Spatial organization reflects the social organization in Bechstein's bats

Barbara Dawo[1,2], Elisabeth K. V. Kalko[1] & Markus Dietz[1,2]

[1] *Institute of Experimental Ecology, University of Ulm, Albert-Einstein-Allee 11, D-89069 Ulm, Germany*
[2] *Institute of Animal Ecology and Nature Education, Altes Forsthaus, D-35321 Gonterskirchen, Germany (*corresponding author's e-mail: barbara.dawo@tieroekologie.com)*

Dawo, B., Kalko, E. K. V. & Dietz, M. 2013: Spatial organization reflects the social organization in Bechstein's bats. — *Ann. Zool. Fennici* 50: 356–370.

An understanding of the spatial organization of endangered species is particularly important in the light of habitat degradation and fragmentation. In bats, little is known about whether and how space is organized between individuals of the same species. We investigated space use in four maternity colonies of Bechstein's bats. We were able to show for the first time that spatial organization reflects the social organization in Bechstein's bats. We found a strong segregation of foraging ranges within colonies, and an even stronger segregation between different colonies. Our results suggest that the spatial organization of females is determined by foraging efficiency. It is crucial to determine the essential characteristics of both feeding and roosting core areas. We provide a precise prediction of effective population size and space requirements. Thereby, implications for the protection of Bechstein's bats and assumedly also for other bat species with a similar social and spatial organization can be deduced.

Introduction

Conservation of endangered species requires a detailed understanding of factors that determine distribution and abundance. Besides extrinsic ecological factors, intrinsic factors such as social interactions among individuals of the same species determine the space required to maintain a population. Up to now, only few attempts have been made to investigate minimum foraging areas required to sustain viable populations (Racey & Entwistle 2003). Knowledge about the spatial organization is particularly important in the light of habitat degradation and fragmentation. In many social mammals, female offspring display natal philopatry. Matrilinear

structures were identified in the social organization of many species (Clutton-Brock *et al.* 1982, Michener 1983, Packer 1986, de Ruiter & Geffen 1998) including bats [*Eptesicus fuscus* (Metheny *et al.* 2008); *Myotis bechsteinii* (Kerth *et al.* 2000)]. Female philopatry often entails adjacent home ranges or increased home range overlap between colony members (Moyer *et al.* 2006, Wronski & Apio 2006, Frere *et al.* 2010), and the inheritance of resources is widespread in social species, including bats [*Rhinolophus ferrumequinum* (Rossiter *et al.* 2002), *Myotis bechsteinii* (Kerth *et al.* 2001b)].

Bat populations are restricted to sites with sufficient and reliable prey availability and enough suitable and highly-connected roosts

(Limpens & Kapteyn 1991, de Jong 1995, Jenkins *et al.* 1998, Dietz & Kalko 2007a). So far, little is known about how space is used by bats. Due to their high specialization and the clear connection to specific habitats, Dietz and Kalko (2007b) suggested to use bats as indicators for ecosystems that require special protection. Since Bechstein's bat is considered to be an indicator species for old-growth broad-leaved woodland of high habitat quality (Kaňuch *et al.* 2008), this bat species could fulfill the role of a target species for ecosystem oriented forest conservation programs, as proposed by Dietz and Kalko (2007b) and Dietz and Pir (2009). In spite of its high priority for conservation issues (Annex II and IV, Habitat Directive), it remains largely unknown how individual *M. bechsteinii* make use of space while foraging. Females show strong natal philopatry with low inter-colony dispersal rates, while males live solitary (Kerth *et al.* 2000, 2002a, 2002b). Colonies form fission-fusion societies that regularly split into several subgroups using different roosts (Kerth & König 1999). *Myotis bechsteinii* has medium-span broad wings and low wing loading, which enables slow and manoeuvrable but energy-consuming flight (Norberg & Rayner 1987, Siemers & Swift 2006b). The species is able to forage close to vegetation and to glean arthropods from vegetation and the ground (Wolz 2002, Siemers & Swift 2006b). Reflecting energy-consuming flight, it is assumed that increased foraging costs arise with increasing distance between foraging range and roosting range (Entwistle *et al.* 1996, Kerth *et al.* 2001b). Bechstein's bats have small home ranges and each female revisits its own foraging ranges over several nights (Dietz & Pir 2009). However, it remains unclear whether there is a high or low amount of overlap between individual home ranges. In particular, little is known about how space is used by individuals of the same colony, and how foraging ranges of different colonies are located to each other. It is known that Bechstein's bats often feed within distances of 1 km from the roosting site and have small individual home ranges, foraging areas and core areas, that are used with strong site fidelity (Kerth & Melber 2009, Napal *et al.* 2010). Between seasons and even between years, females maintained loyal to their individual home range (Kerth *et al.* 2001b). Kerth *et al.* (2000) concluded that this strong female philopatry might reflect the importance of profound roost or habitat knowledge for successful reproduction in Bechstein's bats. Since female Bechstein's bats exploit homogenous and predictable food resources, profound site knowledge could be a crucial 'resource' (Kerth *et al.* 2001b) and increasing hunting efficiency may have selected for site fidelity (Kapfer *et al.* 2008). Kerth *et al.* (2001b) also assumed maternal inheritance of home ranges based on the results of radio-tracked mother–daughter pairs. He found a positive correlation between the degree of MCP (Minimum Convex Polygon) overlap and genetic similarity that would result if daughters inherit part of the hunting areas of their mothers.

The aim of this study was to evaluate whether there is spatial organization in foraging ranges that reflects the social organization of closed societies (Kerth *et al.* 2000) within and between Bechstein's bats' colonies. First, we compared roosting and foraging behavior of one colony in different years to test for continuity in space use patterns. Secondly, we analyzed intra-colony overlap of foraging ranges. Female Bechstein's bats are known to use foraging ranges individually. However, daughters assumedly inherit at least part of the hunting areas from their mothers (Kerth *et al.* 2001b). If relatedness determines spatial distribution of home ranges, this should be reflected by the overlap of foraging ranges. Because of the matrilinear structure in colonies, foraging ranges within a colony might display a certain degree of overlap. Maternity colonies are closed societies, and females even show aggressive behavior when confronted with females from another colony intruding into a roost they occupy (Kerth *et al.* 2000, 2002b).Therefore, we thirdly predicted that females of neighboring colonies should segregate spatially. Indeed, foraging ranges of adjacent colonies, despite being close to each other, should display almost no overlap. Due to wing morphology and foliage gleaning, foraging costs increase with distance between roosts and foraging ranges (Norberg & Rayner 1987, Entwistle *et al.* 1996, Kerth *et al.* 2001b, Siemers & Swift 2006b). Therefore, we expected foraging ranges to be aggregated

around the respective roosting range, in order to minimize flight costs.

Methods

Study site

The study was carried out 2 km west of the town of Echternach in eastern Luxembourg (49°80´N, 6°43´E). Data collection took place in the deciduous forest 'Friemholz', a 126 ha plateau forest. In this homogenous forest stand, up to 180 year-old oak trees (*Quercus robur*) dominate an understory of hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*). This well-structured and closed old-growth forest is characterized by a high amount of dead wood (Heinrich *et al.* 2002, Krippel 2005). It is mainly surrounded by agricultural crop and pasture land. During four summers (2006–2009), we studied a total of 118 female Bechstein's bats, which inhabited almost exclusively woodpecker cavities in oak trees. To assess colony affiliation, since 2006 we individually marked bats with 2.5-mm aluminum split rings. In order to assign individuals to their respective maternity colony, we caught bats emerging from roost trees (*n* = 206). Taking into account frequent roost switching, we caught bats from each roost tree found through radio-tracking whenever possible. The compositions of the captured groups within the respective roost trees showed that there are four distinct maternity colonies in the Friemholz area (col-1, col-2, col-3, and col-4). During four summers, captured groups of females sharing the same roost were assigned to belong to the same maternity colony. We never found a female that shared a roost with females that were, before or afterwards, assigned to another maternity colony. This evidence together with the fact that Bechstein's bats show a very low intercolony dispersal rate supported the conclusion that the females indeed belong to four colonies.

