Intra- and interspecific competition in western barbastelle bats (*Barbastella barbastellus*, SCHREBER 1774):

Niche differentiation in a specialised bat species, revealed via radio-tracking.

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Western barbastelle bats in their tree roost.
Background: View of the brook valley 'Ahringsbachtal'.

Contents.

Abstract.

In the present thesis I examined individual and sex-specific habitat use and site fidelity in the western barbastelle bat, *Barbastella barbastellus*, using data from a four-year monitoring in a Special Area of Conservation in Rhineland-Palatinate, Germany. The western barbastelle occurs in central and southern Europe from Portugal to the Caucasus, but is considered to be rare in large parts of its range. Up to now, long-term field studies to assess interannual site fidelity and the possible effects of intra- and interspecific competition have not been studied in this species. Nevertheless, such data provide important details to estimate the specific spatial requirements of its populations, which in turn can be incorporated in extended conservation actions.

I used radio-telemetry, home range analyses und automated ultrasound detection to assess the relation between landscape elements and western barbastelle bats and their roosts. In addition, I estimated the degree of interspecific niche overlap with two selected forest-dwelling bat species, Bechstein's bat (*Myotis bechsteinii*) and the brown long-eared bat (*Plecotus auritus*).

Intra- and interannual home range overlap analyses of female *B. barbastellus* revealed that fidelity to individual foraging grounds, i.e. a traditional use of particular sites, seems to effect the spatial distribution of home ranges more than intraspecific competition among communally roosting females. The results of a joint analysis of annual maternity roost selection and flight activities along commuting corridors highlight the necessity to protect roost complexes in conjunction with commuting corridors.

Using radio-tracking data and an Euclidean distance approach I quantified the sex-specific and individual habitat use by female and male western barbastelle bats within their home ranges. My data indicated a partial sexual segregation in summer habitats. Females were found in deciduous forest patches and preferably foraged along linear elements within the forest. Males foraged closer to forest edges and in open habitats.

Finally, I examined the resource partitioning between the western barbastelle bat and two syntopic bat species with a potential for interspecific competition due to similarities in foraging strategies, prey selection and roost preferences. Simultaneous radio-tracking of mixed-species pairs revealed a partial spatial separation of the three syntopic bat species along a gradient from the forest to edge habitats and open landscape. Long-eared bats were found close to open habitats which were avoided by the other two species. *B. barbastellus* preferred linear landscape elements (edge habitats) and forests, *M. bechsteinii* also preferred forest habitats. Only little overlap in terms of roost structure and tree species selection was found.

General introduction.

Bat communities are unique in terms of species richness, niche diversity and life history characteristics, which are unusual for mammals of small body size (Kunz & Fenton, 2003). Compared to other mammals, bats show a pronounced seasonality, with specific requirements on each of their seasonal habitats: summer (maternity and male) roosts, mating places and hibernacula (temperate-zone species). The majority of the known bat species needs a set of suitable roosts embedded in a matrix of a variety of habitat patches that provide high quality food resources for at least the reproductive period. Most bat species forage close to each other on the same food resource, flying, and non-flying insects. This requires resource partitioning in one or more niche dimensions: foraging time, foraging habitat and prey type.

Numerous field studies on the home range sizes, flight distances and habitat use of bats are available. They used radio telemetry techniques to either observe individuals via 'homing in on the animal' or synchronised triangulation by two or more observers (White & Garrot, 1990; Millspaugh & Marzluff, 2001). Individuals of the same species and, in particular, members of the same maternity roost, have similar spatial and, if they are in the same reproductive status, energetic requirements and therefore occupy the same ecological niche. To minimise intraspecific competition, mechanisms of resource partitioning within a population's home range should exist, e.g. traditional range use vs. intra- and interspecific competition. Intraspecific interactions between individuals, either simultaneous foraging or exclusive utilisation of individual foraging areas, have been reported (Robinson & Stebbings, 1997; Winkelmann *et al.*, 2000; Kerth *et al.*, 2001; Winkelmann *et al.*, 2003; Goiti *et al.*, 2006). In addition, syntopic bats evolved particular foraging strategies and echolocation calls, and thus became specialised in foraging (micro-) habitats, prey types and/or roosts. Competition can be avoided via selecting different foraging habitats (Nicholls & Racey, 2006), as with the species pair *Myotis myotis* and *M. blythii* (Arlettaz, 1999). Nevertheless, interspecific competition in other, non-sibling species, remains unclear.

In my thesis, I examined habitat use of a population of the western barbastelle bat, *Barbastella barbastellus* (SCHREBER, 1774), via synchronised radio-tracking and automated ultrasound detection in the Special Area of Conservation (SAC) 'Ahringsbachtal' near Frankfurt-Hahn airport, Rhineland-Palatinate, south-western Germany (49°55'38.78" N, 7°13'30.74" E). I included data collected from 2004 to 2007 for detailed analyses. The SAC

'Ahringsbachtal' harbours a newly-discovered maternity colony of the western barbastelle bat in Rhineland-Palatinate (discovered in 2003, Cyrus *et al.*, 2004), the only known maternity colony until 2005. The area also hosts several male roosts, underground swarming sites and hibernacula (abandoned mines). The local population of the western barbastelle bat is subject to a monitoring programme (2004-2010) to assess the effects of the expansion of the Frankfurt-Hahn airport on the local bat fauna, with a special focus on three species protected by European law under the Habitats Directive 92/43/EEC, Annex II: The western barbastelle bat (*B. barbastellus*), Bechstein's bat (*Myotis bechsteinii*) and the Greater mouse-eared bat (*Myotis myotis*).

Individual site fidelity and territorial interaction within and among species may substantially determine the space required by a population to be viable. Therefore, the design of effective nature reserves and action plans has to be based on a detailed knowledge of the factors that shape the spatial structure of a local population or species community. In **Chapter I**, I assessed home range sizes and the spatial distribution of 12 adult females of the *B. barbastellus* maternity colony. I specifically focused on the mechanisms that allowed resource partitioning among colony members and for the first time tested for intraspecific competition to answer the question, how colony members partition their population home range. In addition, I tested for individual foraging site fidelity via home range overlap of individuals that were tracked in two or more years.

Roosts are an important resource for bats, especially for female bats, because they need numerous roosts with different microclimatic features and space to establish maternity colonies. Qualitative roost characteristics, roost niche overlap between species and the potential for interspecific competition have been investigated extensively (Ruczynski & Bogdanowicz, 2005; Barclay & Kurta, 2007; Arnett & Hayes, 2009). Tree-dwelling bats often have high demands on roost quality (e.g., cavity size, ambient temperature, humidity). They have to compensate the lower stability of tree roosts by roost-switching and exploitation of new roosts (Lewis, 1995; Kerth *et al.*, 2006; Barclay & Kurta, 2007). Nevertheless, some studies reported interannual roost site and/or roosting area fidelity (Foster & Kurta, 1999; Barclay & Brigham, 2001; Veilleux & Veilleux, 2004). An additional factor that shapes the spatial structure of roosting areas is the connectivity between habitat patches (e.g. different roosting and foraging areas). Short commuting distances to foraging habitats and available commuting corridors, e.g. linear landscape elements, influence roost selection of bats

(Entwistle *et al*., 1996; Racey & Entwistle, 2003). Due to the rarity of the western barbastelle bat, quantitative data about the structure of roost areas, e.g. the existence of core areas, and the intra- and interannual fidelity to these core areas and commuting corridors, are lacking. In **Chapter II,** I therefore analysed the density and spatial arrangement of roosts, and interannual roost fidelity of the female western barbastelles in the SAC 'Ahringsbachtal'. I used radio-tracking to locate the colony roosts and automated ultrasound detector units to measure and characterise activity patterns at linear landscape elements and different forest locations to determine their function of these landscape elements, e.g. as commuting corridor, and to assess the fidelity to such landscape elements.

I already mentioned above the possible existence of intraspecific competition in bat species. Previous studies showed that sexual segregation in summer habitats, i.e. the sex-specific use of foraging areas which may comprise different habitat structures and provide different prey densities, may reduce inter-sexual competition. Different energetic requirements of females and males (Speakman & Thomas, 2003) and competitive behaviour in males are assumed to be important factors that drive sexual segregation in bats (Senior *et al*., 2005). They have been confirmed for some species, e.g. parti-coloured bats (*Vespertilio murinus*, Safi *et al*., 2007) and Daubenton's bats (*Myotis daubentonii*, Senior *et al*., 2005; Dietz *et al*., 2006). The western barbastelle bat is described as a 'forest bat' and an edge habitat specialist (Meschede & Heller, 2000; Greenaway, 2004). Studies on the echolocation behaviour and the signal repertoire of the western barbastelle revealed an adaptation to 'edge habitats' (forest edges, tree crowns; Denzinger *et al*., 2001; Barataud, 2004) which are used as 'linear foraging grounds' to aerial hawk moths, their main prey, and small dipterans (Beck, 1995; Sierro & Arlettaz, 1997; Rydell *et al*., 1996; Andreas *et al*., 2008). Available literature on the habitat use of *B. barbastellus*, however, does not provide information on sex-specific and individual variability. I therefore investigated the differential habitat use of female and male western barbastelle bats, with special emphasis on linear landscape elements by applying a distance-based approach (**Chapter III**).

Mechanisms of resource partitioning in bat assemblages have been subject of several studies within the fields of ecomorphology and behavioural ecology (Saunders & Barclay, 1992; Siemers & Schnitzler, 2004; Giannini & Kalko, 2005; Schoeman & Jacobs, 2008). However, only few studies focussed on the ability of bats to react individually and flexible to available foraging habitats, roosts and prey densities. The SAC 'Ahringsbachtal' harbours 15 bat species, including several 'forest bats' (Meschede & Heller, 2000), e.g. Bechstein's bat (*Myotis bechsteinii*), Natterer's bat (*M. nattereri*), brown long-eared bat (*Plecotus auritus*), Leisler's bat (*Nyctalus leisleri*), Noctule (*Nyctalus noctula*) and Nathusius' pipistrelle (*Pipistrellus nathusii*). Two of them, Bechstein's bat and the brown long-eared bat, show some niche overlap with the western barbastelle bat in terms of prey selection, foraging style and selection of foraging and roosting habitat. This bears a potential for competition for productive foraging sites in areas where colonies of western barbastelles, brown long-eared and Bechstein's bats live in syntopy.

Interspecific competition for food resources, although widely discussed (e.g. in *Eptesicus nilssonii* and *Pipistrellus pipistrellus* (Rydell, 1992), has rarely been investigated. Western barbastelles and brown long-eared bats show considerable overlap in prey selection, since both prefer (eared) moths and dipterans (e.g. crane-flies, *Tipula* spec.; Rydell, 1989; Beck, 1995; Andreas *et al*., 2008). *Plecotus auritus* uses both aerial hawking and foliage and ground gleaning as foraging strategies (Anderson & Racey, 1991). Bechstein's bats also use aerial hawking and gleaning strategies, feeding on various insects and spiders, but moths can be an important prey type (Wolz, 1993; Wolz, 2002). *Barbastella barbastellus* is an aerial-hawking bat with a potential for foliage gleaning (Rydell *et al*. (1996). A high potential for roost niche overlap is obvious for the cavity-dwelling species *M. bechsteinii* and *P. auritus*, since both use tree roosts, e.g. woodpecker holes and other cavities (Fuhrmann & Godmann, 1994; Kerth & König, 1999; Greenaway & Hill, 2005).

I therefore investigated interspecific differences in individual and species-specific habitat use and interspecific niche overlap in syntopic *B. barbastellus*, *P. auritus* and *M. bechsteinii* in the SAC 'Ahringsbachtal'. I measured the extent of interspecific competition in bat species living in forest habitats (**Chapter IV**) via radio-telemetry. Niche overlap was estimated using a distance-based approach to assess the roosting and foraging area structure on landscape level, and in terms of qualitative characteristics of the tree roosts. All analyses were conducted for females and males separately to incorporate possible effects of sex-specific habitat selection, as I exemplified above (see Chapter III).

Chapters I-IV have been published or submitted for publication in modified form:

Prof. Dr. M. Veith (supervisor) provided valuable suggestions on each of the main parts of this thesis. Dr. A. Kiefer supervised and contributed to the field work 2004-2006 and also gave valuable comments on the manuscripts. T. Kaster, J. Pahle and K. Landsfeld partially conducted the data collection in the field as a part of their Diploma theses at the University of Mainz (mist-netting and radio-tracking bats) and data processing in GIS in 2005 and 2006. JH conducted the field work from 2004 to 2007, data processing and analysis of habitat and roost use applying new approaches (Euclidean distance analysis). O. Elle and E.M. Griebeler (supervisor) provided help in statistical analyses and contributed to fruitful discussions on the manuscripts.

Chapter I:
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Chapter II:
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Chapter III:
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Chapter IV:
Hillen, J., Landsfeld, K., Veith, M. (submitted to Acta Chiropterologica). Resource partitioning in three syntopic forest-dwelling bat species.

Chapter I. Spatial organisation and foraging site fidelity of a population of female western barbastelle bats

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Abstract.

Information about the spatial distribution of individual foraging habitats, which determines the space required by a population to be viable, is vitally important for the conservation of bats. Detailed knowledge of this kind is crucial for the design of nature reserves and management plans. Recent field studies that examined habitat use and home range distribution of bats largely ignored factors like traditional range use vs. intra- and interspecific competition, which may be responsible for the spatial organisation of a population home range. We investigated the home range sizes and distribution of a maternity colony of the western barbastelle bat via radio telemetry in four consecutive tracking sessions (2004–2007). Based on 19 data sets with a total of 2,737 fixes obtained from 12 females, we examined (i) how colony members partition the population home range (home range overlap analysis), and (ii) if individuals tracked over several years exhibit site fidelity. Home range sizes ranged from 125 to 2,551 ha (median: 403 ha), with a median number of 2 core areas (range: 1–5 core areas per individual per year). The core area sizes ranged from 5 to 285 ha (median: 67 ha). A home range and core area overlap analysis showed that site fidelity across years seems to be more important for home range distribution than competition among colony members. This allows researchers to combine information from several years to get a deeper insight into the population's spatial requirements.

1. Introduction.

The viability of natural populations strongly depends on the size and quality of their habitats. These habitats can be differentiated by the kind of resources they provide: roosting sites, foraging grounds, mating places, etc. Profitable habitats may be defended against hetero-specifics or conspecifics through territorial behaviour. Although being costly, territory defence may be energetically profitable and less risky compared to the necessity of repeatedly finding new high-quality habitats. Site fidelity is an alternative way of saving energy in the decision of which habitat to use next; a previously beneficial habitat may have a higher probability of providing sufficient resources than an unexplored new habitat.

