'S BAT (*MYOTIS BECHSTEINII*)

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ABSTRACT - The roosting and foraging habitats of tree-dwelling Bechstein's bats can vary greatly. We hypothesised that the most important determining variables would not vary between different forest habitats and that social constraints may play a role in limiting commuting distances between roosting and foraging sites. Altogether 11 post-lactating adult females were radio-tracked in two predominantly oak forest habitats, where both potential roost and tree stand characteristics differed. We recorded 18 roosts; the distances between occupied roosts and commuting distances to foraging areas were measured. Within a 0.1 ha wide plot centred on each roost, a total of 17 habitat variables were recorded. Regardless of the different habitat structure (canopy closure, stand density) and roost-site availability, tracked females selected tree hollows with similar dimensions. The size of both roosting and foraging areas did not differ between habitats. We suggest that protection from predators and social constraints may determine the spatial distribution of Bechstein's bat roosts.

Key words: tree hollows, habitat, social behaviour, roosting strategy, Chiroptera

RIASSUNTO - ***Fattori influenzanti la selezione dei siti di rifugio arborei da parte del pipistrello di Bechstein (*****Myotis bechsteinii*****)***. Le caratteristiche dei siti di rifugio e foraggiamento del pipistrello di Bechstein variano notevolmente. E' possibile quindi ipotizzare che, in ambienti forestali differenti, i fattori che ne influenzano maggiormente la selezione si mantengano costanti. Inoltre il comportamento sociale della specie potrebbe porre dei limiti alla distanza tra i due siti. Dopo l'allattamento, 11 femmine adulte sono state seguite con la radiotelemetria in due querceti con diversa disponibilità di siti di rifugio. Sono stati individuati 18 roost, per i quali sono state misurate le distanze tra roost occupati e dalle aree di foraggiamento. Entro un cerchio di 0,1 ha centrato su ogni roost, sono state inoltre misurate 17 variabili ambientali. Malgrado sia la struttura del habitat (densità arborea, grado di copertura delle chiome) sia la disponibilità di rifugi siano risultate diverse, le caratteristiche delle cavità utilizzate non sono variate significativamente, così come le dimensioni dei territori. Si suggerisce che la difesa dai predatori e il comportamento sociale del pipistrello di Bechstein ne determinino la distribuzione spaziale dei roost.

Parole chiave: cavità arboree, habitat, comportamento sociale, scelta dei rifugi, Chiroptera

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INTRODUCTION

Roosts provide bats with a place for repose, reproduction and hibernation as well as protection against predators and seasonal weather fluctuations (Altringham 1996; Vonhof and Barclay 1996; Meschede and Heller 2000; Kunz and Lumsden 2003). Social interactions between conspecifics and information sharing may also occur inside roosts (Loughry and McCracken 1991; Kerth and König 1999; Kerth and Reckardt 2003). The type of roost selected also influence the size of bat assemblages (Barclay and Kurta 2007). Tree dwelling bats often show roost-switching behaviour (Meschede and Heller 2000). Some of the proposed benefits gained by individuals that form 'flexible' aggregations, which can split and re-form, include: a) lower flight costs to food resources; b) knowledge of multiple roost sites differing in their microclimate; and c) reduction in parasite loads, predation and competition with other tree-dwelling animal species (Lewis 1996; Vonhof and Barclay 1996; Kunz and Lumsden 2003). In contrast, this behaviour can also increase intra-specific competition for resources (Jones 1990), boost the parasite load and spread diseases (Côte and Poulinb 1995). Although in most mammals social groups consist of kin members (cf. Packer et al. 1990; Symington 1990), in tree-dwelling bats the structure of fission-fusion societies is mediated by individual preferences, which still need to be examined in more details (Metheny et al. 2008).