Radio-tracking

As we intended to compare range use of females in different reproductive states, for radio-tracking we chose only adult and reproductive females (Table 1). Reproductive status was assessed according to Racey (1974, 2009). We excluded females that were within two weeks of giving birth. During radio-tracking, individual bats were located every five minutes via synchronized cross-bearings (Millspaugh & Marzluff 2001) for at least three nights each. Short time intervals may produce temporally autocorrelated fixes (Harris *et al.* 1990, White & Garrott 1990), a negligible fact in Bechstein's bats which are able to cross their entire home range within 5 min (Jones & Rydell 1994). Locations of the animals were calculated using Tracker (version 1.1, Camponotus, Sweden). Between 2006 and 2009, we individually marked 20–39 females from each colony (col-1: *n* = 20; col-2: *n* = 30; col-3: *n* = 39; col-4: *n* = 27). A further estimate of minimum colony size was obtained through visual counts of bats emerging from a roost (col-1: *n* = 32; col-2: *n* = 25; col-3: *n* = 23; col-4: *n* = 28). Counts were conducted before females gave birth, except for col-4. For intra- and inter-colony comparisons, we tracked at least six females from each colony during two consecutive summers. In 2008, we tracked col-3 (*n* = 6) and in 2009 we tracked col-1 (*n* = 7), col-2 (*n* = 6) and col-4 (*n* = 6). We obtained a mean of 167 ± 38 (mean ± SD, range = 107–257) fixes per individual. In order to compare space use of one colony in different years, we compared tracking data from col-1 in 2009 with tracking data obtained from 6 randomly chosen unmarked females in 2005. We also sporadically monitored col-1, col-2 and col-3 in 2006 and 2007, but did no radio-track them.

Home range analysis

Individual home ranges were calculated as 100% Minimum Convex Polygons (MCPs) (Mohr 1947, White & Garrott 1990). Within home ranges, we identified areas of intense use (foraging ranges) using a local convex hull (LoCoH) nonparametric method (Getz *et al.* 2007). This method calculates an animal's probability of occurrence at each point in space (utilization distribution, UD). The shape of the constructed UDs arises directly from the animal's movements (Getz *et al.* 2007). Within foraging ranges,

we distinguished between Foraging Areas (FA) and Core Areas (CA). For many bat species it has been found suitable to define core areas using 50% and 95% isopleths (*see* Harris *et al.* 1990). Hence, in order to ensure comparability with other studies, FAs were defined as areas used for food searching and constructed as isopleths that contain the 95% UD. Consequently, CAs contain the 50% UD as areas of most intense use (cf. Weinbeer & Kalko 2004, Weber *et al.* 2009). CAs and FAs were calculated including only radio-fixes for flying bats to avoid overestimation at roost sites. We calculated roosting ranges for each colony separately. The roosting range of a given colony was defined as 100% MCP that contains all known roost trees for this colony.

We calculated straight-line distances between the day roost of a bat on a given day and all radio-tracking fixes obtained during the following night.

CAs and FAs were calculated using R version 2.10.1 (R Development Core Team 2009) and the R package AdeHabitat (Calenge 2006). We used the *a*-LoCoH algorithm (Getz *et al.* 2007) contained in the AdeHabitat package. This adaptive method uses all radio-fixes within a variable sphere around a given radio-fix, so that the sum of the distances between all included fixes is less than or equal to *a*. For selecting *a*, we followed the heuristic rule, as proposed by Getz *et al.* (2007). MCP calculations were made using ArcView 3.2 (Environmental Sys-

Table 1. Summary of all female radio-tracked *M. bechsteinii* (*n* = 31) belonging to four colonies, roosting in the Friemholz forest in eastern Luxemburg. Females were individually marked since 2006. Reproductive periods of females are pregnancy (grav.), lactation (lac.) and post-lactation (post-lac.).

Year	Colony	Reproductive state	Individual	Ring number	Mass (g)	Number of fixes	Number of tracking nights
2005	Col-1	grav.	F1-1	n.a.	10.4	226	5
		grav.	F1-2	n.a.	9.2	120	4
		grav.	F1-3	n.a.	10.0	217	4
		grav.	F1-4	n.a.	11.8	220	4
		grav.	F1-5	n.a.	12.4	109	4
		lact.	F1-6	n.a.	9.3	191	4
2008	Col-3	grav.	F3-1	H157 550	9.3	174	3
		grav.	F3-2	H157 513	12.5	166	4
		grav.	F3-3	H157 512	12.6	169	3
		post-lac.	F3-4	H157 590	9.8	162	3
		post-lac.	F3-5	H157 591	9.6	159	3
		post-lac.	F3-6	H157 501	9.2	148	3
2009	Col-1	grav.	F1-7	H157 559	9.2	120	3
		grav.	F1-8	H157 622	9.8	122	3
		grav.	F1-9	H157 606	12.4	180	4
		lact.	F1-10	H157 654	9.4	179	4
		lact.	F1-11	H157 604	9.4	257	8
		lact.	F1-12	H157 557	11.4	189	3
		post-lac.	F1-13	H157 580	8.8	107	3
	Col-2	grav.	F2-1	H157 525	9.9	160	3
		grav.	F2-2	H157 532	11.2	159	3
		grav.	F2-3	H157 528	10.2	156	3
		post-lac.	F2-4	H157 539	9.8	221	5
		post-lac.	F2-5	H157 522	8.9	161	4
		post-lac.	F2-6	H157 542	10.1	128	3
	Col-4	post-lac.	F4-1	H157 675	10.2	154	4
		post-lac.	F4-2	H157 677	9.1	133	4
		post-lac.	F4-3	H157 679	10.7	158	4
		post-lac.	F4-4	H157 613	9.5	148	3
		post-lac.	F4-5	H157 686	9.6	226	5
		post-lac.	F4-6	H157 614	10.9	143	3

tems Research Institution, California, USA) with extension Animal Movement (Hooge & Eichenlaub 2000).

Analyses of range use

Home-range overlap

On the basis of the tracking data obtained in 2008 and 2009, where we tracked at least six different females from each colony, we calculated the degree of home range overlap. We used a static interaction analysis, since we did not track all four colonies simultaneously. Thereby, sets of locations are compared without reference to the temporal sequence of locations (Kernohan *et al.* 2001). With regard to the inherent problems of computing overlap in two-dimensional range boundaries, we measured the overlap of UD (Kernohan *et al.* 2001, Fieberg & Kochanny 2005) by applying the Volume of Intersection Index (VI).

$$\text{VI} = \int\limits_{-\infty}^{\infty} \int\limits_{-\infty}^{\infty} \min\left[\hat{U}D_1(x,y), \hat{U}D_2(x,y)\right] dxdy$$

VI denotes the proportion of animal 1's home range that is overlapped by animal 2's home range in a two-dimensional *xy*-plane. $\hat{U}D_1$ is the estimated UD for animal 1 and $\hat{U}D_2$ the estimated UD for animal 2. The outcome potentially ranges between 0 for no overlap to 1 for two home ranges with the same utilization distribution (UD). In order to obtain a more intuitive interpretability, we multiplied VI values, which were originally very small, by 100. Thereafter, they potentially ranged from 0 for no overlap to 100 for two home ranges with the same UD. To determine the degree of inter-colony common space use, we applied the VI index to the foraging ranges of all possible pairs of individuals belonging to different colonies. We determined the degree of intra-colony common space use calculating the VI index for ranges of all possible pairs of individuals within a colony.