In conservation biology, population vulnerability analyses (PVA) are used to measure the consequences of environmental changes. They require information about individual home range sizes and their degree of spatial overlap and the factors that influence the location and size of roosting sites or foraging grounds (Hovestadt *et al.*, 1991). Both territorial behaviour and site fidelity are therefore important factors when interpreting habitat size in terms of population viability. This in turn is required for the design and management of nature reserves. Conservation legislation, such as the European Council Directive 92/43/EEC (the so-called ‘Habitats Directive’), is nowadays supplemented by monitoring guidelines for the assessment of the viability of populations of endangered species. Such recommendations for the appraisal of populations and their habitat use often explicitly include analyses on the size and spatial distribution of individual and population home ranges by means of radio-tracking (Schnitter *et al.*, 2006). However, no information is provided about the interpretation of a given spatial distribution of individual home ranges. Although effective conservation action plans depend on such precise information (Soule´ & Orians, 2001), the possible effects of individual site fidelity and of territorial competition within and among species are not even taken into consideration.

Home range analysis via radio-tracking enables quantification of the size and structural details of individual and population home ranges without overly interfering with behavioural processes. It is increasingly used in wildlife conservation, such as for action plans for endangered species or for habitat management plans (Greenaway, 2004; Boye & Dietz, 2005), and allows for the location and identification of population-specific functional sites (e.g. roosts, mating sites, or feeding grounds) and the detection of individual interactions (territoriality or sociality). Such individual interactions can be analysed via ‘static interaction’ measurements (Kernohan *et al.*, 2001), i.e. the measurement of overlap in home range boundaries or roosting areas. Several radio-tracking studies on bats reported interannual roost and/or roosting area fidelity (Foster & Kurta, 1999; Barclay & Brigham, 2001; Veilleux & Veilleux, 2004) or intraspecific interaction (Robinson & Stebbings, 1997; Winkelmann *et al.*, 2000; Kerth *et al.*, 2001; Winkelmann *et al.*, 2003; Goiti *et al.*, 2006). However, interannual fidelity to foraging areas as well as habitat partitioning among individuals, especially among members of one maternity colony, is still poorly investigated.

Here we present data from a 4-year radio-tracking study of the western barbastelle, *Barbastella barbastellus* (Schreber, 1974). The aim of our study was to quantify home range sizes and distribution of a breeding colony of this forest-dwelling bat. We specifically ask (i) how colony members partition their population home range (test for intraspecific competition), and (ii) to what degree home ranges of tracked individuals overlapped over several years (test for foraging site fidelity). We finally discuss the implications for conservation and monitoring strategies.

2. Materials and methods.

The western barbastelle is among the most endangered European bat species and is protected by European law under the Habitats Directive 92/43/EEC (Annex II). It is listed as 'vulnerable' under the IUCN Red List of Threatened Species. This medium-sized vespertilionid bat is a highly specialised predator of small moths in deciduous or mixed forests and cultivated land. Forests with a high proportion of old and dead trees are preferred (Rydell *et al.*, 1996; Sierro & Arlettaz, 1997). Natural roosts of maternity colonies are mainly found behind the loose bark of trees or in rock crevices (Steinhauser, 2002; Russo *et al.*, 2004; Russo *et al.*, 2005). Little is known about the size and structure of home ranges in different habitats. Home range sizes reported in recent studies vary from 0.6 to 8.8 ha (average individual MCPs; Sierro, 1999), with core regions of about 100–500 m in diameter (harmonic mean; Steinhauser, 2002).

We studied the western barbastelle near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany. Habitats in the study area are characterised by well-structured deciduous forest patches with numerous dead oak and pine trees, interspersed by clearings, meadows and brooks. A large number of abandoned mines is available as hibernacula. The entire area is protected as 'FFH-Gebiet Ahringsbachtal' by European law under the Habitats Directive 92/43/EEC.

Tracking sessions were conducted from June to September in 2004, 2005, 2006 and 2007. Western barbastelles were captured with mist nets close to their maternity roosts. Each individual was marked with an aluminium split ring around the forearm (Deutsche Beringungszentrale, Museum Alexander Koenig, Bonn). They were fitted with 0.4 g LTM radio transmitters (Titley Electronics Pty. Ltd., Australia) glued on the back fur between the shoulder blades (Figure 1). We captured and marked 15 adult female western barbastelles from the maternity colony, 13 of which were fitted with radio transmitters. Females advanced in pregnancy were excluded from the radio-tracking experiment. Since the population size estimated from mark-recapture data (data not shown) averaged to approx. 10 adult females per year, our annual sample sizes of 4, 4, 2 and 7 distributed over 12 different specimens constitute a reasonable sample of the entire population. Body weights ranged from 8.1 to 12.0 g (mean: 10.5 g) in radio-tracked females, so the transmitter weight relative to the females' body weight was always below 5%.

Figure 1. Female western barbastelle bat with ring and radio transmitter.

Three-and five-element Yagi antennas (Telonics Inc., USA; Sirtrack, New Zealand) were combined with Yupiteru MVT 7100 and AOR AR 8200 receivers. We tracked from elevated terrain or wooden towers to maximise the perception range of the transmitted signals (Figure 2). In the first three years, only one bat at a time was tracked per field experiment. In 2007, four pairs of two simultaneously tracked bats each were studied to better quantify intraspecific interactions.

In the first study year, bats were located every 10 min via synchronised triangulation. In the following years, bats were located every 5 min due to the rapid flights of this species. This relatively short time interval may potentially produce temporally autocorrelated fixes, but in fact it was long enough to allow specimens to cross their entire home range. Temporal autocorrelation is a problem inherent in radio-tracking studies based on relatively short time intervals between consecutive fixes. Swihart and Slade (1985) stated that '...animal locations for home range analysis require independence; otherwise they may underestimate the home ranges.' They therefore suggested determination of the 'time to independence (TTI)' in radio-tracking studies to eliminate temporal autocorrelation. However, temporal autocorrelation can be biologically meaningful, and its elimination may overestimate home range sizes and thus bias biological interpretation (De Solla *et al*., 1999). We therefore used the complete data sets after correction for clumped data points (see below). Bat fixes were transferred to 1:25,000 topographic maps, and Gauss–Krüger coordinates were determined. They were imported into

ArcView GIS 3.2 (ESRI, 1999; licensed through the Faculty of Science of the University of Trier) and analysed with the Home Range Extension software, HRE (version 3, Rodgers & Carr, 1998).

Figure 2. One of 10 wooden towers built for the bat monitoring in the SAC 'Ahringsbachtal', used to to maximise the perception range of the transmitted signals.

A variety of analytical tools exist to estimate home ranges. They can be divided into two major classes: the polygon methods, such as the minimum convex polygon (MCP; Mohr, 1947), and contouring methods, such as the bivariate normal ellipse (Jennrich & Turner, 1969) or the kernel density estimation (KDE; Worton, 1989). The MCP is the oldest and most commonly used method of estimating home ranges and it facilitates comparisons with other, especially older, studies. On the other hand, MCP is very sensitive to outliers and requires large data sets for accurate estimations. KDEs are less sensitive to outliers and sample sizes, but they require careful examination of the kernel calculation parameters. In the present paper we rely on KDEs for home range analysis in the western barbastelle. KDE is a non-parametric estimator. It describes home ranges by means of hierarchical probabilities for the intensity of habitat utilisation, so-called isopleths. The isopleths mainly depend on the probability distribution of single locations on an underlying two-dimensional grid. A smoothing factor or bandwidth ‘*h*’ defines the shape and width of this probability distribution. It is largely responsible for the degree of smoothing of the outlines and thus for the size of the estimated home range.

Individual home ranges were estimated as adaptive kernels with the smoothing factor h estimated from the data and optimised via least square cross validation, LSCV (h_{cv}; Worton, 1989). We only used data sets containing more than 30 fixes to calculate reliable home range estimates (Seaman *et al.*, 1999). Silverman (1986) reported a bias in LSCV estimation of h in clumped data points. We therefore eliminated duplicate fixes at roosts prior to hcv estimation. This also eliminates the risk of overestimation of habitat use around roosts due to, for example, swarming behaviour. The females' home ranges were calculated with a mean h_{cv} over the individual h_{cv} to keep annual home ranges comparable among maternity colony members (cp. Kenward, 2001). We defined the 95%-KDEs as 'individual home ranges' and the 50%-KDEs as 'core areas'.

The distribution of home ranges and core areas may be determined by two different mechanisms, intraspecific competition and interannual tradition. If the location of home ranges resulted from intraspecific competition only, i.e. every individual occupied an area that is used exclusively in one year, but selects another suitable area in consecutive years (resulting in a new spatial distribution of home ranges every year), we would expect minor overlap within a year, but higher overlap between different individuals across years. If tradition were the only factor that shaped the home range arrangement, then the interannual overlap of individual home ranges of animals tracked in different years should be larger than the overlap of different animals tracked across years. Pairwise home range and core area overlap was calculated as the mean percentage of area jointly used by two specimens from the area utilised by either of them.

We calculated pairwise overlap between (i) different individuals within a year (test for intraspecific competition) and (ii) annual home ranges of repeatedly tracked individuals across years (test for individual site fidelity). In order to quantify the degree of tradition between two successive tracking periods we used the following equation by Mizutani and Jewell (1998) as a measure of annual foraging site fidelity: $HR'Y1;Y2'=A'Y1;Y2'/A'Y1'$; where $HR'Y1;Y2'$ is the proportion of the individual home range in year 1 overlapped by the individual home range in year 2, $A'Y1;Y2'$ is the area of overlap between the two annual home ranges, and $A'Y1'$ is the area of the home range in year 1 (Kernohan *et al.*, 2001).

Statistical analyses were performed in SsS (version 1.1k, Rubisoft Software GmbH). We tested for significant differences between home ranges (95%-KDE) and core areas (50%-KDE) using Fisher's exact test (level of statistical significance at a = 0.05).

3. Results.

We obtained reliable data with more than 30 fixes from 12 females. Three bats were tracked successfully over 2 years and another two over 3 years (Table 1). In 2007, four pairs of females were tracked simultaneously (BF4 with BF10, BF1 with BF11, BF3 with BF7, and BF12 with BF13). We used a total of 19 data sets and 2,737 fixes in our home range analyses. The mean number of effective tracking nights per bat was 6. The number of fixes per specimen and year included in home range analyses ranged from 32 to 398 (median: 135).

Table 1. Capture date, sex and number of fixes of 13 radio-tracked western barbastelle bats; nr: not reproductive; pr: pregnant; l: lactating; pl: post-lactating; -: specimen not tracked; asterisks indicate data sets too small for further analyses.

ID	Capture date				Reproductive status				n fixes			
	2004	2005	2006	2007	2004	2005	2006	2007	2004	2005	2006	2007
BF1	06.07.	13.07.	11.07.	17.07.	l	l	l	l	98	32	20*	231
BF2	16.07.	20.06.	21.06.	09.07.	l	l	pr	l	112	0	-	44
BF3	04.08.	03.07.	-	25.07.	l	l	-	l	98	42	-	398
BF4	22.08.	-	-	18.06.	pl	-	-	l	135	-	-	183
BF5	-	29.05.	25.07.	-	-	nr	l	-	-	32	96	-
BF6	-	03.06.	-	-	-	g	-	-	-	26*	-	-
BF7	-	01.07.	19.08.	31.07.	-	l	pl	l	-	21*	0	132
BF8	-	15.07.	19.08.	-	-	l	pl	-	-	181	0	-
BF9	-	-	11.07.	-	-	-	l	-	-	-	151	-
BF10	-	-	-	27.06.	-	-	-	l	-	-	-	167
BF11	-	-	-	13.07.	-	-	-	l	-	-	-	192
BF12	-	-	-	10.08.	-	-	-	nr	-	-	-	207
BF13	-	-	-	10.08.	-	-	-	pl	-	-	-	206

We detected a great variability in home range size and number of core areas among the colony members. Home range sizes varied from 125 to 2551 ha (median: 403 ha; Table 2). The median number of core areas per individual and year was 2 (range: 1–5). The core area sizes ranged from 5 to 285 ha (median: 67 ha).

Table 2. Individual annual home range sizes (in ha) for 12 radio-tracked female western barbastelle bats.

ID	95% home range area				50% core area			
	2004	2005	2006	2007	2004	2005	2006	2007
BF1	714	127	-	534	107	19	-	81
BF2	2,551	-	-	160	186	-	-	5
BF3	539	207	-	583	79	36	-	92
BF4	343	-	-	403	27	-	-	75
BF5	-	922	198	-	-	67	15	-
BF7	-	-	-	2,097	-	-	-	285
BF8	-	125	-	-	-	14	-	-
BF9	-	-	399	-	-	-	34	-
BF10	-	-	-	258	-	-	-	22
BF11	-	-	-	352	-	-	-	50
BF12	-	-	-	1,622	-	-	-	254
BF13	-	-	-	1,835	-	-	-	101

All the home ranges of radio-tracked females overlapped with at least one other home range, but only 41% of the females' core areas overlapped with another female's core area. The degree of spatial overlap between annual home ranges of different individuals was low (means: 13.1% in 95%-KDE; 2.4% in 50%-KDE; see Table 3).

Table 3. Percent home range and core area overlap among different groups of female western barbastelle bats; ind.: individuals.

comparison	percent overlap of						
		95% home range			50% core area		
	N	mean	median	range	mean	median	range
among simultaneously tracked ind. in 2007	4	11.9	11.3	5.6-19.4	2.8	1.8	0.0-7.6
between non-simultaneously tracked ind. in 2007	32	13.4	10.3	0.9-57.2	2.2	0.0	0.0-16.3
between all ind. within years	49	13.1	10.2	0.9-57.2	2.4	0.0	0.0-19.8
between repeatedly tracked ind. across years	9	27.6	20.4	6.2-56.5	8.9	7.2	0.0-22.4
between different ind. across years	115	13.0	10.3	0.8-43.4	3.2	0.0	0.0-33.1

Spatial overlap between bats tracked at the same time in 2007 (n = 4) did not differ significantly from pairs of bats tracked at different times within this year (n = 32; 95%-KDE: P = 0.567; 50%-KDE: P = 1.000), indicating that home range overlap within a year did not depend on the time when home ranges were determined. Hence we pooled annual home ranges (annual core areas) of simultaneously and non-simultaneously tracked bats into one sample for further comparisons. To test for territoriality among foraging specimens, all pairwise overlaps of annual home ranges and core areas within a year were compared to all possible overlaps across years (n = 115). We could not reject our null hypothesis of equal home range and core area overlaps between these two types of comparisons (95%-KDE: P = 0.682; 50%-KDE: P = 1.000), indicating that there is no competition for foraging areas within a year. To test for foraging area fidelity across years, we compared the spatial overlap between the annual home ranges and core areas of repeatedly tracked bats (n = 9) with the overlap of all possible combinations of different individuals across years. Overlap of 95%-KDE (P = 0.001) and 50%-KDE (P = 0.039) was significantly larger in repeatedly radio-tracked specimens.