Appropriate bat management and conservation entails the knowledge of population and species requirements, including their preference for different roost and foraging sites (e.g. Crampton and Barclay 1998; Lacki and Baker 2003; Russo et al. 2004; Kaňuch et al. 2008). We studied roost-site selection by Bechstein's bat, *Myotis bechsteinii* (Kuhl, 1817), a species endangered in many parts of Europe. This non-migratory, medium-sized (forearm 39–45 mm, body mass 7–14 g), long-lived bat roosts and breeds in tree cavities (the approximate size of maternity colonies is 10–50 females; Dietz et al. 2009). Although occurring in various types of woodlands, it is typically associated with old natural broadleaved forests, such as oak stands (Meschede and Heller 2000; Kaňuch et al. 2008; Dietz et al. 2009). The proportion of dead wood, canopy closure and the availability of insect prey have been reported as variables determining habitat selection in this species (Schofield and Morris 2000; Fitzsimons et al. 2002; Napal et al. 2009; 2010).

The aim of our study was to point out the main factors influencing the choice of roost-sites by Bechstein's bat, based on comparison of two different forest habitats with varying characteristics. We hypothesised that the most important determining variables would not vary between forest habitats. Fission-fusion behaviour being an important social and ecological mechanism in tree-dwelling bat colonies (Lewis 1996; Kerth and König 1999; Kerth and Reckardt 2003), we also expected that commuting distances between roosting and foraging sites represent a major constraint in the selection of roost sites by Bechstein's bats.

MATERIAL AND METHODS

1. Study area

The standard commercial dense forest (thereafter *DF*) is characterized by 80–100 year-old deciduous trees. The dominant species (with diameter at breast height, DBH, > 30 cm) are oaks (*Quercus robur*, *Q. petrea*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). Managed harvesting of timber is regular; however, no extensive clear-cuts have occurred. This forest type is widespread in the region and data were collected from three plots in eastern Slovakia (N48°41–48°52', E21°29'–22°04', 222–458 m a.s.l. Fig. 1). The sparse forest (thereafter *SF*) consists of plain woodland (central Slovakia, N48°28', E19°08', 470 m a.s.l.), including solitary 200–300 year-old oaks (*Quercus robur* agg., *Q.cerris*). This area is not harvested, but cattle grazing is used as a conservation management strategy (for details see Kaňuch and Ceľuch 2007).

2. Radio-tracking of bats

In July and August 2007 and 2009 post-lactating females were captured by placing 2.5 × 7 m mist-nests above a water pit or pool. Bats were banded by incoloy rings (Porzana Ltd., United Kingdom), equipped with Pip3 radio-transmitters (Biotrack Ltd., UK) and released at the site of capture. Transmitters that did not exceed 5% of a bat weight were attached between the bat's scapulae using surgical adhesive after clipping the fur. To track bats, we used two TRX-3S receivers (Wildlife Materials Inc., USA) fitted with three-element Yagi antennas.

We tracked bat movements for a total of 53 nights. Whenever possible, tracking was carried out during the entire night, or at least during the first half of the night. When bats actively foraged, locations were acquired by the biangulation method in 10 minute interval throughout the night. The locations made during night-roosting were excluded from analyses. We used the "homing-in" method to locate day-roosts (White and Garrot 1990). Recorded bat locations were transformed into ArcView GIS 3.2 (ESRI, Inc., USA) and both pair-wise distances between occupied roosts and commuting distances from each roost to foraging areas were measured. The first measures allowed to determine the size of roosting territories, while the sizes of foraging territories and their core areas were assessed by 95% and 50% kernel polygons, respectively, in Animal Movement extension for ArcView GIS 3.2. Fission-fusion social relation among bats was confirmed by random harp-trapping at their roosts in each study plot.

To test for variation in the sizes of roosting and foraging territories between the two habitats, we used standard *t*-tests, after having checked the data by Shapiro-Wilk's normality test.

3. Characteristics of roosting habitats

Stand characteristics were measured within a 0.1 ha (ca. 18 m radius) plot around each roosting tree. The level of canopy closure around the roost was categorised visually as follows: 1 – sparse (three or more trees were missing); 2 – discontinuous (one or two trees were missing); 3 – open (tree crowns did not influence each other); 4 – loose (crowns did not touch each other, but influenced each other); 5 – full (crown touched and influenced each other); 6 – dense (branches interfere with adjacent tree crowns). Within each plot we also measured stand density (i.e. the number of trees with DBH > 25 cm) and assess the number of potential roosts (tree hollows and cavities counted from the ground).