Spatial distribution of core areas

To determine where bats foraged in relation to

their neighbouring colonies, we used a subject-centred system of angular units of 60 degrees in a clockwise direction from the vertical. To determine in which directions foraging ranges of a given colony were located, we scored the centroids of each CA and FA within the six angular units. The centre of the angular system was the centroid of the associated roosting site. We defined all angular units containing the centroids of a neighbouring colony as in direction 'towards' neighbouring colonies. Angular units opposite to the centroids of a neighbouring colony were characterized as 'away' from neighbouring colonies.

To compare distances from foraging areas to maternity colonies, we measured linear distances from each animal's centroids of CAs to the centroid of its own roosting range and the centroids of neighboring roosting ranges. Polygon centroids were determined within ArcView using the center of mass extension (Jenness 2006).

Statistical analysis

When conditions of normality were not met, non-parametric tests were applied. The significance level was set at $p < 0.05$. To correct for multiple uses of the same set of observations, we applied Holm's method, i.e. a sequential Bonferroni correction (Rice 1989). Corrected *p* values were then given as α. Non-normally distributed values were expressed as medians and interquartile ranges (IQR), otherwise means and standard deviations (SD) were given.

Results

Colony site fidelity

We analysed colony site fidelity for col-1, which was repeatedly radio tracked. Col-1 used a total of 35 roost trees during the two monitoring summers (2005 and 2009), and during sporadic observations in 2006, 2007 and 2008. The roosting range in 2005 had a size of 5.15 ha. In 2009, it comprised 6.79 ha. Roosting ranges from 2005 and 2009 overlapped by 77% (Fig. 1). We comparatively tracked col-1 in 2005 and 2009.
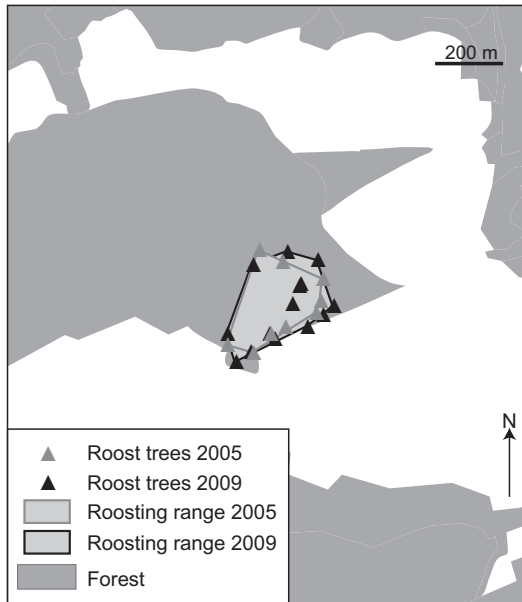
Fig. 1. Roosting ranges and roost trees of a maternity colony of *M. bechsteinii* (col-1) roosting in the Friemholz forest in eastern Luxemburg. Col-1 was repeatedly radio-tracked in 2005 (*n* = 6) and 2009 (*n* = 7).

Fig. 2. Boxplots showing home range (MCP), foraging area (FA) and core area (CA) sizes of *M. bechsteinii* belonging to four maternity colonies (col-1: *n* = 7; col-2, col-3, col-4: each *n* = 6) roosting in the Friemholz forest in eastern Luxemburg. The bar and box denote the median, and the 25th and 75th percentiles, respectively. Whiskers represent the 1.5 interquartile range. Small circles indicate outliners.

Individual MCP sizes were similar in both years (2005: mean ± SD: 37.9 ± 22.9 ha, *n* = 6; 2009: mean ± SD: 39.4 ± 19.5 ha, *n* = 7). CAs were twice as big in 2009 as in 2005 (2009: median ± IQR: 1.8 ± 1.5 ha, *n* = 7; 2005 median ± IQR: 0.9 ± 0.6 ha, *n* = 4). The comparison between both years revealed no significant difference in MCPs and CAs (MCP: Mann-Whitney *U*-test: $U = 19$, $n_1 = 6$, $n_2 = 7$, $p = 0.836$, $\alpha = 0.017$; CA: Mann-Whitney *U*-test: $U = 5$, $n_1 = 4$, $n_2 = 7$, $p = 0.109$, $\alpha = 0.025$). FA sizes in 2009 were significantly larger than in 2005 (Mann-Whitney *U*-test: $U = 2$, $n_1 = 6$, $n_2 = 7$, $p = 0.005$, $\alpha = 0.05$). FAs in 2005 and 2009 had mean sizes of 4.9 ± 1.3 ha and 9.7 ± 2.6 ha, respectively.

Range use

Overall, we documented 124 roost trees with a mean of 31 roosts per colony. The maximum distance between roosts occupied by one colony was 1.3 km. In contrary, neighboring colonies roosted within a distance of 0.5 km between the midpoints of roosting ranges.
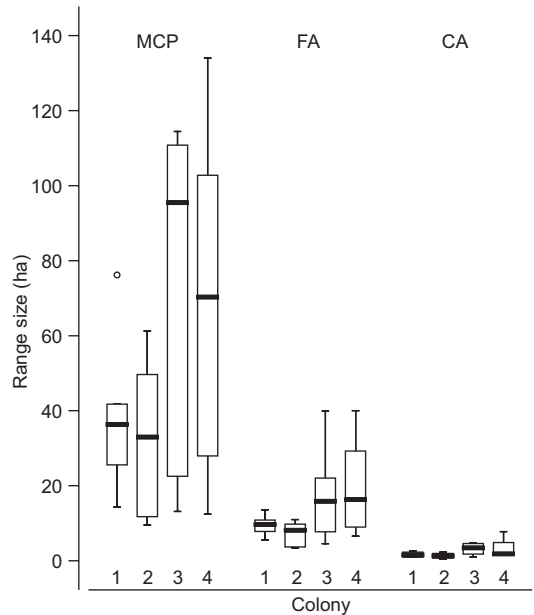
We calculated range use for 25 females from four maternity colonies in 2008 and 2009 (Fig. 2). Individual MCP sizes varied considerably. MCPs included much smaller FAs with yet smaller CAs (Fig. 3). Each bat revisited the same FA over several nights. Most individuals used two FAs and one CA, whereas every animal had at least one FA close to the roosting range (< 540 m). CAs mainly concentrated around the vicinity of the roost trees (32–543 m). Although no statistically significant differences were found in range sizes based on reproductive state, post-lactating females tended to have larger MCPs, FAs and CAs (Table 2). Range sizes during gravidity barely exceeded range sizes during lactation, except for median home range size (Table 2). We found no significant differences in range sizes for females from different colonies or for females of different reproductive states (Table 3). Straight-line distances between roosts and radio fixes ranged from 4 to 2754 m. Reproductive state significantly influenced the distance
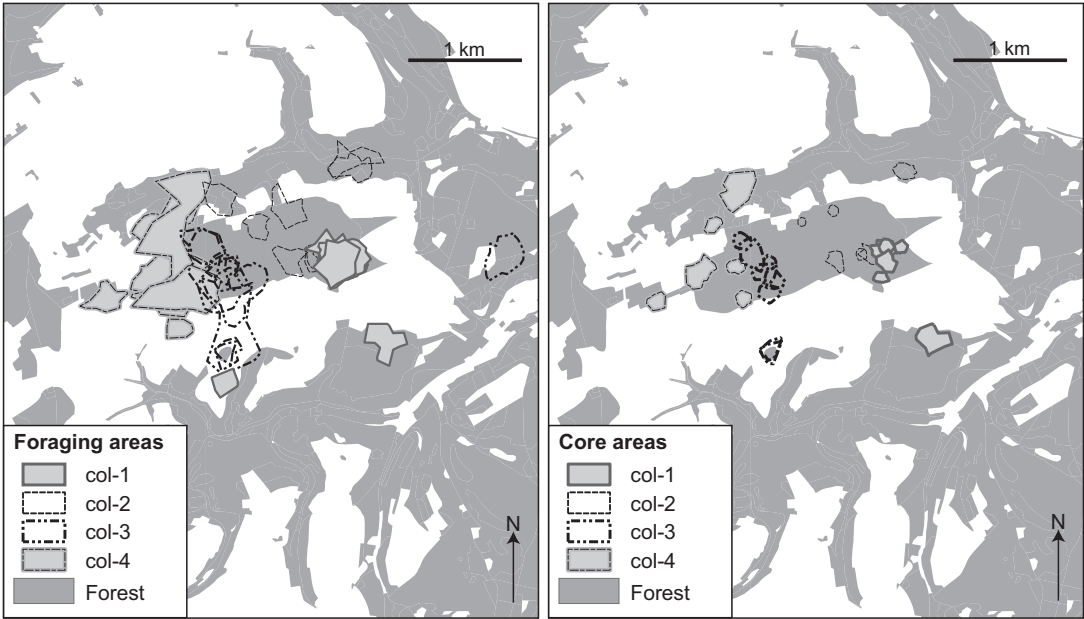
Fig. 3. Foraging areas (left) and core areas (right) of all four colonies of *M. bechsteinii* roosting in the Friemholz forest in eastern Luxemburg. Radio-tracking took place in 2008 (col-3: *n* = 6) and 2009 (col-1: *n* = 7; col-2 and col-4: each *n* = 6).