Five female western barbastelles were tracked successfully in 2 or 3 years. Three of them, BF1, BF3 and BF4, were found in the same areas of our study site as in previous years, but with varying shapes of the home range boundaries (for an example see Figure 3) and, to a greater extent, in the location of core areas. This also indicates their fidelity to foraging areas once selected. The home ranges of all individuals largely fit within available forest patches. In 2007, BF2 used a much smaller home range than in 2004, and in 2005, BF5 even used an area that was not used again in 2006. When averaged over all specimens, the percentage of overlap between different years, hence the degree of site fidelity, was significantly smaller for core areas than for home ranges (P = 0.015; Figure 4).

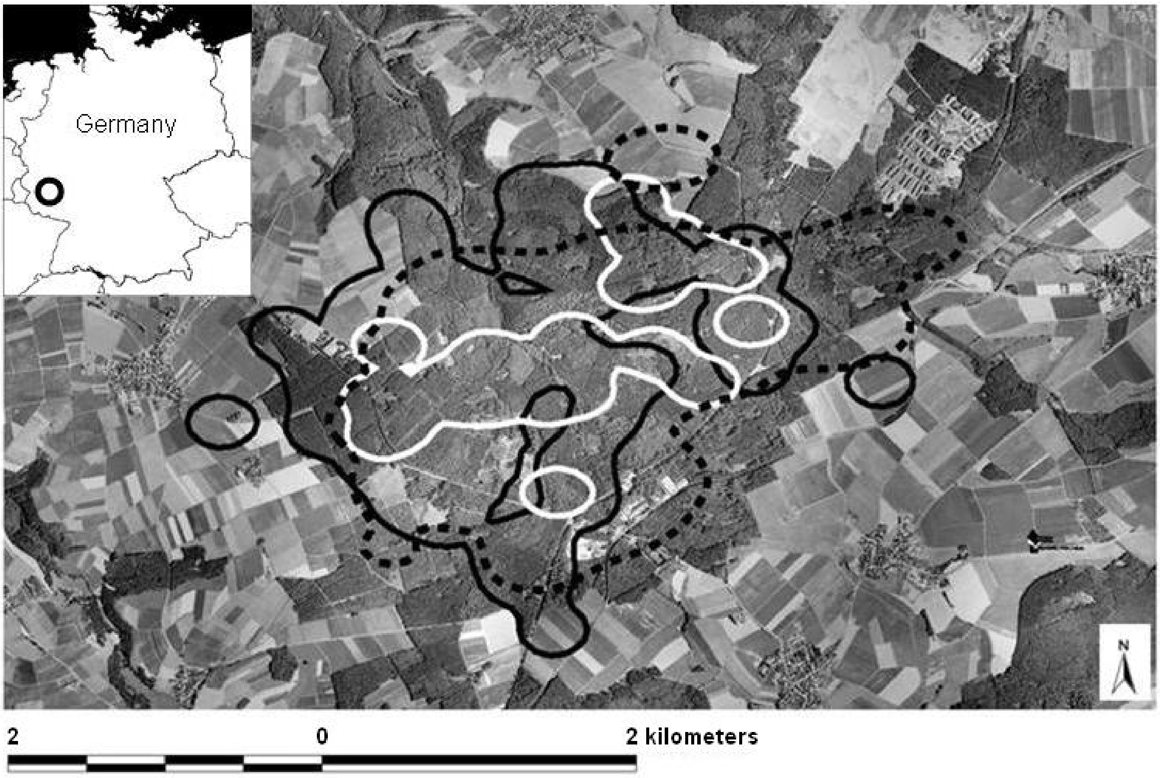

Figure 3. Example of the individual annual home range (95%-KDE) overlap between different years (female barbastelle bat BF3); black solid: 2004; white solid: 2005; black dashed: 2007; drawn on digital orthophotos, ©Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz; licence no. 26 722-1.51; the inlet shows the study area within Germany.

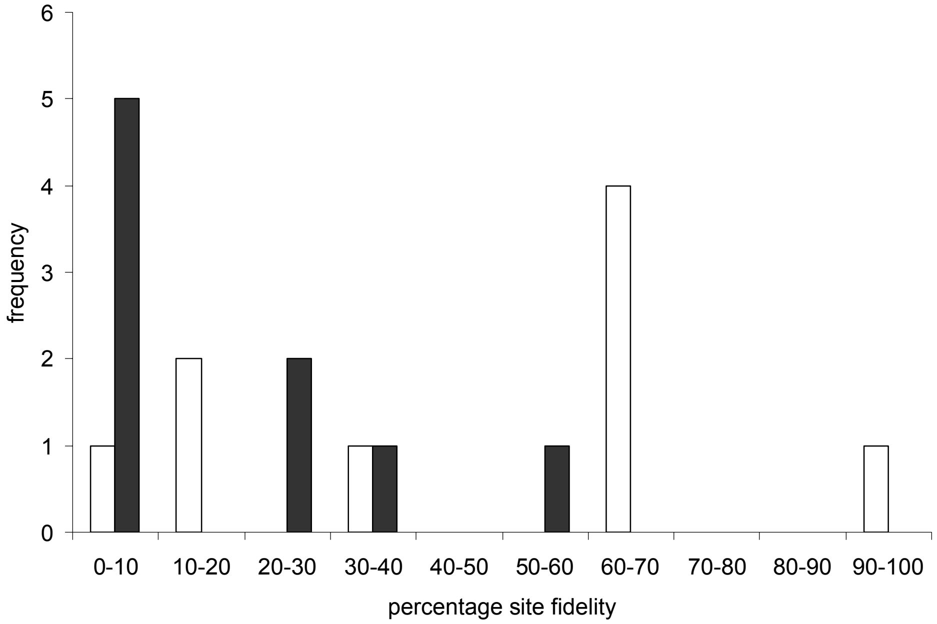

Figure 4. Percentage site fidelity in annual home ranges and core areas of four western barbastelle bats tracked in two or three different years; black: site fidelity in core areas; white: site fidelity in home ranges.

4. Discussion.

The spatial organisation of foraging areas found in our maternity colony of the western barbastelle strongly indicates that females partition the foraging area of the entire colony and keep their individual hunting areas constant over time (foraging site fidelity). Although each individual home range of female western barbastelles overlapped with at least one other individual home range, the degree of spatial overlap between annual home ranges of different specimens was low (mean: 13.1%).

A comparably small home range overlap between colony members within a year was reported for *Myotis bechsteinii* (12.3%; Kerth *et al*., 2001). In both species, a sufficient and stable availability of food may allow females to utilise more or less ‘private’ foraging areas without interfering too much with conspecifics (see also Chaverri *et al*., 2007). The impact of food availability on home range overlap is supported by simulation experiments (Barta & Szép, 1992) and confirmed by several field and laboratory studies on birds and mammals (as cited in Kerth *et al*., 2001). In case of stable or increasing food availability and decreasing home range overlap the development of tradition will avoid costs for repeated searching for profitable hunting grounds and for resource defence (Chaverri *et al*., 2007).

Although our data show that site fidelity is a major factor that shapes the spatial distribution of home ranges and core areas in our western barbastelle population, competition cannot be ruled out as being responsible for the initial establishment of home ranges and core areas with small overlap. Bonaccorso *et al*. (2005) suggested that territorial behaviour in both male and female *Melonycteris melanops* (a nectarivorous Pteropodid) tracked simultaneously in two consecutive years could be responsible for an exclusive use of individual core areas (minimum area probabilities) and for some overlap in their home range boundaries. One male tracked in both years showed fidelity to core areas, but an extension of its home range resulting from some excursions to a female’s home range, indicating seasonal behaviour (mating season). Of all tracked females BF5 was the only female that was not reproductive during the first radio tracking period, but it was lactating in the following year. Therefore we cannot exclude that in this single case of foraging area selection was influenced by a seasonal change in behaviour. All other repeatedly tracked females had reproduced (tracking periods: lactation and early post-lactation), and thus their annual home ranges are comparable.

In our study, the individual home range sizes (95%-outlines) of western barbastelles varied from 125 to 2,551 ha, with sometimes more than one core area. These home ranges are among the largest known for the species. Sierro (1999) reported home range sizes, measured as average individual MCP, ranging from 0.6 to 8.8 ha. Steinhauser (2002) located lactating females in foraging core areas, measured as harmonic means, covering up to 20 ha that were located at a distance of 3–4.5 km away from the roosts. It seems that lactating western barbastelles are able to compensate for their increased energy demand during lactation by exploiting productive foraging sites at greater distances from their roost (Greenaway, 2004). Studies on maternity colonies of other bat species (e.g. *Nyctalus leisleri*; Shiel *et al*., 1999) also showed that females were able to compensate for their increased energy demand during lactation by different strategies, for example through an intense use of multiple core areas close to the roost.

The strong site fidelity of female western barbastelles has several important implications for conservation strategies and monitoring programs. First, and from a technical point of view, radio-tracking of different specimens across years but during comparable seasonal periods may in fact suffice to describe home range and habitat utilisation of an entire breeding colony. Many forest-dwelling bat species live in small colonies like the western barbastelle and show comparable population structures and space use (e.g. the Bechstein's bat, *M. bechsteinii* (Kerth *et al*., 2001), the New Zealand longtailed bat, *Chalinolobus tuberculatus* (O'Donnell, 2001), the Rafinesque's big-eared bat, *Corynorhinus rafinesquii* (Hurst & Lacki, 1999). To our knowledge, reduced individual home-range overlap (including foraging areas) has been shown for all bat species studies so far with the exception of two studies (*Nyctalus noctula* (Mackie & Racey, 2007); *Eptesicus serotinus* (Robinson & Stebbings, 1997)). A reduction of radio-tracking efforts in one year in favour of a cumulative monitoring across consecutive years may therefore be a suitable approach to in general reduce the potential invasiveness of a radio-tracking monitoring programme on forest bats. Second, analysing the size and distribution of individual home ranges that only slightly overlap allows one to draw a realistic picture of the spatial requirements of an entire population. Knowing the importance of tradition (measured in terms of site fidelity) on foraging area location will help to assess the plasticity with which populations may react to habitat alterations.

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Chapter II. Interannual fidelity to roosting habitat and flight paths by female western barbastelle bats.

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Abstract.

The roost area selection of reproductive female western barbastelles was examined throughout four study seasons (2004–2007) via radio-tracking and automated acoustic monitoring. We specifically analysed the spatial structure of the roosting habitat and roost fidelity including a flight path connecting the roosts. We radio-tracked 13 colony members to 46 natural roosts, mainly dead oaks with large pieces of loose bark. Simultaneous tracking of four pairs of females revealed the existence of subgroups and fission-fusion-behaviour in Barbastella barbastellus. The colony displayed fidelity to the roost area rather than to single roost trees, although some trees were reused in two or three study seasons. Bimodal activity patterns obtained from acoustic monitoring indicated that the flight path connecting two core roosting areas functioned as a commuting corridor.

1. Introduction.

Bats have specific requirements for foraging grounds, hibernacula and summer roosts. Roosts play a crucial role for bats, because they provide shelter for single animals and reproductive groups (maternity colonies) from predators and unfavourable weather conditions. Roost quality (e.g., microclimate, space) and the structural composition of the roosting habitat influence the reproductive success of individuals and even shape patterns of behaviour in populations of bats (Lewis, 1995, 1996). Forest-dwelling bats often have high demands on roost quality (e.g., cavity size, ambient temperature, humidity), but as these types of roosts are less permanent compared to others (e.g., caves) the bats have to compensate by roost-switching and exploitation of new roosts (Lewis, 1995; Kerth *et al.*, 2006; Barclay & Kurta, 2007).

The western barbastelle bat (*Barbastella barbastellus*) is one of the most endangered forest-dwelling bat species in Europe (Temple & Terry, 2007). Numerous roosts of western barbastelle bats have been located in man-made structures as they can easily be observed in crevices in walls, in old barns or behind wooden window shutters. Today, radio-telemetry enables researchers to study the roosting behaviour of the western barbastelle under more natural conditions. Through radio-telemetry studies, this species has been identified as a forest-dweller relying on old-growth forests that provide a high density of potential roosts and maternity colonies have mainly been found behind the loose bark of trees or, in exceptional cases, in rock crevices (Steinhauser, 2002; Russo *et al.*, 2004, 2005). Such qualitative findings have been implemented in practice guidelines for woodland management that consider the qualitative roosting requirements of bat colonies and other wildlife (Boye & Dietz, 2005).

Unfortunately, quantitative data about the structure of roost areas of western barbastelle bats as well as other forest-dwelling bats, e.g., the existence of core areas and the intra- and interannual fidelity to these core areas are lacking, although these data would improve existing conservation strategies. Despite the fact that the degree of connectivity between the habitat patches (e.g., roost areas) drives the spatial distribution of bat populations (Racey & Entwistle, 2003), there are still but a few studies that reveal long-term fidelity to linking landscape elements, e.g., forest tracks or hedgerows. These linear elements are often used as commuting corridors to hunting grounds, as shelter from predators, or as hunting grounds (Limpens & Kapteyn, 1991; Verboom & Huitema, 1997; Verboom *et al.*, 1999; Greenaway, 2004; Goiti *et al*., 2008). Therefore, it would be interesting to find out, if the roost area of a bat colony comprises commuting corridors facilitating orientation and, possibly, communication between colony members.

In the present study, we analysed quantitative aspects of roost areas, especially the density and spatial arrangement of roosts, and roost fidelity of female western barbastelles throughout four radio-tracking seasons. We specifically wanted to know how the bats utilise available landscape elements surrounding the roost areas and whether they display interannual fidelity to specific landscape elements.

2. Materials and methods.

The study was carried out in the Special Area of Conservation (SAC) Ahringsbachtal near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany. This area comprises large patches of 100–180 year old deciduous and mixed forests (*Fagus sylvatica*, *Quercu robur*, *Q. petraea*, *Pinus sylvestris*) with numerous dead trees. Some bat boxes also were available (flat rectangular boxes for crevice-dwelling species and round wood-concrete boxes). Tracking sessions were conducted from June to September in 2004, 2005, 2006 and 2007. Capture and mark- ing of adult females are described in Hillen *et al.* (2009). A total of 13 females were fitted with 0.4 g LTM radio transmitters (Titley Electronics Pty. Ltd., Australia). The transmitter weight relative to the females'body weight was always below 5%. In the first three years, only one bat at a time was tracked successfully over several nights. In 2007, four pairs of simultaneously tracked bats were tracked successfully to assess the occurrence and spatial organisation of subgroups.

Bats were radio-tracked to their individual roosts every morning until transmitter failure or loss (mean number of tracking nights per bat: six nights). The approximate locations of the roosts were estimated via triangulation, and the exact determination of location as well as description of roost characteristics were conducted in the afternoon. We recorded the following roost characteristics: roost type (natural, e.g., tree; artificial, e.g., crevice in a house wall, bat box), tree species and roost height (in metres; Laser-Hypsometer, Opti-Logic 400 LH). We used emergence counts to assess the height and number of occupied pieces of loose bark or other crevices and to estimate the number of females in each subgroup.