From each tree-roost we recorded: 1 – species; 2 – total height; 3 – DBH; 4 – distance from the nearest neighbouring tree; and 5 – number of hollows visible from the ground on trunk and main branches. Whenever the roost hollow was located, we recorded: 1 – its origin (i.e. natural hollow, woodpecker hollow, crevice, under the bark); 2 – position (main trunk, side-branches); 3 – aspect of the entrance; 4 – minimal and maximal entrance dimensions;

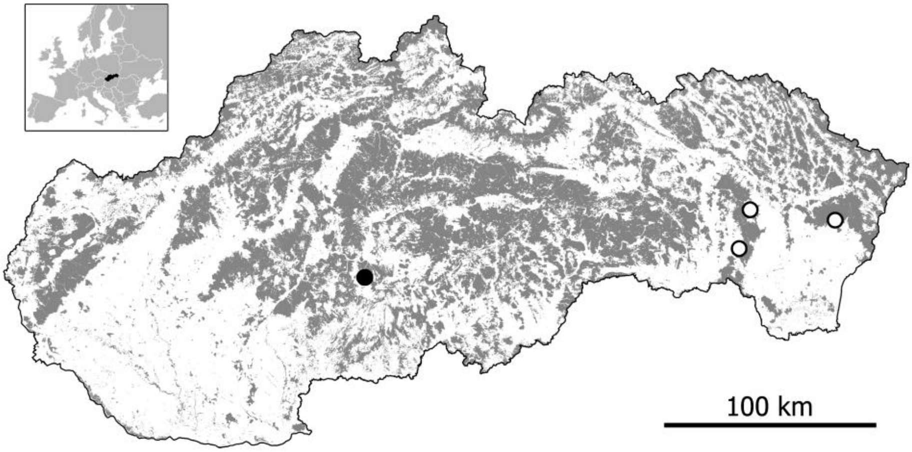

Figure 1 - Location of the study plots (white circles, dense forest habitat; black circle, sparse forest habitat) in Slovakia. Forested areas are shown in grey.

5 – internal height over the entrance of the hollow; 6 – internal diameter of the hollow; 7 – external diameter of the trunk or branch at the level of the entrance; and 8 – the height of the entrance over the ground.

Since most data was not normally distributed (Shapiro-Wilk's normality test), variation between habitats was tested by Mann-Whitney *U*-test.

RESULTS

We tagged 5 females in *SF* (2007) and 8 females in *DF* (2009). Two bats in 2009 were never detected after release and were excluded from further analyses. The mean monitoring time ± S.E. per individual was 3.3 ± 0.7 days (range 1–5 days) in *DF* and 6.6 ± 0.9 days (range 5–10 days) in *SF* (Tab. 1).

In total, we located 18 roosts of Bechstein's bats (11 in *DF* and 7 in *SF*; Tab. 1). In *DF* four bats (out of six tracked) used two or three roosts, while one of them was found in four different roosts. For three bats only one roost was found before losing the radio contact. Similarly, in *SF*, three bats (out of five tracked) used two roosts, one bat used three different roosts and one bat only one. The number of occupied roosts per tracked individual did not differ significantly between the two habitats ($U = -0.09$, $P = 0.93$). Switching of roosts confirmed also other banded bats which were recaptured during harp-trapping (data not shown).

Table 1 - Radio-tracking data on post-lactating adult females of Bechstein's bat in dense (N = 6) and sparse (N = 5) forest (Days: number of tracking days; Locations: number of radio-locations during foraging; Roosts: number of tree roosts occupied).