travelled (Kruskal-Wallis test: H_2 = 89.793; *p* < 0.001). Post-lactating females foraged farthest away from day roosts (median ± IQR: 369 ± 291 m, *n* = 1840). Lactating females foraged closest to the day roosts (median ± IQR: 250 ± 190 m, *n* = 625). Pregnant females traveled somewhat farther to foraging areas than lactating females (median ± IQR: 262 ± 456 m, *n* = 1396). Pair-wise multiple comparisons revealed significant differences between all reproductive states (Dunn's method: grav./lac. *Q* = 2.691, lac./post-lac. *Q* = 8.256, grav./post-lac. *Q* = 7.120; *p* < 0.05).

Intra-colony spatial organization

VI values between FAs within colonies were small (median ± IQR: 13.0 ± 32.3, *n* = 66) and ranged from 0 to 72.7 for all individuals. VI values between CAs were even smaller (median ± IQR: 0 ± 0, *n* = 66) and ranged from 0 to 58.4.

The degree to which FAs and CAs overlapped within each of the four colonies varied significantly (Kruskal-Wallis test: CA: H_3 = 11.946, *p* = 0.008, *α* = 0.010; FA: H_3 = 13.923, *p* = 0.003, *α* = 0.008). CAs within col-2 (Fig. 4) and col-4 overlapped significantly less than CAs within the two other colonies (Table 4). FAs within col-2

Table 2. Range sizes of female *M. bechsteinii* radio-tracked in 2008 and 2009 (*n* = 25). Females belonged to four maternity colonies roosting in the Friemholz forest in eastern Luxemburg. Home range sizes (MCP), foraging area (FA) and core area (CA) sizes for each reproductive state are given.

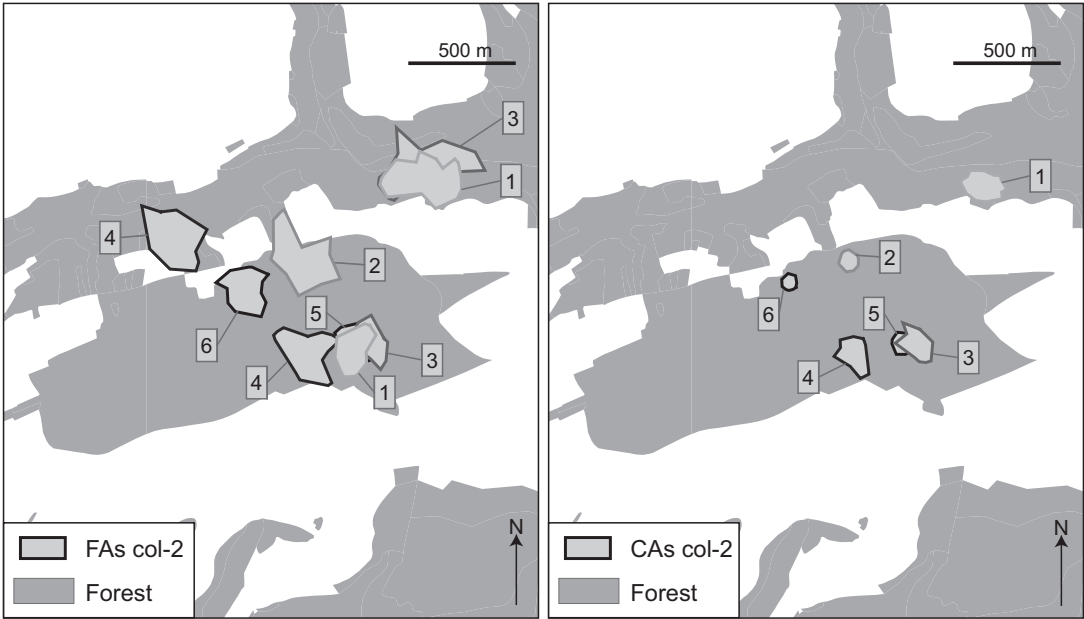|	Gravidity (*n* = 9)		Lactation (*n* = 3)		Post-Lac. (*n* = 13)	
	Median ± IQR (ha)	Range (ha)	Median ± IQR (ha)	Range (ha)	Median ± IQR (ha)	Range (ha)
MCP	41.3 ± 78.8	9.6–114.4	41.8 ± 33.6	31.3–76.2	45.0 ± 59.1	12.4–134.0
FA	18.7 ± 13.2	6.5–35.2	16.4 ± 5.2	12.8–19.7	19.0 ± 14.0	9.1–54.1
CA	2.8 ± 2.0	1.7–5.1	2.4 ± 0.6	1.9–2.7	2.5 ± 1.2	1.9–5.1

Fig. 4. Example of foraging areas (left) and core areas (right) of a colony of female *M. bechsteinii* (col-2: $n = 6$) roosting in the Friemholz forest in eastern Luxemburg. Radio-tracking took place in 2008 (col-3: $n = 6$) and in 2009 (col-1: $n = 7$; col-2 and col-4: each $n = 6$). Numbers indicate different individuals.

overlapped significantly less than FAs within all other colonies.