The exact roost locations were measured using GPS (Garmin 12 XL), and the resulting Gauss-Krüger-coordinates were imported into ArcView 3.2 (ESRI, 1999). The distances between the colony roosts were calculated using the Animal Movement Extension software (Hooge & Eichenlaub, 1997). We delineated the roost area via kernel density estimation (95%-kernel; Worton, 1989) and core areas (50%-kernel) including all roosts (2004–2007) using the Home Range Extension software, HRE (version 3, Rodgers & Carr, 1998). The smoothing parameter h was estimated via least square cross validation, LSCV (h_{cv}; Worton, 1989). We excluded duplicate records in our kernel analysis (i.e., every roost was taken only once) to avoid an underestimation of the colony roost area.

Several western barbastelles were mist-netted along a specific forest track (6–8 m width, Figure 5) that runs from a patch of old deciduous forest in the central SAC to a patch of mixed forest in the South. These forest patches are separated by a patch of coniferous forest (plantation of *Picea abies*) and a small federal street. This forest track emerged as a major commuting corridor for the colony.

Figure 5. Forest track used as a commuting corridor between roosts.

In 2006 and 2007, we additionally recorded *B. barbastellus* echolocation calls along this corridor to measure the activity patterns with the automated detector system Anabat II (Titley Electronics Pty. Ltd., Australia). In 2006, we started with one Anabat II-unit placed at the southern entrance of the flight path (fp1; Figure 8). In 2007, we used three units simultaneously to test whether the flight path was used over its full length (fp1, fp2 and fp3; Figure 8). We placed the detector units (including the zero-crossings analysis interfaces module (Anabat CF Storage ZCAIM)) into a waterproof box. The microphones were protected from rain by using small housings that were mounted on a reflector at a 45 degree angle to direct the calls into the microphones. The microphones were mounted on poles to record the calls in a clutter-free space (Figure 6). The Anabat detectors monitored bat activities from dusk till dawn (June–September 2006 and May–August 2007; one repeated measurement per site, i.e., two samples of call recordings per site) with an Anabat division ratio set to 16. One sample of site-specific call recordings comprised between 10 and 21 consecutive nights. This method of recording calls provides information about the characteristic activity pattern at a given site and considers the varying bat activities depending on weather conditions and insect densities at a site (Hayes, 1997). We used Analook (version 4.9j, Corben, 2004) for call analysis.

Figure 6. Anabat detector microphone with reflector.

Western barbastelles usually alternate between two different echolocation calls (starting frequencies: type 1: 33–38 kHz; type 2: 42–46 kHz) when flying in semi-cluttered and open space (Ahlén, 1981; Russ, 1999; Denzinger *et al*., 2001; for example sequences in ANABAT format see Appendix Figure A-1). The number of call sequences (comprising at least 3 calls each) per hour was summed up over all successful recording nights. Since single calls may be misclassified due to their similarity to call fragments of other species, we excluded them from the analysis. We compared two different types of activities: (a) activities of *B. barbastellus* at the southern entrance of the flight path in 2006 and 2007, recorded in the main lactation period, to assess the fidelity to this flight path, and (b) activities of *B. barbastellus* at three sites along the flight path in 2007 to test whether the flight path was used over its full length. For comparison, we recorded flight activities at 17 other sites (forest tracks, forest edges) throughout the central SAC to test whether the activity patterns at the flight path represented a characteristic of our study area or a special pattern different from those recorded at other sites. We only compared data from nights with successful simultaneous recordings by applying Craddock-Flood’s $\chi 2$-test (pairwise tests, $\alpha = 0.05$; Craddock & Flood, 1970) in BIAS 8.4.5 (epsilon-Verlag).

3. Results.

We radio-tracked 13 females to 46 natural roosts within deciduous or mixed forest patches (Table 4). We also obtained data on individual roosts of three females that were tracked over two years (BF 2, 4, 5 and 8; see Table 4) and another twothat were tracked over three years (BF3 and 7). One female (BF 1) was tracked over four years. Most occupied roost trees were dead oaks with large pieces of loose bark (*n*= 38; Figure 7), followed by dead pines (*n*= 6), dead spruce (*n*= 1) and one living oak with dead branches and loose bark. We never found colony members roosting in one of the bat boxes, crevices or tree hollows. In five cases the emergence counts showed that the colony used more than one piece of bark per tree. Most occupied roosts were found at a height of 8–10 m (*n*= 18, *n* total = 46 roost trees, range = 2.5–17.1 m). The roost area (95%-kernel) comprised 183 ha, and the core area (50%-kernel) was 27 ha. The allocation of the roosts indicated the existence of three main roost clusters (see Figure 8); two smaller ones (cluster A and A') situated in the central SAC and another one (cluster B) in the southern part of the study area. Two roost trees were not included in the clusters (Table 4: single trees, S). All clusters defined a separate part of the 50%-core area and comprised 120–180 year old patches of deciduous or mixed forest. The distances between the colony roosts ranged from 6 to 2,014 m (median 751.9 m).

Figure 7. Roost structures: dead oak with loose bark.

Table 4. Reproductive status, allocation and number of individual roosts of 13 radio-tracked western barbastelle bats; nr: not reproductive; pr: pregnant; l: lactating; pl: post-lactating; A, A' and B: roost clusters; S: single tree outside the clusters; n_r: number of roosts; n_{obs}: number of days with roost observation; 0: no data on the roosts.

ID	Reproductive status				Utilised cluster of roosts				n_r, n_{obs}			
	2004	2005	2006	2007	2004	2005	2006	2007	2004	2005	2006	2007
BF1	l	l	l	l	A,S	S	B	A,S	3,8	1,1	1,1	2,6
BF2	l	l	pr	l	B,S	0	-	B,S	4,13	0,0	-	2,3
BF3	l	l	-	l	A',B,S	A,S	-	B	5,8	2,7	-	4,10
BF4	pl	-	-	l	A,A',S	-	-	A,S	6,8	-	-	2,10
BF5	-	nr	l	-	-	A,B	B,S	-	-	4,4	3,5	-
BF6	-	pr	-	-	-	A,S	-	-	-	2,10	-	-
BF7	-	l	pl	l	-	S	S	B	-	1,2	1,4	1,4
BF8	-	l	pl	-	-	A,S	0	-	-	4,12	0,0	-
BF9	-	-	l	-	-	-	B	-	-	-	4,6	-
BF10	-	-	-	l	-	-	-	A,S	-	-	-	2,5
BF11	-	-	-	l	-	-	-	B	-	-	-	4,7
BF12	-	-	-	nr	-	-	-	B,S	-	-	-	6,7
BF13	-	-	-	pl	-	-	-	A',B	-	-	-	6,7

The radio-tracked individuals inhabited 1–6 roosts (median 3.5 roosts) without a clear fidelity to a specific roost area cluster (Table 4). The bats that were tracked over more than one year also selected different trees and roost clusters in different years. We never observed a reuse of a certain roost tree by the same animal in our radio-tracking experiments, although we cannot exclude a reuse over the years. By comparing data from four pairs of simultaneously tracked bats a division of the colony into several subgroups or even single bats was revealed, e.g., BF4 representing one group (three bats in total) and BF10 another one (comprising three bats, too; see Table 5). The pairs of simultaneously tracked bats occupied the same piece of bark in all cases of exact roost height measurement and emergence count.

We also observed a pronounced swarming behaviour around the roost in the evening after roost emergence and in the morning when the bats returned to the roost. Single bats switched frequently between roosts (every 2.0 ±1.8 day (0± SD) and regularly crossed the small road that separates the roost clusters A/A’ and cluster B. The simultaneously tracked bats switched between the roost area clusters and roosted with a varying number of conspecifics (Table 5). The number of bats (including volant juveniles) emerging from a single roost tree ranged from 1 to 15.

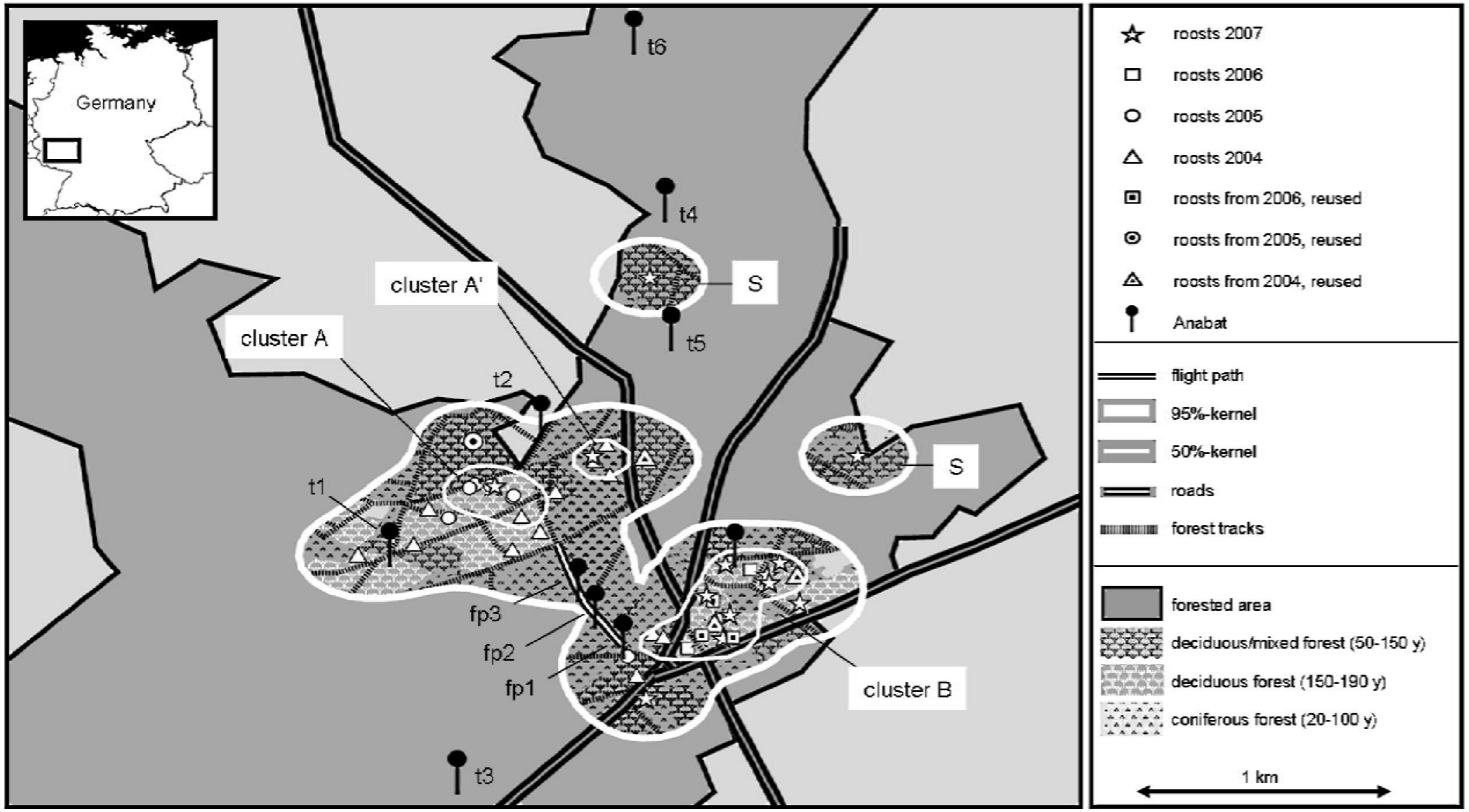

Figure 8. Map of the roost area including forest types and age classes (in years, y), roost allocation, 95%-kernel (roost area) and 50%-core areas estimated from all 46 colony roost trees; fp1-fp3: Anabat sampling sites along a flight path; t1-t6: further Anabat sites within and around the roosting habitat.

Table 5. Grouping behaviour and number of emerging bats per subgroup obtained from four pairs of simultaneously tracked western barbastelle bats; s: bats found in separate trees; t: bats found together in one tree; * no emergence count possible.

Pair	Tracking days with both animals observed simultaneously	Roost occupancy						
		day 1	day 2	day 3	day 4	day 5	day 6	day 7
BF4 + BF10	30.06. - 02.07.2007	s	t	t	-	-	-	-
BF1 + BF11	18.07. - 21.07.2007	s	s	s	s	-	-	-
BF3 + BF7	01.08. - 04.08.2007	s	t	t	t	-	-	-
BF12 + BF13	11.08. - 16.08. and 18.08.2007	t	t	t	s	t	t	s
		number of emerging bats per roost						
		day 1	day 2	day 3	day 4	day 5	day 6	day 7
BF4 + BF10	30.06. - 02.07.2007	3 + 3	*	3	-	-	-	-
BF1 + BF11	18.07. - 21.07.2007	3 + 4	4 + 6	3 + 13	4 + 15	-	-	-
BF3 + BF7	01.08. - 04.08.2007	1 + *	*	*	15	-	-	-
BF12 + BF13	11.08. - 16.08. and 18.08.2007	*	3	2	3 + 2	2	10	* + *

Seven trees were used in two or more different years. Three trees first found in 2004 were occupied in one of the following tracking sessions (2005, 2006 or 2007). Further, three trees found in 2006 were reused in 2007. One tree from 2005 was reused in 2006 and 2007 (Figure 8). Occupied roosts were located in the central SAC (cluster A and A') as well as in the southern part of the area (cluster B) in all tracking sessions. Automatically recorded activity patterns at the three sites along the flight path (fp1, fp2 and fp3) indicated that it was used over its full length, although Craddock-Flood's Chi-square tests resulted in significant differences between fp1 and the other two sites in June (Table 6 and Figure 9a). We did not find any differences between the three sites in August (Table 6 and Figure 9b).