Habitat	Days	Locations	Roosts
Dense forest			
Mean	3.3	74.2	2.2
Range	1–5	17–144	1–4
Total	20	445	11
Sparse forest			
Mean	6.6	38.2	2.0
Range	5–10	23–53	1–3
Total	33	191	7

In *DF*, seven roosts occurred in *Quercus robur*, two in *Fagus sylvatica*, and one in both *Fraxinus excelsior* and *Carpinus betulus*. In *SF*, all roosts were found in *Quercus robur*, which was the dominant tree species there. It was quite difficult to assess the origin of the hollows due to the natural decay of the wood. Nevertheless, in *DF* five natural and three woodpecker-created hollows were recorded in the main trunk. The remaining three roosts (one woodpecker hollow, one crevice and one roost under exfoliated bark) were located in side-branches. In one case, the entrance of the hollow had been adjusted with mud by nuthatch *Sitta europea*. In *SF* two natural hollows, one woodpecker's hollow and a crevice were found in the main trunk. Two natural and one woodpecker hollows were located in side-branches.

All variables of the forest stands and roosting trees exhibited significant differences (Tab. 2). Canopy closure as well as stand density were significantly higher in *DF* than in *SF* ($U = 3.49$, $P < 0.001$ and $U = 3.22$, $P < 0.001$), while the number of potential roosts was higher in *SF* ($U = –3.31$, $P = 0.001$). In *DF* roost trees were taller, when compared with *SF* ($U = 2.81$, $P = 0.005$), however, the diameter at breast height was significantly smaller ($U = –3.49$, $P < 0.001$). The distance of the roosting tree to the nearest tree was significantly smaller in *DF* ($Z = –3.49$, $P < 0.001$). The number of hollows in the roosting tree was higher in *SF* ($Z = –2.49$, $P = 0.013$). Roost entrances were mostly oriented towards east - south-east in both *SF* and *DF* ($U = –0.23$, $P = 0.821$). The hollow's minimum entrance diameter did not differ significantly between the two habitat types ($U = 1.85$, $P = 0.064$), while the maximum entrance diameter was larger at *DF* ($U = 2.44$, $P = 0.015$). While the internal diameter of the roost was smaller in *DF* ($U = –2.73$, $P = 0.006$), internal height did not vary ($U = –1.32$, $P = 0.188$), as so as the external diameter of the trunk or branch at the level of the entrance ($U = –0.09$, $P = 0.928$) and the height of the roost above ground ($U = 1.68$, $P = 0.094$).

We discovered a total of 631 (445 in *DF* and 191 in *SF*) foraging locations (Tab. 1). All radio-tracked females foraged exclusively in the forest interior. Despite the fact that the bats in *DF* had foraging sites less distant from their roosts than those in *SF* ($t = –9.47$, d.f. = 584, $P = 0.000$), the mean size of both bat total ($t = –2.01$, d.f. = 9, $P = 0.075$) and core foraging areas ($t = –1.67$, d.f. = 9, $P = 0.129$) did not differ between the two habitats. Similarly, the size of roosting territories did not differ between the compared habitats ($t = 1.81$, d.f. = 36, $P = 0.079$). The longest distance between two roosts was 842 m in *DF* and 887 m in *SF* (Tab. 3).

DISCUSSION

Local habitat conditions may vary greatly between habitats and roosting sites selected by tree-dwelling bat species (Lacki and Baker 2003). Dominant tree species composition associated with potentially different climatic conditions and food and roost availability can influence population densities as well as the behaviour of the species (Vonhof and Braclay 1996; Russo et al. 2003; Napal et al. 2010). In our study, radio-tracked females selected tree hol-

Table 2 - Characteristics of roosting habitats occupied by Bechstein's bats in dense (N = 11 roosts) and sparse (N = 7 roosts) forests (Mann-Whitney *U*-test; *: P < 0.05, **: P < 0.01, ***: P < 0.001, N.S.: not significant). Variables as the tree species, origin of roost and its position on tree are shown in the text only.