We found a significant effect of reproductive state on the degree of overlap within colonies (Kruskal-Wallis test: CA: $H_2 = 16.697$, $p < 0.001$, $\alpha = 0.006$; FA: $H_2 = 22.950$, $p < 0.001$, $\alpha = 0.006$). Pair-wise multiple comparisons (Table 5) revealed that CAs of lactating females

$(0 \pm 25.5, n = 18)$ overlapped significantly more than CAs of post-lactating females $(0 \pm 0, n = 66)$. Median VI for gravid females was 0 ± 6.2 $(n = 48)$. FAs significantly differed in relation to reproductive states. FAs of lactating females overlapped most $(32.4 \pm 23.1, n = 18)$, followed by significantly lower overlap of gravid-female FAs $(13.9 \pm 44.2, n = 48)$. FAs of post-lactating females overlapped the least $(6.0 \pm 21.9, n = 66)$.

Inter-colony spatial organization

We determined the degree of inter-colony joint

Table 3. Comparison of range sizes of four different maternity colonies of female Bechstein's bats roosting in the Friemholz forest in eastern Luxemburg. We used a General Linear Mixed Model (GLMM) to compare the sizes of CA, FA, and MCP for different colonies (col-1: $n = 7$; col-2, col-3, col-4: each $n = 6$) and for females of different reproductive stages (grav.: $n = 9$; lac.: $n = 3$; post-lac.: $n = 13$). We included reproductive stage as a fixed factor and colony as a random factor in the GLMM.

	Reproductive state	Colony
CA	$F_{2,19} = 0.175$ $p = 0.841$	$F_{3,19} = 1.262$ $p = 0.316$
FA	$F_{2,19} = 0.029$ $p = 0.972$	$F_{3,19} = 1.757$ $p = 0.189$
MCP	$F_{2,19} = 0.485$ $p = 0.623$	$F_{3,19} = 2.495$ $p = 0.091$

Table 4. Degree of overlap within the four maternity colonies of female Bechstein's bats roosting in the Friemholz forest in eastern Luxemburg (col-1: $n = 7$; col-2, col-3, col-4: each $n = 6$) given as the Volume of Intersection Index (VI, median ± IQR).

Colony	CA	FA
1	8.1 ± 18.3	35.4 ± 21.2
2	0 ± 4.5	4.1 ± 11.9
3	5.5 ± 4.3	14.1 ± 16.8
4	0 ± 0	14.2 ± 18.1

space use calculating the VI index for ranges of all possible pairs of individuals belonging to different colonies. VI values range from 0 for no overlap to 100 for two ranges with the same UD. VI values between FAs of different colonies ranged from 0 to 23.9 (median ± IQR: 0 ± 0, n = 468). For CAs, VI values ranged from 0 to 14.0 (median ± IQR: 0 ± 0, n = 468). There was no significant difference in the degree of inter-colony joint space use among colonies (Kruskal-Wallis test; CA: H_3 = 5.335, p = 0.149, α = 0.0125; FA: H_3 = 0.455, p = 0.929, α = 0.05). No significant difference was found for females in different reproductive states (Kruskal-Wallis test; CA: H_2 = 3.171, p = 0.205, α = 0.017; FA: H_2 = 0.484, p = 0.785, α = 0.025).

Comparing intra- and inter-colony joint space use for FAs, we found that intra-colony overlap was significantly higher than inter-colony overlap (ANOVA: $F_{3,42}$ = 13.037, p = < 0,001, α = 0.005). We performed pair-wise comparisons within each colony (Table 6). Significantly higher intra-colony overlap was found in three colonies. In colony 2, there was no significant difference between intra- and inter-colony overlap.

Across reproductive states, we found a significant difference between intra- and inter-colony overlap of FAs (ANOVA: $F_{1,44}$ = 50.573; p < 0.001, α = 0.007). Pair-wise comparisons for each reproductive state revealed that intra-colony overlap was always significantly higher than inter-colony overlap (Table 6).

A picture of the spatial pattern in foraging ranges was constructed by scoring each CA and FA within the six angular units centred on each colony. Significantly more foraging ranges were oriented away from neighbouring colonies than towards them (Chi-square test; CA:

χ^2 = 4.481, df = 1, p = 0.034, α = 0.05; FA: χ^2 = 10.939, df = 1, p = 0.001, α = 0.025).

To compare distances from foraging ranges to maternity colonies, we measured for each individual linear distances from centroids of CAs to centroids of their own roosting range and to the neighbouring roosting range. Distances from CAs to their own roosting range ranged between 41 and 1289 m (mean ± SD: 360 ± 280, n = 25). Distances to neighboring roosting ranges were between 283 and 1535 m (mean ± SD: 674 ± 293). Distances from CAs to their own roosting range were significantly shorter than to the nearest neighboring roosting range (paired *t*-test: t_{24} = –10.018; p = < 0.001).

Discussion

The purpose of this study was to evaluate potential patterns in the space use of *M. bechsteinii*. Our results from a radio-tracking study on 25 individuals belonging to four neighboring maternity colonies of *M. bechsteinii* showed that spatial organization reflects the social organization of this species. Low intra-colony overlap between foraging ranges indicates that reproductive females partition their colony home range. Furthermore, our results highlight a strong segregation between adjacent colonies. Our data on a colony tracked over several seasons reveal that colonies stay loyal to a defined roosting range.

Table 5. Pair-wise comparisons of VI values (of all CAs and FAs per colony) in different reproductive periods for all four colonies of female Bechstein's bats roosting in the Friemholz forest in eastern Luxemburg based on Dunn's method. For each comparison, Q values with significance levels are given. ** = p < 0.01.

Tracking period	CA	FA
Grav.–lac.	1.160	2.730**
Lac.–post-lac.	2.149	2.440**
Grav.–post-lac.	2.739**	4.578**

Table 6. Pair-wise comparisons of VI values for FAs within and among colonies of female *M. bechsteinii* roosting in the Friemholz forest in eastern Luxemburg. Based on the Holm-Sidak test, t values with significance levels are given for each of the four colonies and for each reproductive state. ** = p < 0.01; *** = p < 0.001.

	Difference (VI intra *vs*. VI inter)
Colony	
1	9.903***
2	1.193
3	3.626***
4	3.309**
Reproductive state	
Grav.	4.475***
Lac.	4.780***
Post-lac.	3.184**

Colony site fidelity

Repeated radio-tracking confirmed the conservative use of home ranges. Usually, environmental changes in forests occur gradually, involving a relatively predictable and consistent prey source for bats. Consequently, females might benefit from a profound site knowledge combined with a constant use of the site. Indeed, females well acquainted with their environment can avoid unnecessary flight costs.

Females used many different roost trees, but were loyal to their roosting range. This is consistent with results from other studies on Bechstein's bats (Kerth & König 1999, Kerth *et al.* 2002b) and studies on other bat species (Vonhof & Barclay 1996, O'Donnell & Sedgeley 1999, Willis & Brigham 2004). Possibly, roosting range fidelity in combination with fission fusion behavior facilitates exploring new roosts and thus provides communal knowledge of many potential roost trees (Lewis 1995, Kerth *et al.* 2000, 2001a, 2006). This is beneficial, since forest dwelling bats have changing preferences for different abiotic roost characteristics and since natural roosts in tree holes are not permanent (Kerth *et al.* 2001a).

Repeated radio-tracking revealed no significant difference in range use between the years 2005 and 2009. Our findings are consistent with other studies on Bechstein's bats. The observed pattern may be a result of strong loyalty to foraging ranges during the season and even over several years (Kerth *et al.* 2001b). Hunting site fidelity is also reported for other species in Europe [*Myotis myotis*, (Audet 1990); *Myotis emarginatus*, (Krull *et al.* 1991); *Plecotus auritus*, (Entwistle *et al.* 1996); *Myotis daubentonii*, (Dietz & Kalko 2007a), *Barbastella barbastellus* (Hillen *et al.* 2009)]. For Bechstein's bats, conservative space use probably reflects the importance of profound habitat knowledge (Kerth *et al.* 2000).