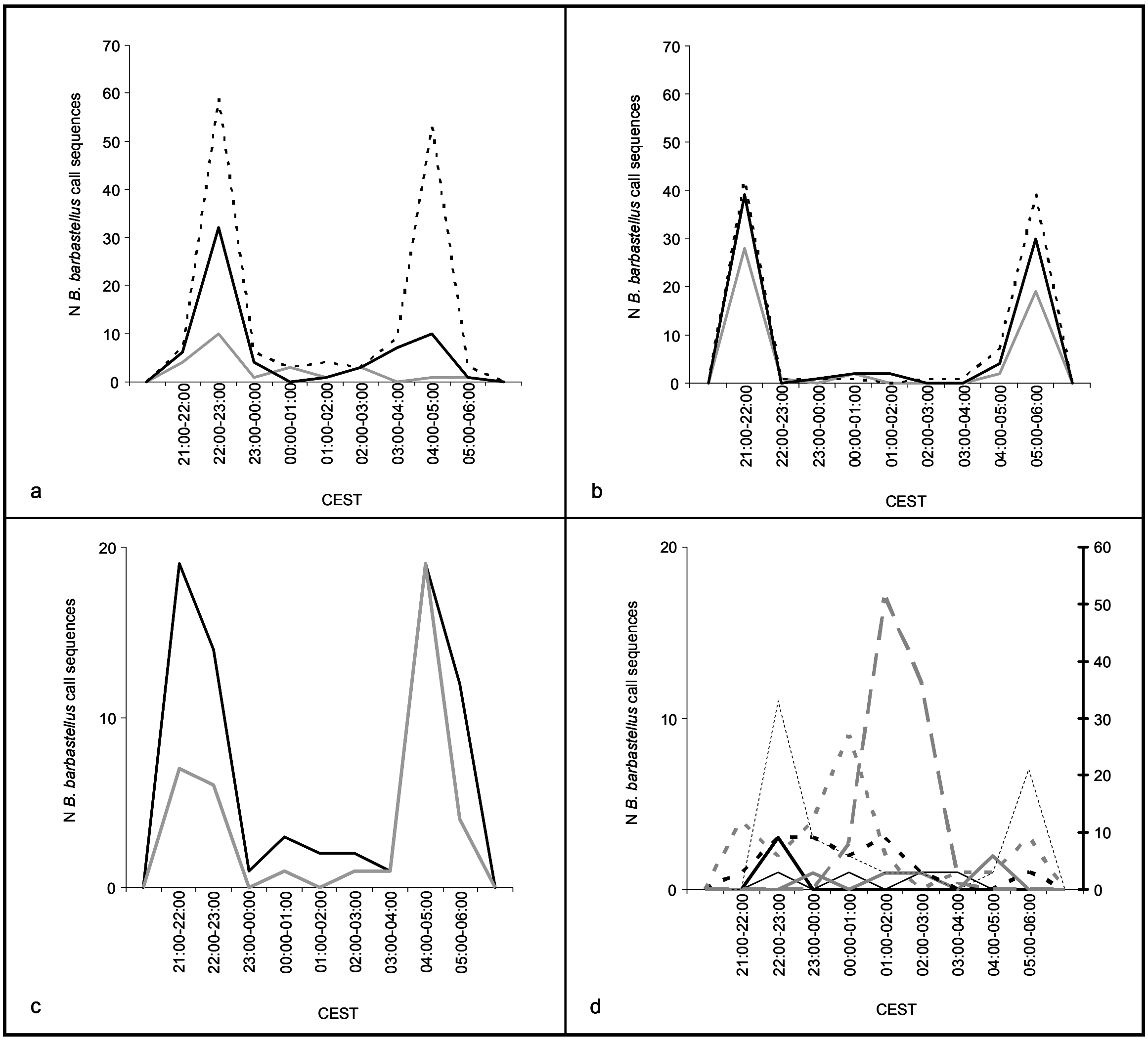

Figure 9. Comparison of automatically recorded *B. barbastellus* activity patterns; CEST: Central European Summer Time.

a) Activity patterns recorded at three sites along a flight path (fp1-fp3) in 2007; n = 8 nights (18.06. - 25.06.2007); grey line: *B. barbastellus* activities at fp1; black solid line: *B. barbastellus* activities at fp2; black dashed line: *B. barbastellus* activities at fp3;

b) *B. barbastellus* activity patterns recorded at three sites along a flight path (fp1-fp3) in 2007; n = 14 nights (31.07. - 13.08.2007); grey line: fp1; black solid line: fp2; black dashed line: fp3;

c) Activity patterns recorded at the southern entrance of a flight path (fp1) 2006 and 2007; n = 7 nights; 15.07. - 21.07.2006 (2007); black line: *B. barbastellus* activities at fp1 in 2006; grey line: *B. barbastellus* activities at fp1 in 2007;

d) *B. barbastellus* activity patterns recorded at six sampling sites (test sites t1-t6) around the roost area; black solid line (bold): t1; black solid line: t2; grey dashed line (bold): t3; black dashed line (bold): t4 (June 2007); grey dashed line: t4 (August 2007); grey solid line (bold): t5; black dashed line: t6; t3 drawn on secondary y-axis.

The activity patterns that resulted from the mean numbers of *B. barbastellus* calls per hour and night were bimodal. Our data showed a first activity peak at dusk (21:30–22:30 CEST) and a second peak in the morning (04:30– 05:30 CEST), whereas calls of other species were recorded throughout the whole night (data not shown).

Activity patterns that were recorded at the southern entrance of the flight path (fp1) measured in 2006 did not differ significantly from the activity patterns in 2007 (Craddock-Flood's $\chi 2$-test, $\chi 2=3.285$, *d.f.* = 2, *P*= 0.194; *n*= 112 call sequences; Figure 9c). Of the 17 additional sites where we recorded flight activities of *B. barbastellus* only six of them ('t1'–'t6'; Figure 8) could be included in further analyses due to the low number of recorded call sequences. We recorded various activity patterns (unimodal, multimodal or bimodal with one large peak followed by a smaller one; Figure 9d). In most cases they differed significantly from those recorded at the flight path ('t1'–'t6'; Table 6).

Table 6. Recording nights and number of call sequences used for comparison between three sites along a flight path connecting colony roosts western barbastelle bats (fp1-fp3) and six other sampling sites around the roost area (t1-t6). Results of pairwise comparisons (*P*-values; Craddock-Flood's Chi-square test) are given.

Recording nights	N	comparison				
04.06.-05.06.2007			fp1	t1	t2	t3
	8	fp1	-	-	-	-
	3	t1	0.461	-	-	-
	4	t2	0.472	0.139	-	-
	96	t3	<0.001	<0.001	0.003	-
18.06.-25.06.2007			fp1	fp2	fp3	t4
	24	fp1	-	-	-	-
	64	fp2	0.005	-	-	-
	147	fp3	<0.001	0.072	-	-
	14	t4	0.691	<0.001	<0.001	-
31.07.-13.08.2007			fp1	fp2	fp3	t4
	52	fp1	-	-	-	-
	78	fp2	0.858	-	-	-
	93	fp3	0.459	0.440	-	-
	26	t4	<0.001	<0.001	<0.001	-
17.07.-27.07.2007			fp1	t5	t6	-
	47	fp1	-	-	-	-
	5	t5	0.002		-	-
	26	t6	<0.001	0.298	-	-

4. Discussion.

All members of our western barbastelle colony roosted in dead trees (mainly oaks) with large pieces of loose bark which occur in great quantities through out our study area. Forest-dwelling barbastelles selected similar roost types in other study areas across Europe (Dietz *et al.*, 2007). However, the occurrence of the species seems not to depend on a specific forest type (e.g., deciduous, mixed or coniferous forest; Spitzenberger, 1993; Steinhauser, 2002; Russo *et al.*, 2005; Hillen *et al.*, 2009). One exception is reported by Sierro (1999) who radio-tracked lactating western barbastelles to a rock crevice in the Swiss Alps. Russo *et al.* (2005) reported varying roost switches depending on the reproductive status. They found that lactating females switched roosts less often, probably because frequent movements would require more energy. Since most of our study animals were lactating, we could not test for an effect of reproductive status on the roost switching rate. However, our data at least indicate a high variability among females with regard to roost switching rate and roost selection.

Loose bark is among the least stable roost type for bats as it can be easily destroyed by heavy rain, wind and other agents (Barclay & Brigham, 2001). In general, roosts in trees are less permanent compared to caves or artificial roosts in buildings. Bat species that occupy instable roosts often display a pronounced roost-switching behaviour (Lewis, 1995; Barclay & Kurta, 2007). Trousdale *et al.* (2008) described a correlation between roost quality and roost-switching rate in Rafinesque`s big-eared bats (*Corynorhinus rafinesquii*) which use natural and artificial roosts. Bats roosting in natural sites switched more frequently than those occupying artificial ones. Colony members have to remember a large number of alternative roost trees and to explore new roosts within their range. There are two main behavioural patterns to overcome this problem (not mutually exclusive), both of which have already been observed in forest-dwelling bats (Lewis, 1995): a) fission and fusion of subgroups that are spread over a colony’s home range, and b) fidelity to large roosting areas instead of single roosts.

Fission-fusion behaviour has been reported for other bat species, including *Myotis bechsteinii* (Kerth & König, 1999) and *Eptesicus fuscus* (Willis & Brigham, 2004). Their colony members frequently moved between roosts and thus kept in contact with other communally roosting females. The behaviour of simultaneously tracked females with changing association to other colony members (Table 5) is in concordance with a fission-fusion behaviour also in *B. barbastellus*. The pronounced swarming behaviour around the roost in the evening and in the morning indicated social interaction between the colony members and a joint decision for a specific roost tree. We interpret this behaviour as fission-fusion behaviour, although the bats may have occupied different (but adjacent) pieces of loose bark. Fidelity to roost areas with a variety of different roosts is an important characteristic of forest-dwelling bats which may have direct consequences on the management of forested areas where maternity colonies exist. We showed that western barbastelles display fidelity to a roost area over at least four years and to single roost trees over at least three years (see also Russo *et al.*, 2004). Repeated tracking of the same individuals emphasised their plasticity with regard to roosting habitat. A similar behaviour has been shown in a variety of other forest-dwelling species such as *Myotis sodalis*(Kurta & Murray, 2002), *Myotis californicus* (Barclay & Brigham, 2001), *Pipistrellus subflavus* (Veilleux & Veilleux, 2004) and *Myotis nattereri* (Smith & Racey, 2005).

The results of our automated call records also support the roost area fidelity hypothesis in the western barbastelle. Animals regularly used a forest track that connects the roost clusters A/A’ and B. This corridor was evidently used over its full length and fulfilled a function as a straight-line connection between different core areas over at least two years. The bimodal activity patterns that characterised this flight path also indicated a function as a commuting corridor between the roosts: the first peak coincidedwith the roost emergence and the second peak in the morning with the return to the roost and swarming (pers. observation). Additional and numerous captures of western barbastelle bats along this flight path in previous years indicated that it was already in use for more than two years. We also analysed the ranging patterns of the barbastelle bats whose roosts were analysed in the present work (Hillen *et al.*, 2009). These bats foraged in individual home ranges within a radius of 13 km, and they travelled to their foraging grounds on a straight path. The flight path connecting the core roosting areas was not used to travel to the foraging grounds. Swarming behaviour at the roosts and increasing commuting activities between the roosts coincided with the first flights of the juveniles (July–August). In two cases we were able to simultaneously capture a female and a juvenile in the same mist-net at the entrance of the flight path (fp1). A similar fidelity to commuting corridors was shown for *M. sodalis* through a capture-recapture experiment (Kurta & Murray, 2002). Lewis (1995) suggested that fidelity to roost areas may facilitate locating new roosts and thus may help to save energy. The same may be true for the reuse of commuting corridors as they facilitate orientation, especially for juvenile bats that exploit the colony home range, and thus maintain the ‘social network’ of colony members.

Our findings accentuate the need for an intensive investigation of the spatial organisation of roosts and commuting corridors in endangered bat species, such as the western barbastelle. These bats display a pronounced fidelity to a roost complex including commuting corridors, rather than to single roost trees within the home range. This characteristic emphasises the need for the conservation of entire forest patches with numerous suitable roost trees as well as the potential to provide such trees for the future rather than the protection of single roost trees. The obvious fidelity to commuting corridors has additional implications for conservation practise at the interface of infrastructure development (e.g., expansion of road networks) and nature conservation (see Greenaway, 2004). Underpasses or other wildlife crossings are sometimes considered adequate substitutes for commuting corridors that have been trenched by roads. However, such artificial crossings are still up for debate (see Kerth & Melber, 2009).

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Chapter III. Sex-specific habitat selection in an edge habitat specialist, the western barbastelle bat.

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Abstract.

Niche variation hypothesis suggests that a population's ability to react to varying environmental conditions depend on the behavioural variability of its members. However, most studies on bats, including work on the habitat use of the western barbastelle bat, *Barbastella barbastellus*, have not considered sex-specific and individual variability. We studied the habitat use of 12 female and five male western barbastelle bats within their home ranges with respect to available habitat types by applying kernel methods and Euclidean distances. Our results indicate individual habitat preferences within and among sexes of this species. Females preferred deciduous forest and linear elements within the forest. Males used habitat patches in the vicinity of the maternity colony and preferred forest edges and open habitats. Our results strongly suggest that both sexes' as well as individual variability in habitat choice are to be considered to assess a population' s true potential to react on habitat alterations.

1. Introduction.

Information on the habitat use of animals is usually based on a set of individual data collected from a random sample of population or maternity colony members that are later on pooled for analysis. Recent studies increasingly focused on individual niche variation since animals often respond individually to varying habitat conditions (Bolnick *et al.*, 2003). Individual niche variation within species may be influenced by different factors, such as reproductive status, age class or sex, and even by the individual character (Wolf *et al.*, 2007; Biro & Stamps, 2008; Boon *et al.*, 2008). Most such studies focused on the behavioural differences leading to sexual segregation (Durell, 2000; Lewis *et al.*, 2002; Ruckstuhl & Neuhaus, 2002; Long *et al.*, 2009; Senior *et al.*, 2009). Sexual segregation can be a result of dimorphism, e.g. in body size, length of bills, or wing load (Durell, 2000), but it is also reported for species with only little morphological variation in the two sexes, such as bats.

Bats, especially those living in temperate zones, display a pronounced sexual segregation in summer. Females form maternity colonies to rear their young, while males usually live alone or, in a few species, form male groups at a great distance from the female colonies (Barclay, 1991; Kunz & Fenton, 2003). Observations of male bats living together with the females are rare and are often linked to a special thermoregulatory behaviour (e.g. in *Plecotus auritus*, Entwistle *et al.*, 2000; *Myotis myotis*, Rodrigues *et al.*, 2003). In late summer and autumn, females and males meet at special swarming sites (often underground sites which may also function as hibernacula) to mate (Parsons *et al.*, 2003; Veith *et al.*, 2004).

Sexual segregation may also affect migration behaviour in both short- (Cryan *et al.*, 2000) and long-distance migrations (Ibanez *et al.*, 2009). Different energetic requirements of females and males (Speakman & Thomas, 2003) and competitive behaviour in males, leading to the exclusion of males from profitable foraging habitat in proximity to the female colony, are assumed to be important factors that drive sexual segregation in bats (Senior *et al.*, 2005). The western barbastelle (*Barbastella barbastellus* Schreber, 1774), which occurs all over Europe except for northern Scandinavia, northern Great Britain, and southern Spain (Dietz *et al.*, 2007), is one of the most endangered European bat species. Previous studies on the summer habitat of western barbastelle bats showed that, depending on the study area, the species used a great variety of different habitats such as coniferous forest (Sierro, 1999), mixed and deciduous forests (Russo *et al.*, 2004) or hedgerow landscapes with small to medium- sized forest patches.

However, it always preferred richly structured forests with a high proportion of old and dead trees that provide roosts for maternity colonies (Rydell *et al.*, 1996; Sierro & Arlettaz, 1997). Such forest habitats also provide a high diversity ofinsects, namely Lepidopterans, the major prey of western barbastelles (Beck, 1995; Rydell *et al.*, 1996; Sierro & Arlettaz, 1997; Barataud, 2004).