	Dense forest			Sparse forest		
Variable	Median	Range	P-value	Median	Range	Units
Stand (0.1 ha)						
Canopy closure	5	2–6	***	1	1–1	(scale)
Stand density	10	4–18	***	4	1–5	-
Potential roosts	1	0–5	***	6	4–9	-
Tree						
Height	20	10–30	**	15	9–18	m
DBH	36	30–66	***	130	110–140	cm
Distance from other tree	3	1–3	***	10	8–20	m
No. of hollows	0	0–5	*	2	2–7	-
Tree hollow						
Aspect	90	0–315	N.S.	135	0–270	°
Entrance (min)	4.5	1.5–7.0	N.S.	3.5	2.5–8.0	cm
Entrance (max)	5.0	4.5–11.0	*	4	2.7–10.0	cm
Internal height	10	0–20	N.S.	15	0–50	cm
Internal diameter	10	6–15	**	15	10–25	cm
External diameter	36	30–66	N.S.	50	28–60	cm
Height of entrance	10	5.5–14	N.S.	9	2.5–10	m

Table 3 - Roosting and foraging areas of Bechstein's bats in two distinct forest habitats (*t*-test; ***: P < 0.001, N.S.: not significant).

	Dense forest			Sparse forest	
Variable	Mean ± S.E.	Range	P-value	Mean ± S.E.	Range
Roosting-foraging distance (m)	389±11	12–1968	***	839±73	18–4407
50% Kernel estimate (ha)	8.3±2.0	4.1–17.8	N.S.	19.9±5.9	1.7–37.8
95% Kernel estimate (ha)	63.8±17.8	20.4–148.3	N.S.	131.7±39.3	17.5–233.1
Distance between roosts (m)	516±56	29–842	N.S.	379±51	0–887

lows with similar dimensions regardless of the different habitat structure (canopy closure, stand density) and potential roost-site offer. Likewise, the size of both roosting and foraging territories did not differ between two very distinct habitats. These similarities suggest some constraints on roost-site selection by tree-dwelling Bechstein's bats, which are discussed below.

Roosts were found mainly in oak trees, which were dominant tree species in both studied forest types and may supply more cavities for bats than other European trees (Boonman 2000). The degree of wood decay of the roosting tree and the number of potential roosts in its vicinity have been found to be determining factors for most tree-dwelling bats (Vonhof and Barclay

1996; Brigham et al. 1997; Rabe et al. 1998; Cryan et al. 2001; Lacki and Baker 2003; Lučan et al. 2009; Napal et al. 2009). However, we did not find bats roosting in dead trees. The limited size of the entrance, which is located well above the ground, suggests that protection from predators may play a major role in tree-dwelling bat choice for a roost-site, as reported for other tree-dwelling species (Vonhof and Barclay 1996; Betts 1998; Ruczyński and Bogdanowicz 2005). Other variables of tree-hollows which did not differ between the two distinct habitats (aspect of the entrance, external diameter of the trunk or branch at the level of entrance) may suggest a preference for specific microclimatic conditions. As microclimatic preferences of bats vary according to the season, such hypothesis needs experimental evidence (Crampton and Barclay 1998; Kalcounis and Brigham 1998).

Interestingly, the distance between pairs of roosts did not differ between the two forest types, despite the strikingly different availability of potential roost-sites (but see Fuhrmann et al. 2002). Foraging strategies depend on habitat structure (Brigham et al. 1992; Crampton and Braclay 1998; Patriquin and Barclay 2003). However, Bechstein's bats forage exclusively in the forest interior, hence commuting distances between roosts and foraging sites should reflect other qualitative characteristics (e.g. prey density) of wood stands (cf. Kronwitter 1988; Schrocht et al. 2002). Although foraging sites in *SF* were more distant from roosts than in *DF*, the mean size of both total and core foraging areas did not differ, suggesting that a trade-off between prey availability and energy demands of bats determines the spatial distribution of occupied roosts. In the stand offering high roost availability, occupied roosts were not located closer to each other. We hypothesise that higher spatial density of switched roosts may increase the risk of predation. On the other hand, bats performing fission-fusion behaviour need to maintain social contacts (Lewis 1996; Kerth and König 1999; Kerth and Reckardt 2003) and hence may select roost-sites within "socially acceptable" distances. Considering our field-based observations, we suggest that protection from predators and the maintenance of social contacts may be major determining factors in roost-site selection by Bechstein's bats. These hypotheses need to be experimentally tested in the future.

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