Individual foraging ranges

Our data revealed that individual bats seemed to avoid too much overlap between their ranges. While median overlap of FAs was low, median overlap of CAs was even lower with values close to zero. We conclude that this might be the result of individual segregation in order to avoid the depletion of resources.

There are studies on intraspecific spacing behavior in species with different foraging strategies. For example, aerial foraging species specialized on ephemeral prey are assumed to benefit from improved foraging efficiency through information transfer during times of high food availability (Dechmann *et al.* 2010). In contrast to species that feed on airborne prey, gleaning bats seem to be solitary foragers, as reported in several studies (Rydell 1989, Brigham 1991, O'Donnell 2001). An even distribution of prey and constant food availability might benefit solitary foragers. Since female Bechstein's bats exploit homogenous and predictable food resources, profound site knowledge could be crucial (Kerth *et al.* 2000, 2001b), and increasing hunting efficiency may select for foraging site fidelity (Kapfer *et al.* 2007). According to optimal foraging theory (Stephens & Krebs 1986), natural selection leads to the evolution of a behavior that maximizes foraging efficiency (Lacki *et al.* 2007). Within a species, individuals have similar morphology and echolocation call structures, and consequently make use of the same habitat and prey types. This fact together with their strong loyalty to foraging sites might have selected for a mechanism to avoid resource depletion. The spatial partitioning observed in this study may thus be an evolutionary strategy to avoid resource depletion and to lead to reliable available food sources for every colony member throughout the season and even over several years.

Home ranges of colonies

The observed foraging pattern leads to the assumption that coexistence between neighboring colonies is facilitated through spatial segregation and thus resource partitioning. Our results reveal a pronounced spatial segregation between the four colonies. Despite the fact that roosting ranges lay close to each other, colonies were strictly separated. Foraging ranges were mainly mutually exclusive for all colonies.

Distances between midpoints of roosting ranges amount to less than half of the longest distance between roosts of the same colony. This strict separation reflects the high degree of natal philopatry in this species (Kerth *et al*. 2000, 2002a, 2002b). It indicates a segregation of the resource 'roosts' between different colonies. This is in accordance with results from a confrontation test. It demonstrated that female *M. bechsteinii* show aggressive behavior to prevent the intrusion of females from a foreign colony into a occupied roost (Kerth *et al*. 2002b).

The observed roosting range segregation in female Bechstein's bats reflects social organization and might be the result of a past selection favoring spatially segregated foraging ranges as 'the ghost of competition past' (Connell 1980). The high degree of natal philopatry as well as maternal inheritance of home ranges might result in this significant spatial segregation despite the absence of current competition or interference while foraging.

Bechstein's bats have individual home ranges (Kerth *et al*. 2001b, Dietz & Pir 2009, Napal *et al*. 2010) and the overlap between foraging areas of a given bat in two years is significantly higher than the overlap between foraging areas of different individuals (Kerth & Melber 2009). In the present study, we showed that the segregation of different colonies was even more pronounced than the segregation of individuals within a colony. Additionally, females of a given colony not only had separate foraging ranges; they even preferably chose foraging ranges away from neighbouring colonies instead of foraging areas closer to them. This indicates that spatial organization reflects the social organization of colonies in Bechstein's bats, where females of different colonies live in very closed societies (Kerth *et al*. 2000).

Coexisting animal species frequently differ in resource use in at least one niche dimension. In bats, there is evidence for interspecific resource partitioning through differences in habitat use and diet (Saunders & Barclay 1992, Arlettaz 1999, Siemers & Swift 2006b). Even for very similar cryptic species, it is assumed that coexistence is facilitated through spatial segregation (Nicholls & Racey 2006b, 2006a). Conversely, for studies on intraspecific spacing

behaviour results are inconsistent. Rydell (1986) documented feeding territoriality including aggressive chases and vocalizations for female *E. nilssonii*. Alternatively, there are species that feed at least partially in groups or with considerable overlap among foraging areas: [*Eptesicus nilssoni*: (de Jong 1994); *E. serotinus*: (Catto *et al*. 1996); *M. lucifugus*: (Barclay 1982); *N. humeralis*: (Wilkinson 1992); *Nyctalus leisleri*: (Shiel *et al*. 1999); *Pipistrellus pipistrellus*: (Racey & Swift 1985); *M. capaccinii*: (Almenar *et al*. 2006)]. Aggregation of individuals that forage on airborne prey is suggested to be affected by distribution of the prey. Aerial foraging species are assumed to benefit from information transfer about high prey occurrences (Dechmann *et al*. 2010). In contrast, solitary foraging has been found in several gleaning bat species (Racey & Swift 1985, Audet 1990, Entwistle *et al*. 1996, Siemers & Swift 2006a). Moreover, individuals within a species have many fundamental features in common. Therefore, coexistence within a species might also be facilitated through spatial segregation. For example, many group living species exclude neighboring groups from their core feeding range (Herrera & Macdonald 1989, Stewart *et al*. 1997).

In many cases, competing individuals do not interact with one another directly. For example, if a feeding range has been overlapped by the 'resource depletion zone' of a neighboring individual, competition may be described as exploitation. Mutual avoidance can create range exclusion without active defense (Kaufmann 1983). Within a species, it has been shown that avoidance of exploitation competition between groups of the European badger (*Meles meles*) may be an important factor in shaping this species' home ranges (Stewart *et al*. 1997).

Implications for conservation

Our results suggest that the spatial organization of female Bechstein's bats is determined by foraging efficiency. During energy demanding phases of reproduction, we found a significantly more pronounced though still low overlap of individual inner range cores within colonies. We can not exclude that this finding is a side effect

of the unbalanced study design, since reproductive stages of females were not equally spread across colonies. Higher overlap was not a result of different range sizes. However, we found significant differences in straight-line distances between roosts and radio fixes depending on reproductive states. The concentration of foraging activity around roosting ranges during lactation may result from constraints imposed by time and energy required for nursing. The strong segregation of individual CAs even during lactation is remarkable and leads to the assumption that exclusive CAs implies advantages in terms of foraging efficiency. Furthermore, neighboring colonies preferably foraged close to their colony roosting range, but still showed almost no overlap with foraging ranges from other colonies.

This approach provides implications for the protection of Bechstein's bats and assumedly also for other bat species with a similar social organization, e.g. *Barbastella barbastellus* (Hillen *et al*. 2009). Our data advocate that conservation measures should concentrate on core areas of habitat usage. Therefore, it is crucial to identify the essential characteristics of core areas for feeding and roosting (Lacki *et al*. 2007). For the conservation of maternity colonies, it is vitally important to protect potential roosting sites with a high amount of old growth woodland that are well connected to foraging habitats providing high quality prey and enough space for the exclusive usage of core areas for all colony members (Dietz & Pir 2009). Changes in natural landscapes occur gradually. Consequently, in the light of evolution, female Bechstein's bats benefit from profound site knowledge and conservative use of these sites (*see* Hillen *et al*. 2009). Knowledge about the spatial organization of female Bechstein's bats provides an understanding of how bat populations would respond to changing land or forest management. It also highlights the fact that protection strategies have to be effective in the long term. Our study offers the possibility to estimate intra-specific spatial intersection between and within colonies, and provides a more precise prediction of effective population size and space requirements. As intensive anthropogenic land use and forest management often results in a pattern of degraded, fragmented or unsuitable habitats (*see* Hayes &

Loeb 2007), we expect high population densities only in well-structured mature woodlands providing high quality core areas for feeding and roosting. Our data highlight the fact that habitat degradation or destruction in a colony's home range cannot be compensated without negative effects by selecting new sites. Available habitats nearby might already be saturated and used by other colony members or even other colonies.