Several authors suggested that the western barbastelle prefers linear landscape elements such as tree lines and forest edges as commuting flight corridors (Meschede & Heller, 2000; Steinhauser, 2002; Greenaway, 2004) and foraging habitats (Goldsmith, 2002; Simon *et al.*, 2004). Studies on differential echolocation behaviour and the signal repertoire of the western barbastelle also support the idea of an adaptation to 'edge habitats' (forest edges, tree crowns; Denzinger *et al.*, 2001; Barataud, 2004). However, such assumptions were solely based on only few direct observations of flying bats or on a comparison of habitat types at foraging sites with those available in general (Simon *et al.*, 2004).

We therefore study the habitat use of a population of the western barbastelle, with special emphasis on linear landscape elements. We specifically focus on male and female habitat preferences within individual home ranges by applying a distance-based approach.

2. Materials and methods.

Our study was carried out in the Special Area of Conservation 'Ahringsbachtal' near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany (Figure 10). The area covers ca. 2,000 ha and is located at the edge of a tributary of the river Moselle (mean elevation: 380 m a.s.l.). It is characterised by richly structured deciduous and mixed forests (mainly *Fagus sylvatica*, *Quercus, robur*, *Quercus petraea* and *Pinus sylvestris*) with numerous dead trees, meadows and brooks. Tracking sessions were conducted from June to September in 2004, 2005, 2006 and 2007. Mist-netting, marking and radio- tracking via triangulation of bats is described in more detail in Hillen *et al.* (2009). In total 13 adult females and eight males were fitted with 0.4 g LTM radio transmitters (Titley Electronics Pty. Ltd., Australia). Tracking intervals were 5 to 10 minutes (Hillen *et al.*, 2009). The results of our study presented below are based on data obtained from 12 females and 5 males due to transmitter loss or difficulties in tracking the other animals. The transmitter weight relative to the bats' body weight was always below 5%. Three females were tracked successfully in two years and another two in three years. All bats were tracked in the breeding season when they formed a maternity colony of approx. 10 adult females per year (Hillen, unpubl. data), whereas the males always roosted alone.

Bat fixes were transferred to 1:25,000 topographic maps, and Gauss-Krüger coordinates were determined. They were imported into ArcView GIS 3.2 (ESRI, 1999) and analysed with the Home Range Extension software, HRE (version 3, Rodgers & Carr, 1998). Based on digital orthophotos (resolution 0.5 m per pixel; scale 1:5,000; Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz; licence no. 26 722–1.51), four dominant areal habitat types were distinguished according to their structural properties. In addition, we defined two types of linear habitats as stripes of 10 m width (Table 7 and Appendix Figure A-3). In 2007, 23 ha of coniferous and deciduous forest close to the airport were cleared and the resulting open habitat patches were included in the habitat selection analyses (Appendix Figure A-3).

Table 7. Definition of the habitat types included in habitat selection analysis.

habitat type	characteristics
edge habitat 1	linear elements within forest, i.e. forest tracks and aisles
edge habitat 2	linear elements representing ecotones, i.e. forest edges, hedges, clearings
deciduous forest	dominant species: *Fagus sylvatica*, *Quercus robur/Quercus petraea*
coniferous forest	dominant species: *Picea abies* (plantation)
mixed forest	*Fagus sylvatica*, *Quercus* spec., *Pinus sylvestris*, *Picea abies*
open landscape	meadows, pastures and arable land

The two most commonly used methods that had been used in literature to test for preferences in the habitat use of animals are the Chi-square goodness-of-fit tests for comparison of 'observed' vs. 'expected' habitat use (Neu *et al*., 1974) and the Compositional Analysis (Aebischer *et al*., 1993). Both are based on the classification of single fixes by habitat types, which may be difficult for fixes that fall into habitat edges. An alternative method is based on the measurement of the Euclidean distances between animals' fixes and the nearest patch of a given habitat type (Conner & Plowman, 2001). These 'observed distances' of fixes (representing the observed habitat use) are compared to the distances of random fixes, which would represent a habitat use without any preferences. Conner *et al*. (2003) compared the performance of the Euclidean distance approach to the Chi-square goodness-of-fit test and to the Compositional Analysis. They concluded that patterns of habitat use resulting from the two classification-based analyses may be biased depending on the radio-tracking error and habitat patch sizes. In contrast, distance-based approaches are superior to classification approaches, because they do not require an independent analysis of the radio-tracking error. In the distance-based approach, the distances of imprecise fixes to the preferred habitat will still be lower than random fixes (Conner & Plowman, 2001). Furthermore, this method is applicable to linear and areal habitat types and it is increasingly used in studies of habitat selection (e.g. Menzel *et al*., 2005; Cox *et al.,* 2006; Howell *et al*., 2007; Perry *et al*., 2007; van Etten *et al*., 2007; Korte, 2008).

We here used an implementation of the Euclidean distance approach to assess the individual habitat use of western barbastelle bats. We examined habitat preferences within individual home ranges ('third-order selection'; Johnson, 1980). The study of individual home ranges is an objective approach to define the 'available habitat', especially for highly mobile species such as bats. Individual home ranges (95%-outlines) were estimated for data sets of ≥30 fixes per individual (Seaman *et al*., 1999) and for bats with data from at least three nights via adaptive kernel density estimation with a smoothing factor h_{cv} estimated via least square cross validation, LSCV (Worton, 1989). For across female comparison we applied the mean h_{cv} of all females for individual kernel estimation (Kenward, 2001). The males' home ranges were calculated with the individual smoothing parameters h_{cv}. We then generated an equal number of random fixes within individual home ranges (one random data set per individual and year) in ArcView GIS 3.2 (ESRI, 1999) using the Random Point Generator extension (version 1.3, Jenness, 2005).

We applied a distance-based approach to test for non-random habitat use. We adopted the method of Conner & Plowman (2001) with the exception of ranking of habitat types. They used a MANOVA to test for non-random habitat use across all habitat types. Since our Euclidean distance data did not fit a normal distribution (Kolmogorov-Smirnov-test), we applied non-parametric statistics (Bortz *et al.*, 2008). We calculated the median distance from original fixes to a specific habitat (u) and the median distance from random fixes to this habitat (r) for each individual and each habitat type.

In order to avoid pseudo-replication caused by including several annual data sets of repeatedly tracked females we calculated the median distance from all original fixes across years and used every individual as sampling unit. This procedure was repeated to calculate the median distance from all random fixes to this habitat (r) for the respective animals. We then calculated distance ratios (d) by dividing the elements in u by the elements in r for every habitat type and individual. These distance ratios indicate preference or avoidance of a habitat, with $d < 1$ indicating preference and $d > 1$ indicating avoidance (Conner & Plowman, 2001). The mean vector Δ (termed 'p' in Conner & Plowman, 2001) (= mean of distance ratios (d)) was then tested via Mann-Whitney U-test for a significant difference from a vector of 1 which represents random use of a specific habitat type (exact test). This test was conducted for every habitat type separately. Additionally, we reported annual individual habitat distance ratios d of repeatedly tracked females to show the interannual variability in habitat use.

We finally compared pair-wise distance ratios d to rank the habitats relative to habitat availability via Wilcoxon signed ranks-test (exact test). We used the same methods to analyse the males' radio-tracking data and hereafter we compared the habitat preferences of males and females. Statistical analyses were performed in SPSS 15.0 (SPSS Inc., 2007). The level of statistical significance was always set to $\alpha = 0.05$.

3. Results.

We analysed a total of 12 successfully tracked females, altogether comprising 2,737 fixes (Hillen *et al.*, 2009 and Figure 10), to depict the habitat use by female western barbastelle bats. The number of fixes per animal and year which were included in home range analyses ranged from 32 to 398. Female home range sizes (95%-kernels; with mean $h_{cv} = 0.142$) ranged from 125 to 2,551 ha (Table 8). The home ranges of five successfully tracked males (N = 472 fixes, 58−167 fixes per male; h_{cv} (BM1) = 0.158; h_{cv} (BM2) = 0.050; h_{cv} (BM3) = 0.297; h_{cv} (BM5) = 0.053; h_{cv} (BM6) = 0.328) were smaller than ranges of females, ranging from 88 to 864 ha (Table 8). The home ranges of four males were located in the 'Ahringsbach' valley close to the river Moselle, but one male foraged in close proximity to the maternity colony roosts (see Hillen *et al.*, 2010a).

The availability of habitat types varied between the individual home ranges. Although open landscape dominated the females' home ranges (mean 28%), deciduous forest patches (mean 27%) and coniferous forest (median 19%) also constituted a major part of their home ranges. The males' home ranges were composed mainly of deciduous forest (33%) and open landscape (27%). One male home range lacked patches of mixed forest. Linear landscape elements of edge habitat 1 (forest tracks) and edge habitat 2 (ecotones) formed a dense 'network', although they comprised only a small area within the home ranges of the tracked bats (Table 9).

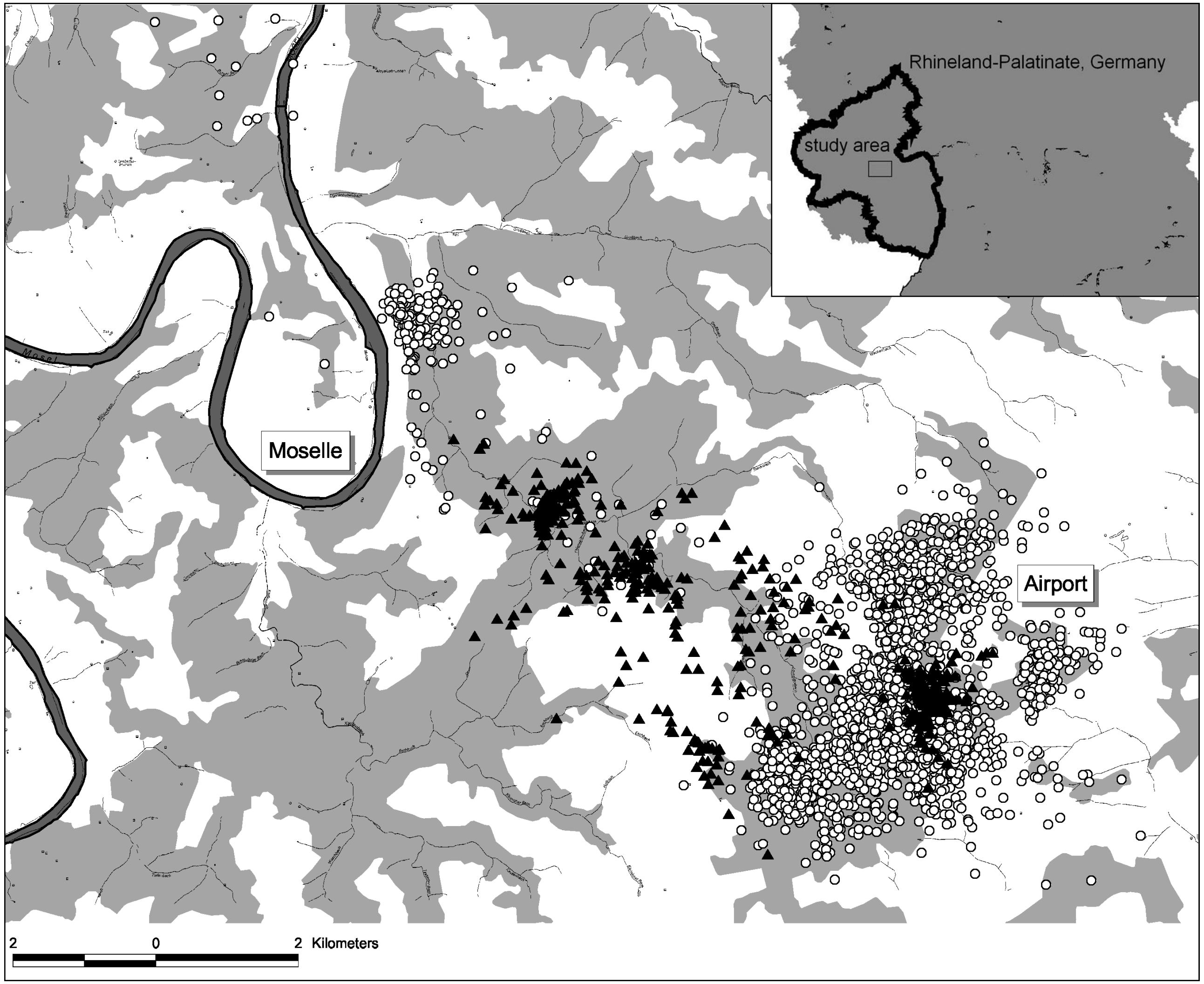

Figure 10. Spatial distribution of bat fixes (12 female and five male western barbastelle bats radio-tracked 2004-2007); white points: female fixes; black triangles: male fixes; grey: forested areas (CORINE Land Cover, data set for Germany, 2000; modified); airport: Frankfurt-Hahn Airport, Rhineland-Palatinate.

Table 8. Number of fixes and home range size of 17 western barbastelle bats (*Barbastella barbastellus*) radio-tracked near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany. Home range sizes were derived from 95%-kernels; x: individual was radio-tagged, but the radio-tracking experiment failed (transmitter loss, battery malfunction).

	# fixes				95% home range size (ha)			
	2004	2005	2006	2007	2004	2005	2006	2007
females								
BF1	98	32	x	231	714	127	-	534
BF2	112	x	-	44	2,551	-	-	160
BF3	98	42	-	398	539	207	-	583
BF4	135	-	-	183	343	-	-	403
BF5	-	32	96	-	-	922	198	-
BF7	-	x	x	132	-	-	-	2,097
BF8	-	181	x	-	-	125	-	-
BF9	-	-	151	-	-	-	399	-
BF10	-	-	-	167	-	-	-	258
BF11	-	-	-	192	-	-	-	352
BF12	-	-	-	207	-	-	-	1,622
BF13	-	-	-	206	-	-	-	1,835
males								
BM1	91	-	-	-	558	-	-	-
BM2	78	-	-	-	344	-	-	-
BM3	-	90	-	-	-	-	93	-
BM5	-	-	167	-	-	-	88	-
BM6	-	-	58	-	-	-	864	-

Table 9. Mean habitat availability within home ranges of 17 western barbastelle bats (12 females, five males); * mean of four male home ranges).

habitat type	mean availability (% home range area)	
	females	males
edge habitat 1 (forest tracks)	6	8
edge habitat 2 (ecotones)	5	2
deciduous forest	27	33
coniferous forest	19	17
mixed forest	4	6 *
open landscape	28	27

We were able to reject the hypothesis of a random habitat use across 12 females for edge habitat 1 (Mann-Whitney U = 24, P = 0.005), edge habitat 2 (U = 36, P = 0.039) and deciduous forest (U = 90, $P \leq 0.001$). We excluded one male (BM 3) from this analysis to maintain comparability with the females' data because mixed forest was not available to this male, whereas all females' home ranges contained mixed forest. Four males used edge habitat 2 and open landscape in a non-random fashion (U = 0, P = 0.029 for both habitat types), but there were no significant differences between the habitat types (pair-wise tests). Females` fixes were significantly closer to deciduous forest than to mixed forest (Wilcoxon Z = -2.040, P = 0.042), edge habitat 1 (Z = -2.040, P = 0.042), edge habitat 2 (Z = -2.353, P = 0.016) and open landscape (Z = -2.432, P = 0.012). They were also closer to edge habitat 1 than to open landscape (Z = -2.118, P = 0.034) and closer to edge habitat 2 than to open landscape (Z = -2.353, P = 0.016). There were no significant differences between other pairs of habitats. The five repeatedly tracked females (BF1−5) showed varying habitat use across years regarding areal habitat types, but a preference for edge habitats, indicated by individual distance ratios *d*, tended to remain constant over time (Table 10).