Acknowledgements

References

Almenar, D., Aihartza, J., Goiti, U., Salsamendi, E. & Garin, I. 2006: Habitat selection and spatial use by the trawling bat *Myotis capaccinii* (Bonaparte, 1837). — *Acta Chiropterologica* 8: 157–167.

Arlettaz, R. 1999: Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. — *Journal of Animal Ecology* 68: 460–471.

Audet, D. 1990: Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). — *Journal of Mammalogy* 71: 420–427.

Barclay, R. M. 1982: Night roosting behavior of the little brown bat, *Myotis lucifugus*. — *Journal of Mammalogy* 63: 464–474.

Brigham, R. M. 1991: Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). — *Canadian Journal of Zoology* 69: 117–121.

Calenge, C. 2006: The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. — *Ecological Modelling* 197: 516–519.

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. — *Journal of Zoology* 238: 623–633.

Clutton-Brock, T., Guinness, F. & Albon, S. 1982: *Red deer: behaviour and ecology of two sexes*. — University of

Chicago Press, Chicago.

Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of competition past. — *Oikos* 35: 131–138.

de Jong, J. 1994: Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssonii*, in a hemoboreal coniferous forest. — *Mammalia* 58: 535–548.

de Jong, J. 1995: Habitat use and species richness of bats in a patchy landscape. — *Acta Theriologica* 40: 237–248.

de Ruiter, J. & Geffen, E. 1998: Relatedness of matrilines, dispersing males and social groups in long-tailed macaques (*Macaca fascicularis*). — *Proceedings of the Royal Society of London B* 265: 79–87.

Dechmann, D., Kranstauber, B., Gibbs, D. & Wikelski, M. 2010: Group hunting — a reason for sociality in molossid bats? — *PLoS ONE* 5(2): e9012, doi:10.1371/journal.pone.0009012.

Dietz, M. & Kalko, E. K. V. 2007a: Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentonii*. — *Canadian Journal of Zoology* 85: 653–664.

Dietz, M. & Kalko, E. K. V. 2007b: Fledermäuse als Schlüsselarten für einen ökosystem-orientierten Naturschutz im Wald. — *Natschutz Biol Vielfalt* 60: 101–106.

Dietz, M. & Pir, J. 2009: Distribution and habitat selection of *Myotis bechsteinii* in Luxembourg: implications for forest management and conservation. — *Folia Zoologica* 58: 327–340.

Entwistle, A. C., Racey, P. A. & Speakman, J. R. 1996: Habitat exploitation by a gleaning bat, *Plecotus auritus*. — *Proceedings of the Royal Society Biological Sciences B* 351: 921–931.

Fieberg, J. & Kochanny, C. O. 2005: Quantifying home-range overlap: the importance of the utilization distribution. — *Journal of Wildlife Management* 69: 1346–1359.

Frere, C. H., Kruetzen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., Connor, R., Bejder, L. & Sherwin, W. B. 2010: Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. — *Animal Behaviour* 80: 481–486.

Getz, W. M., Fortmann-Roe, S., Cross, P., Lyons, A. & Ryan, S. 2007: LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization distributions. — *PLoS ONE* 2(2): e207, doi:10.1371/journal.pone.0000207.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T. & Wray, S. 1990: Home-range analysis using radio-tracking data — a review of problems and techniques particularly as applied to the study of mammals. — *Mammal Review* 20: 97–123.

Hayes, J. P. & Loeb, S. C. 2007: The influences of forest management on bats in North America. — In: Lacki, M. J., Hayes, J. P. & Kurta, A. (eds.), *Bats in forests: conservation and management*: 207–235. Johns Hopkins University Press, Baltimore, Maryland.

Heinrich, C., Junck, C., Takla, M. & Sowa, F. 2002: *Naturwaldkonzept für Luxemburg*. — Das vorgeschlagene Schutzgebietsnetz; Olm, Biologesch Statioun Westen.

Herrera, E. A. & Macdonald, D. W. 1989: Resource utilization and territoriality in group-living capybaras (*Hydro-*

choerus hydrochaeris). — *Journal of Animal Ecology* 58: 667–679.

Hillen, J., Kiefer, A. & Veith, M. 2009: Foraging site fidelity shapes the spatial organisation of a population of female western barbastelle bats. — *Biological Conservation* 142: 817–823.

Hooge, P. N. & Eichenlaub, B. 2000: *Animal movement extension to Arcview. ver. 2.0*. — U.S. Geological Survey, Anchorage, AK, USA.

Jenkins, E. V., Laine, T., Morgan, S. E., Cole, K. R. & Speakman, J. R. 1998: Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. — *Animal Behaviour* 56: 909–917.

Jenness, J. 2006: *Center of Mass (center_of_mass.avx) extension for ArcView 3.x*. — Jenness Enterprises. [Available at http://www.jennessent.com/arcview/centermass.htm].

Jones, G. & Rydell, J. 1994: Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. — *Philosophical Transactions of the Royal Society of London B* 346: 445–455.

Kaňuch, P., Danko, Š., Celuch, M., Krištín, A., Pjenčák, P., Matis, Š. & Šmídt, J. 2008: Relating bat species presence to habitat features in natural forests of Slovakia (central Europe). — *Mammalian Biology* 73: 147–155.

Kapfer, G., Rigot, T., Holsbeek, L. & Aron, S. 2007: Roost and hunting site fidelity of female and juvenile Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) (Chiroptera: Vespertilionidae). — *Mammalian Biology* 73: 267–275.

Kapfer, G., Rigot, T., Holsbeek, L. & Aron, S. 2008: Roost and hunting site fidelity of female and juvenile Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) (Chiroptera : Vespertilionidae). — *Mammalian Biology* 73: 267–275.

Kaufmann, J. H. 1983: On the definitions and functions of dominance and territoriality. — *Biological Reviews (Cambridge)* 58: 1–20.

Kernohan, B. J., Gitzen, R. A. & Millspaugh, J. J. 2001: Analysis of space use and movements. — In: Marzluff, M. a. (ed.), *Radiotelemetry and animal populations*: 125–166. Academic Press, San Diego, California, USA.

Kerth, G. & König, B. 1999: Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). — *Behaviour* 136: 1187–1202.

Kerth, G. & Melber, M. 2009: Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. — *Biological Conservation* 142: 270–279.

Kerth, G., Mayer, F. & König, B. 2000: Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. — *Molecular Ecology* 9: 793–800.

Kerth, G., Weissmann, K. & Konig, B. 2001a: Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. — *Oecologia* 126: 1–9.

Kerth, G., Wagner, M. & König, B. 2001b: Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). — *Behavioral Ecology and Sociobiology* 50: 283–291.

Kerth, G., Mayer, F. & Petit, E. 2002a: Extreme sex-biased dispersal in the communally breeding, nonmigratory

Bechstein's bat (*Myotis bechsteinii*). — *Molecular Ecology* 11: 1491–1498.

Kerth, G., Safi, K. & König, B. 2002b: Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteinii*). — *Behavioral Ecology and Sociobiology* 52: 203–210.

Kerth, G., Ebert, C. & Schmidtke, C. 2006: Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. — *Proceedings of the Royal Society Biological Sciences B* 273: 2785–2790.

Krippel, Y. 2005: *Die Kleine Luxemburger Schweiz: geheimnisvolle Felsenlandschaft im Wandel der Zeit.* — Société des naturalistes luxembourgeois, Musée national d'histoire naturelle & Administration des eaux et forêts, Luxembourg.

Krull, D., Schumm, A., Metzner, W. & Neuweiler, G. 1991: Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). — *Behavioral Ecology and Sociobiology* 28: 247–253.

Lacki, M. J., Amelon, S. K. & Baker, M. D. 2007: Foraging ecology of bats in forests. — In: Lacki, M. J., Hayes, J. P. & Kurta, A. (eds.), *Bats in forests: conservation and management*: 83–127. Johns Hopkins University Press, Baltimore, Maryland.

Lewis, S. E. 1995: Roost fidelity of bats: a review. — *Journal of Mammalogy* 76: 481–496.

Limpens, H. J. G. A. & Kapteyn, K. 1991: Bats, their behaviour and linear landscape elements. — *Myotis* 29: 39–48.

Metheny, J. D., Kalcounis-Rueppell, M. C., Bondo, K. J. & Brigham, R. M. 2008: A genetic analysis of group movement in an isolated population of tree-roosting bats. — *Proceedings of the Royal Society B* 275: 2265–2272.

Michener, G. 1983: Kin identification, matriarchies, and the evolution of sociality in ground dwelling sciurids. — In: Eisenberg, J. & Kleiman, D. (eds.), *Advances in the study of mammalian behavior*: 528–572. American Society of Mammalogists, Shippenburg, Spec. Publ. 7.

Millspaugh, J. J. & Marzluff, J. M. 2001: *Radio tracking and animal populations.* — Academic Press, San Diego, California, USA.

Mohr, C. O. 1947: Table of equivalent populations of North American small mammals. — *American Midland Naturalist* 37: 223–249.

Moyer, M. A., McCown, J. W., Eason, T. H. & Oli, M. K. 2006: Does genetic relatedness influence space use pattern? A test on Florida black bears. — *Journal of Mammalogy* 87: 255–261.

Napal, M., Garin, I., Goiti, U., Salsamendi, E. & Aihartza, J. 2010: Habitat selection by *Myotis bechsteinii* in the southwestern Iberian Peninsula. — *Annales Zoologici Fennici* 47: 239–250.

Nicholls, B. & Racey, P. 2006a: Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. — *Ecography* 29: 697–708.

Nicholls, B. & Racey, P. 2006b: Contrasting home-range size and spatial partitioning in cryptic and sympatric pipistrelle bats. — *Behavioral Ecology and Sociobiology*

61: 131–142.

Norberg, U. M. & Rayner, J. M. V. 1987: Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. — *Philosophical Transactions of the Royal Society of London B* 316: 335–427.

O'Donnell, C. F. J. 2001: Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. — *Journal of Zoology (London)* 253: 253–264.

O'Donnell, C. F. J. & Sedgeley, J. A. 1999: Use of roosts by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate rainforest in New Zealand. — *Journal of Mammalogy* 80: 913–923.

Packer, C. 1986: The ecology of sociality in felids. — In: Rubenstein, D. & Wrangham, R. (eds.), *Ecological aspects of social evolution*: 429–451. Princeton University Press, Princeton, NJ.

R Development Core Team 2009: *R: A language and environment for statistical computing.* — R Foundation for Statistical Computing, Vienna, Austria.

Racey, P. A. 1974: Ageing and assessment of reproductive status of pipistrelle bats, *Pipistrellus pipistrellus*. — *Journal of Zoology (London)* 173: 264–271.

Racey, P. A. 2009: Reproductive assessment in bats. — In: Kunz, T. H. & Parsons, S. (eds.), *Behavioural and ecological methods for the study of bats*: 249–264. Johns Hopkins University Press, Baltimore.

Racey, P. A. & Swift, S. M. 1985: Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. — *Journal of Animal Ecology* 54: 205–215.

Racey, P. A. & Entwistle, A. C. 2003: Conservation ecology of bats. — In: Kunz, T. H. & Fenton, M. B. (eds.), *Bat ecology*: 680–743. University of Chicago Press, London.

Rice, W. R. 1989: Analyzing tables of statistical tests. — *Evolution* 43: 223–225.

Rossiter, S. J., Jones, G., Ransome, R. D. & Barratt, E. M. 2002: Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). — *Behavioral Ecology and Sociobiology* 51: 510–518.

Rydell, J. 1986: Feeding territoriality in female northern bats, *Eptesicus nilssoni*. — *Ethology* 72: 329–337.

Rydell, J. 1989: Food habits of northern (*Eptesicus nilssonii*) and brown long-eared (*Plecotus auritus*) bats in Sweden. — *Holarctic Ecology* 12: 16–20.

Saunders, M. B. & Barclay, R. M. R. 1992: Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. — *Ecology* 73: 1335–1345.

Shiel, C. B., Shiel, R. E. & Fairley, J. S. 1999: Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. — *Journal of Zoology (London)* 249: 347–358.

Siemers, B. & Swift, S. 2006a: Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis natteri* (Chiroptera: Vespertilionidae). — *Behavioral Ecology and Sociobiology* 59: 373–380.

Siemers, B. M. & Swift, S. M. 2006b: Differences in sensory

ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). — *Behavioral Ecology and Sociobiology* 59: 373–380.

Stephens, D. W. & Krebs, J. R. 1986: *Foraging theory*. — Princeton University Press, Princeton, New Jersey.

Stewart, P., Anderson, C. & Macdonald, D. 1997: A mechanism for passive range exclusion: evidence from the European badger (*Meles meles*). — *Journal of Theoretical Biology* 184: 279–289.

Vonhof, M. J. & Barclay, R. M. R. 1996: Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. — *Canadian Journal of Zoology* 74: 1797–1805.

Weber, N., Kalko, E. K. V. & Fahr, J. 2009: A first assessment of home range and foraging behaviour of the African long-tongued bat *Megaloglossus woermanni* (Chiroptera: Pteropodidae) in a heterogeneous landscape within the Lama Forest Reserve, Benin. — *Acta Chiropterologica* 11: 317–329.

Weinbeer, M. & Kalko, E. K. V. 2004: Morphological characteristics predict alternate foraging strategy and microhabitat selection in the orange-bellied bat, *Lampronycteris brachyotis*. — *Journal of Mammalogy* 85: 1116–1123.

White, G. C. & Garrott, R. A. 1990: *Analysis of wildlife radio-tracking data*. — Academic Press, San Diego, California.

Wilkinson, G. S. 1992: Information transfer at evening bat colonies. — *Animal Behaviour* 44: 501–518.

Willis, C. K. & Brigham, R. M. 2004: Roost switching, roost sharing and social cohesion: fortest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission-fusion model. — *Animal Behaviour* 68: 495–505.

Wolz, I. 2002: Beutespektren der Bechsteinfledermaus (*Myotis bechsteinii*) und des Großen Mausohrs (*Myotis myotis*) aus dem Schnaittenbacher Forst in Nordbayern. — In: Meschede, A., Heller, K.-G. & Boye, P. (eds.), *Ökologie, Wanderungen und Genetik von Fledermäusen in Wäldern*: 71: 213–224. Landwirtschaftsverlag, Münster.

Wronski, T. & Apio, A. 2006: Home-range overlap, social vicinity and agonistic interactions denoting matrilineal organisation in bushbuck, *Tragelaphus scriptus*. — *Behavioral ecology and sociobiology* 59: 819–828.