The males' fixes were closer to open habitats and ecotones, such as forest edges, whereas the females foraged in deciduous forest patches and along the linear landscape elements within the forest, as indicated by the mean of the distance ratios (**Δ**, Table 11). The males' preferences appeared to be the opposite of the females' (Figure 11), even though habitat availability within the home ranges of both sexes was similar.

Table 10. Annual individual habitat distance ratios d of tracked western barbastelle bats including annual data for five repeatedly tracked females; d < 1 indicating preference; d > 1 indicating avoidance; conf: coniferous forest; mixf: mixed forest; decf: deciduous forest; open: open landscape; edg 1: edge habitat 1; edg 2: edge habitat 2; x: habitat not available within home range.

animal	year	*d* conf	*d* mixf	*d* decf	*d* open	*d* edg 1	*d* edg 2
BF1	2004	0.705	1.089	0.347	1.101	0.716	0.740
BF1	2005	0.981	1.083	0.000	1.493	0.885	1.216
BF1	2007	0.562	1.135	0.167	0.902	0.473	0.670
BF2	2004	0.312	1.131	0.347	0.818	0.804	0.721
BF2	2007	0.619	0.273	6.289	1.995	1.053	1.572
BF3	2004	0.796	0.861	0.813	1.251	0.720	1.431
BF3	2005	2.208	1.362	0.480	0.725	0.775	0.781
BF3	2007	1.365	0.905	0.698	0.889	0.963	0.833
BF4	2004	1.046	1.147	0.725	0.200	0.840	0.931
BF4	2007	1.784	1.358	1.203	0.000	1.321	1.022
BF5	2005	0.661	0.486	0.324	2.197	1.393	1.032
BF5	2006	0.032	0.385	1.697	1.944	0.615	1.134
BF7	2007	1.365	0.905	0.698	0.889	0.963	0.833
BF8	2005	1.914	1.124	0.000	0.879	0.605	0.789
BF9	2006	0.523	0.703	0.256	2.755	0.683	1.098
BF10	2007	1.519	1.244	0.000	1.400	0.799	0.844
BF11	2007	0.706	1.135	0.791	0.878	1.037	0.821
BF12	2007	1.311	1.420	0.001	1.970	0.524	0.914
BF13	2007	0.473	0.450	0.408	1.048	0.459	0.637
BM1	2004	0.786	0.375	5.797	0.498	0.703	0.814
BM2	2004	1.773	2.750	0.302	0.633	0.524	3.111
BM3	2005	0.514	x	0.000	0.739	0.712	1.897
BM5	2006	1.224	0.688	1.065	0.879	0.884	0.877
BM6	2006	1.136	0.754	0.609	0.000	0.580	0.836

Table 11. Mean habitat distance ratios Δ (= mean (d)) of 17 western barbastelle bats (12 females, five males); Δ < 1 indicating preference; Δ > 1 indicating avoidance; conf: coniferous forest; mixf: mixed forest; decf: deciduous forest; open: open landscape; edg 1: edge habitat 1; edg 2: edge habitat 2.

	Δ conf	**Δ** mixf	**Δ** decf	**Δ** edg 1	**Δ** edg 2	**Δ** open
females	0.94	0.93	0.53	0.76	0.89	1.31
males	1.23	1.14	1.94	1.41	0.67	0.50

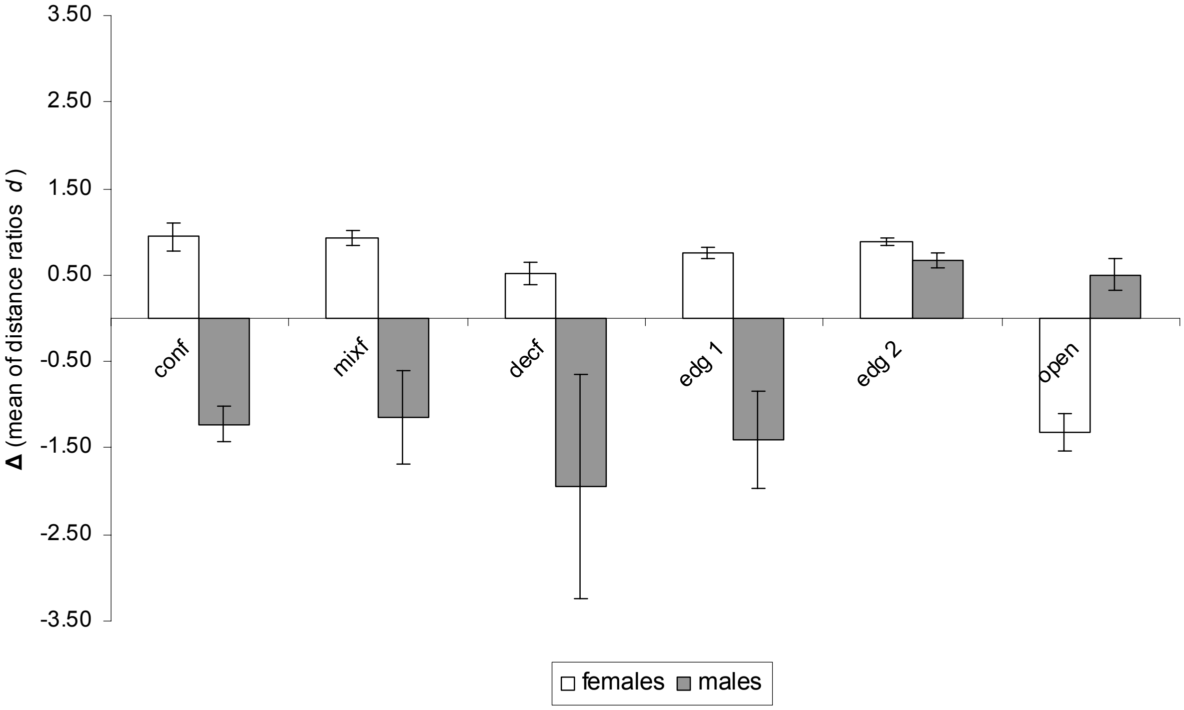

Figure 11. Mean distance ratios (Δ) and standard errors of 12 female and four male western barbastelle bats. Δ < 1 indicate preference; Δ > 1 indicate avoidance; original Δ -values and standard errors > 0; mean distance ratios and standard errors were multiplied by −1 to facilitate the differentiation of preferred and avoided habitat types by females and males; conf: coniferous forest; mixf: mixed forest; decf: deciduous forest; edg 1: edge habitat 1; edg 2: edge habitat 2; open: open landscape; * significant non-random use of habitat type.

4. Discussion.

Our distance-based approach resulted in different patterns of habitat use in females and males. Females preferred deciduous forest and the linear elements within the forest stands, whereas the males preferred open landscape and forest edges. Females tracked in different years showed a high across year fidelity to their home ranges (95% kernel estimations), but with varying core areas (Hillen *et al.*, 2009) and varying, in one case (mixed forest in BF3) even reverse, annual habitat preferences (this study). Like other mammals, western barbastelle bats seem to react to varying prey densities, although its food range is narrow compared to other bat species' food ranges. Barbastelle bats mainly feed on small to medium-sized moths, but it does not rely on certain prey species. A recent study conducted by Andreas *et al.* (2008) revealed an opportunistic niche widening ability during period of decreasing abundance of the preferred prey, e.g. hunting for larger Lepidopterans. Other prey taxa (Neuroptera, Arachnida) can also play an important role (Steinhauser, 2002). This opportunistic behaviour may explain why habitat preferences within and among individuals are highly variable, and illustrates the species' high plasticity in foraging habitat choice regarding vegetation type (coniferous, mixed or deciduous forest), but not regarding landscape elements.

Depending on the landscape, western barbastelle populations preferred either hedgerow landscapes in the lowland, forested low mountain ranges or even alpine valleys (Dietz *et al.*, 2007). However, they always showed a preference for forested areas (Sierro, 1999; Meschede & Heller, 2000; Steinhauser, 2002; Spitzenberger, 1993), albeit without preference for any specific forest type. Linear landscape elements are of major importance for western barbastelle bats. They may be used as commuting corridors or as specific hunting grounds, as has been shown in a variety of other bat species such as *Myotis emarginatus* (Krull *et al.*, 1991), *Myotis dasycneme* (Verboom *et al.*, 1999), *Pipistrellus pipistrellus* (Verboom & Huitema, 1997), *Rhinolophus euryale* (Goiti *et al.*, 2008), *Corynorhinus townsendii* (Clark *et al.*, 1993; Fellers & Pierson, 2002) and *Chalinolobus tuberculatus* (O'Donnell & Christie, 2006). Edge habitats are assumed to function either as shelter from predators, or as profitable foraging area with a high insect density, or as acoustic landmarks for commuting flights across the landscape. Linear elements within forested areas and hedgerows may certainly provide shelter for specimens that emerge early from the roost (Limpens & Kapteyn, 1991; Verboom & Huitema, 1997; Greenaway, 2004). Roost emergence in our study area started early in the evening (20 minutes after sunset; females and males), therefore predator avoidance may certainly be invoked as a factor that influences the observed behaviour, but it does not 261 sufficiently explain the preference for edge habitats that was found in our study. Fixes along linear landscape elements were found throughout all radio-tracking nights and in the home ranges of all animals, but only some of them were situated near roosts or along distinct commuting corridors.

A major factor that causes a preference for linear landscape elements may be the higher densities of insects, especially moths, the major prey of *B. barbastellus*, along hedge rows or forest corridors (Lewis, 1969; Pasek, 1988; Pedgley *et al*., 1990). An experimental field study (Fukui *et al*., 2006) showed that bat activity along a stream, another type of linear landscape element, is influenced by the number of emerging aquatic insects. The ability of bats to respond to varying prey densities may explain a shift of core hunting areas and variable use of habitat types within their home ranges which are used for years (Hillen *et al*., 2009).

The differential habitat use of females and males observed in our study area still remains to be explained. The radio-tracked males were recorded in more open habitats (pastures etc.) and forest edges, although all habitat types were available to them. Additionally, the home ranges of four males were located along the 'Ahringsbach' valley, but they used the forested valley itself as well as the plains. In contrast, the females' home ranges concentrated on a plateau near the roosting area, but they also foraged along the valley and even crossed the river Moselle to reach hunting areas. We do not assume that the home range distribution results from the distribution of suitable roosts only, because natural roosts (trees with loose bark, see Hillen *et al*., 2010a) and alternative roosts (houses with slate cladding, bat boxes) were available in large numbers throughout the study area.

Sexual segregation in bats has been reported for several species. Safi *et al.* (2007) found that male parti-coloured bats (*Vespertilio murinus*) covered larger foraging areas and were more flexible in habitat use than females that were restricted to more profitable hunting areas near lakes. Reproductive females need more energy during lactation and thus occupy high-quality habitats (Speakman & Thomas, 2003), whereas the males are able to use suboptimal habitats (open landscape) and to compensate lower energy intake by extended torpor, as suggested by Barclay (1991). Wilkinson & Barclay, (1997) obtained similar data from radio-tagged male big brown bats (*Eptesicus fuscus*) that covered longer commuting distances and foraging grounds than females. In other bat species (*Corynorhinus townsendii*, Fellers & Pierson, 2002; *Rhinolophus euryale*, Goiti *et al.*, 2006) females covered significantly greater distances to their foraging grounds than males. Nevertheless, individuals of both sexes displayed a pronounced variability in commuting distances and home range sizes. *Corynorhinus* and *Rhinolophus* are described as gleaning species, while western barbastelles and parti-coloured bats are aerial hawkers. In general, behavioural patterns within and between sexes vary across species and foraging mode.

Our results indicate that foraging pattern and habitat availability may influence behavioural differences between sexes. In our study, males had smaller home ranges than females, while both sexes showed variable home range sizes. The latter indicates flexibility in habitat use as reported for other species (*Myotis bechsteinii*, Kerth *et al.,* 2002). Steinhauser (2002) also reported very small home ranges for male western barbastelles. Female barbastelle bats are not restricted to profitable areas near the maternity roosts (as reported for *V. murinus*; Safi *et al.*, 2007), rather they are able to cover large distances to reach hunting areas without being disadvantaged. We identified linear landscape elements within the forests and deciduous forest as preferred foraging habitats, both may provide high insect densities (Lewis, 1969) and shelter facilitating extended foraging even in cold or rainy nights and thus increasing the energy intake of the females. Males may also avoid competition with the females that display inter-annual site fidelity to their home ranges, but competition between sexes still remains to be examined in more detail.

Our data indicate sexual segregation in western barbastelle bats, although we analysed a small sample of 12 females (due to the fact that the study colony is very small) and four males only. Nevertheless, our analyses clearly show that characterising habitat preferences of bats through an analysis of individual behaviour is well suited to account for the variability across all members of a population. Variation in individual niches, e.g. reflected by individual foraging behaviour, may positively affect the viability of populations (Bolnick *et al.*, 2003), but it also highlights the need for detailed analysis of habitat requirements of both sexes of a species to design effective conservation strategies for entire populations.

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Chapter IV. Resource partitioning in three syntopic forest-dwelling bat species.

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Abstract.

Resource partitioning in syntopic bats is mainly studied through comparative ecomorphology and behavioural ecology. Only few studies focussed on direct observation of syntopic bats and their ability to react individually on competition for foraging habitats and roosts. Here we used simultaneous radio-tracking of syntopic forest-dwelling bats, the western barbastelle (*Barbastella barbastellus*), Bechstein's bat (*Myotis bechsteinii*) and the brown long-eared bat (*Plecotus auritus*) to analyse individual and species-specific foraging habitat and roost site selection. We estimated niche partitioning via Euclidean distance analyses to landscape elements and via Pianka's niche overlap index for roost types. We analysed a total of 2,278 fixes and 54 roosts of 15 bats. Home range overlap ranged from 0 to 52% in interspecific pairs and from 0 to 35% in intraspecific pairs, indicating some spatial segregation between and within species. Western barbastelles and Bechstein's bats stayed significantly closer to the forest than brown long-eared bats. Female barbastelles also foraged significantly closer to forest tracks, which were avoided by female brown long-eared and Bechstein's bats. Female and male brown long-eared bats were found close to open habitats which were avoided by the other two species. We found a high niche overlap in terms of roost height, but low overlap in terms of roost type and roost tree species among the three bat species. Woodpecker holes and natural cavities in live oaks appeared to be the preferred roost structures of Bechstein's bats, crevices and basal hollows in live beeches were preferred by brown long-eared bats. Western barbastelles roosted almost exclusively under the loose bark of dead oaks. Across all studied niche dimensions our results indicate a partial segregation of the three species in syntopy. Individual niche variation may allow these specialised forest-dwelling bat species to minimize competition when foraging and roosting in syntopy.

1. Introduction.

Bat communities are unique among mammals. Even in the temperate climatic zone they usually comprise a much great number of ecologically similar species than any other mammalian order. This is even more amazing since all temperate zone species basically utilise the same food resource: flying nocturnal insects. Consequently, within this comparatively narrow trophic niche, syntopic bat species must further specialize to avoid or at least minimize competition for food resources.

Within forests, available space for roosting is restricted to only a few principle roost types available at trees. This adds further competitive pressure on syntopic forest species. Therefore, different strategies that facilitate resource partitioning must have evolved to allow for coexistence of forest dwelling bat species.

Among syntopic forest bats, differences in habitat use are well documented (Russo *et al.*, 2005 a; Nicholls & Racey, 2006). Differential prey selection (Arlettaz *et al.*, 1997; Arlettaz, 1999) as well as temporal habitat partitioning and exploitative competition (Bonaccorso *et al.*, 2006) have been described. Differences in echolocation signals and ecomorphological traits, such as the wing aspect ratio, are further indicators of resource partitioning among forest bats through foraging in different microhabitats and on special prey items (Norberg 1981; Saunders& Barclay, 1992; Siemers & Schnitzler, 2004).

Ecomorphology is an indirect measure of resource partitioning in bats and may not always suffice to explain habitat selection in syntopic species. *Myotis myotis* and *M. blythii,* two morphologically similar species, are clearly adapted to different habitat structures and prey items (Arlettaz, 1999). Other syntopic species differ in foraging behaviour, foraging habitat and roost preferences (Lee & McCracken, 2004; Campbell *et al.*, 2006; Jacobs & Barclay, 2009; Timpone *et al.*, 2009). Direct and synchronous observation of roost selection and foraging behaviour may therefore best describe niche segregation among syntopic forest species.

The western barbastelle (*Barbastella barbastellus*), Bechstein's bat (*Myotis bechsteinii*) and the brown long-eared bat (*Plecotus auritus*) are typical forest-dwelling species of Central Europe. They mainly forage in forest habitats (Schlapp, 1990; Meschede & Heller, 2000;

Greenaway & Hill, 2005; Kerth *et al*., 2002; Russo *et al.*, 2005 b; Dietz *et al*., 2007; Hillen *et al*., 2011; Fuhrmann & Seitz, 1992; Entwistle *et al.*, 1996), although occasionally they also hunt outside forests (Howard, 1995; Goldsmith 2002; Dietz, 2009; Hillen *et al*., 2010 b). Brown long-eared bats appear to be most flexible in their foraging habitat choice, since they are more often observed to hunt along tree lines, hedgerows as well as in orchards and gardens (see references in Meschede & Heller, 2000) than the other two species. They use both aerial hawking and foliage and ground gleaning as major foraging strategies (Anderson & Racey, 1991). Bechstein's bats use aerial hawking as well as foliage and ground gleaning to feed on various insects and spiders, although moths constitute their most important prey (Wolz, 1993; Wolz, 2002). In contrast, the western barbastelle predominantly hunts inside forests as an aerial-hawking species, although some indirect evidence exists for gleaning (Rydell *et al.* 1996 found plant remains, spiders and crane-flies in their droppings). They usually feed on small prey items with a wing span <30 mm (Geometridae, Pyralidae; Beck, 1995; Sierro & Arlettaz, 1997; Rydell *et al*., 1996), with some potential to feed on larger insects (Arctiidae and others; wing span >30 mm) due to seasonal shifts in prey availability (Andreas *et al*., 2008).

Western barbastelles prefer roosts under the loose bark of dead or ill trees (Russo *et al*., 2005 b; Hillen *et al*., 2010 a). Roost preferences of brown long-eared bats and Bechstein's bats are different, with both usually occupying woodpecker holes and other tree cavities.

We here test the hypothesis that, despite the evidence for substantial overlap in single niche dimensions, *B. barbastellus*, *P. auritus* and *M. bechsteinii* clearly segregate in syntopy. We use radio-tracking to quantify individual and species-specific home ranges, foraging habitat preferences and roost site selection.

2. Materials and methods.

Our study was carried out in the Special Area of Conservation 'Ahringsbachtal' near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany. A total of 15 bat species including several cavity-dwelling species (*Myotis nattereri*, *Nyctalus noctula*, *Nyctalus leisleri*) were recorded via mist-netting. Tracking sessions were conducted in 2006 from June to September.

Bats were captured with mist nets in potential foraging grounds or along flight paths close to their maternity roosts. Individuals were marked with aluminium split rings around the forearm (Deutsche Beringungszentrale, Museum Alexander Koenig, Bonn). For radio-tracking we used 0.4 g LTM radio transmitters (Titley Electronics Pty. Ltd., Australia) and LB-2 radio transmitters (Holohil Systems, Ltd., Canada, Figure 12). Transmitter weight relative to body weight was always below 5% in the Bechstein's bats and the western barbastelles and ranged between 4.6-5.6% in the brown long-eared bat. Three- and five-element Yagi antennas (Telonics Inc., USA; Sirtrack, New Zealand) were combined with Yupiteru MVT 7100 and AOR AR 8200 receivers to track the bats via synchronised triangulation.

We simultaneously tracked species pairs in order to obtain data that allowed for direct comparison. Animal fixes were usually taken every 5 min. For some animals we had to switch to 10 min intervals. In total, four barbastelle bats (two females, two males), seven Bechstein's bats (four females, three males) and four brown long-eared bats (two females, two males) were tracked simultaneously. Females were tracked during lactation and early post-lactation period. The radio-tracked males lived solitary in the vicinity of the maternity colonies.

Emergence from roosts was observed to assess roost height and the number of used roost structures. Hand-held bat detectors (Pettersson D240x, Pettersson Elektronik AB, Uppsala) were used for additional species identification.

Bat fixes were transferred to 1:25,000 topographic maps, and Gauss-Krüger coordinates were determined and imported into ArcView GIS 3.2 (ESRI, 1999). A map of habitat types and linear landscape elements was produced on the basis of digital orthophotos (resolution 0.5 m per pixel; scale 1:5,000; Hillen *et al.*, 2011).

Figure 12. A male brown long-eared bat (left) and a male Bechstein's bat (right), both fitted with radio-transmitters.

We compared the habitat use of syntopic *B. barbastellus*, *M. bechsteinii* and *P. auritus* using Euclidean distances of bat fixes from habitat types. Available forest types (coniferous, mixed and deciduous forest) were merged into a single habitat type (‘forest') since all focal species are known to utilise a variety of different forest habitats (Dietz *et al.*, 2007; Benzal, 1991; Sierro, 1999; Albrecht *et al.,* 2002; Meschede & Heller, 2000). Further landscape elements distinguished for analysis are forest tracks ('edge habitat 1'), ecotones ('edge habitat 2') and 'open landscape' (meadows etc.).

Euclidean distances were pooled for each sex and species. Habitat use of females and males was analysed separately since recent studies have shown that sexual segregation is widespread in bats (Senior *et al.,* 2005, and references therein). Female and male bats have different roosting requirements and energy demands, so they are likely to use different habitats. Euclidian distances were compared for all landscape elements via median tests for the three species together and via Mann-Whitney-U-test for pairwise comparisons. Females and males were analysed separately.

We included additional roost data of one male brown long-eared bat and two female western barbastelle bats that could not be radio-tracked successfully in their foraging habitats in 2006, but that were located in their roosts.

Roosts were located every morning via triangulation. Exact roost positions were then determined using a GPS (Garmin 12 XL). As roost characteristics we recorded if the roost was of natural or artificial origin, the roost type (woodpecker hole, basal hollow, loose bark etc.), the tree species and the roost height (measured in metres with a laser-hypsometer, Opti-Logic 400 LH; roost height was transferred into height classes). Since some roosts were not visible from the ground we were not able to determine their respective roost characteristics.

Frequency distributions of qualitative roost characteristics (roost structure and height, tree species) were compared using Craddock-Flood-tests for small sample sizes or Haldane-Dawson-tests for contingency tables with more than five rows and/or columns and small sample sizes (Haldane, 1940; Craddock & Flood, 1970; Bortz *et al.,* 2008) using BIAS 8.4.5 (epsilon-Verlag, 2008). Niche overlap was assessed through Pianka's index (Pianka, 1973) using roost characteristics instead of food resources. This index ranges from 0 (no overlap) to 1 (total overlap). We calculated Pianka's index for roost height, tree species and roost type.

In order to assess differential spatial roost selection among species we calculated Euclidean distances of the roosts to three landscape elements ('open landscape', 'edge habitat 1' and 'edge habitat 2') and pooled them for each sex and species. We had to omit the habitat type 'forest' from this analysis since all roost were found inside forests. Again females and males were analysed separately (median tests for all three species and Mann-Whitney-U-test for pairwise comparisons).

Unless otherwise indicated, all analyses were run in SPSS 15.0 (SPSS Inc., 2007), box-plot graphics were produced in Statistica 7.1 (StatSoft Inc., 2005).

3. Results.

We collected 2,278 fixes from 15 individuals (Table 12). Two pairs of *B. barbastellus* - *P. auritus*, two pairs of *M. bechsteinii* - *P. auritus* and one pair of *B. barbastellus* - *M. bechsteinii* were tracked simultaneously. Home range sizes ranged from 44 to 864 ha, core areas were much smaller (6-177 ha, Table 12). Bechstein's bats had smaller home ranges and core areas than brown long-eared bats and barbastelles. Both females and males foraged within a radius of 1-3 km around their roosts (Figure 13). Home ranges and core areas overlapped between 0 to 52% and 0 to 42% in interspecific pairs and between 0 to 35% and 0 to 40% in intraspecific pairs. Within species, females showed 0 to 35% home range and 0 to 26% core area overlap.

Table 12. Sample sizes, home range and core area sizes and commuting distances of 15 successfully radio-tracked bats near Frankfurt-Hahn airport, Rhineland-Palatinate.

	N fixes	95% kernel home range size (ha)	50% kernel core area size (ha)	median distance roosts - fixes (m)	maximum distance roosts - fixes (m)
females:					
BF5	96	198	34	355	2,929
BF9	151	399	15	528	2,638
males:					
BM5	155	88	14	408	1,429
BM6	58	864	177	1,472	2,621
females:					
BEF1	136	201	19	616	1,818
BEF2	87	205	19	647	2,596
BEF3	242	98	13	289	1,185
BEF4	61	87	14	236	1,108
males:					
BEM2	79	139	15	239	898
BEM3	77	44	6	287	740
BEM4	297	126	18	360	1,117
females:					
LF1	35	266	33	291	1,296
LF2	256	566	77	582	2,121
males:					
LM2	116	435	47	1,103	2,907
LM3	432	217	17	218	1,424

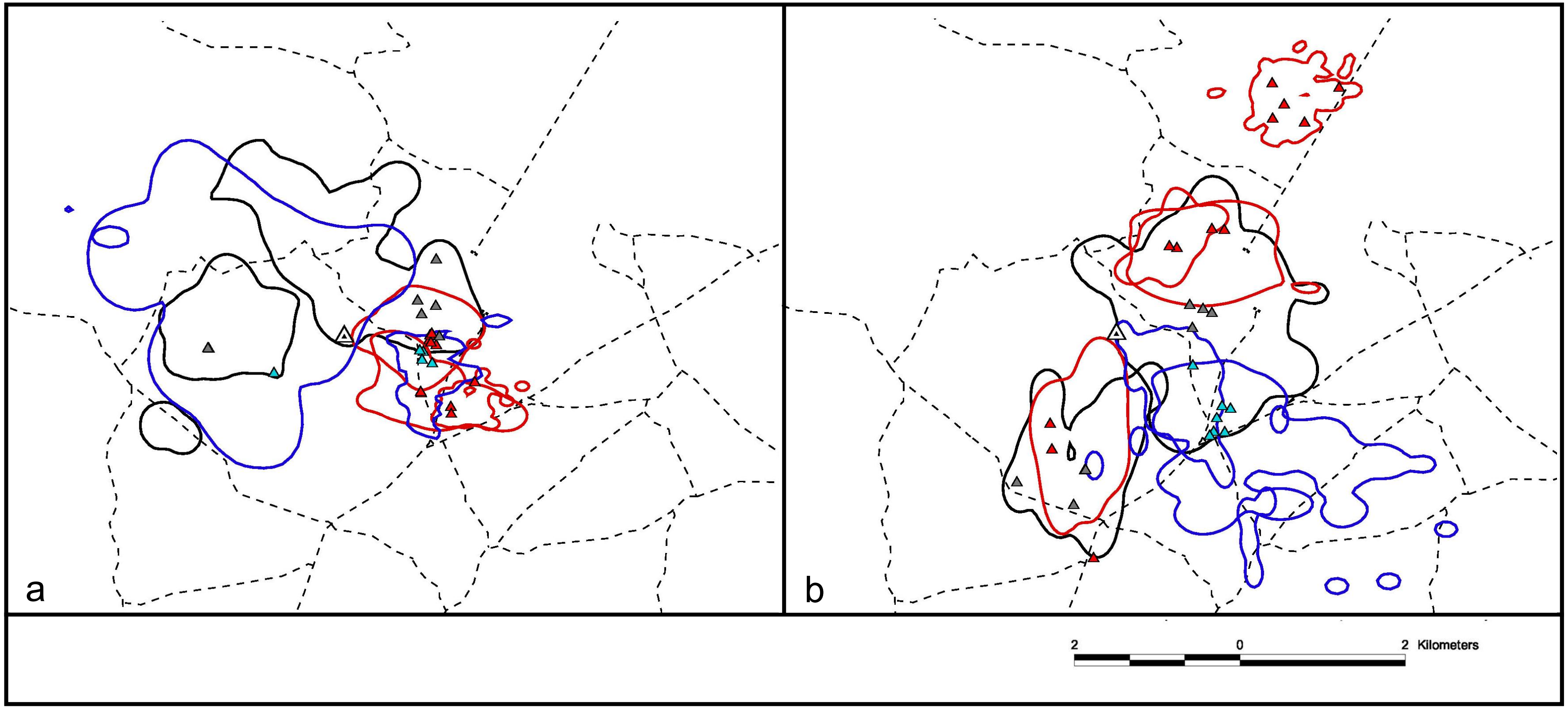

Figure 13. Spatial arrangement of the home ranges and roosts of a) male and b) female bats; blue lines: *B. barbastellus*; black lines: *P. auritus*; red lines: *M. bechsteinii*; blue triangles: *B. barbastellus* roosts; grey triangles: *P. auritus* roosts; red triangles: *M. bechsteinii* roosts; black dashed lines: roads; white triangle: a trig point (49°55'38.78" N, 7°13'30.74" E) in the central SAC; all home ranges were located around this trig point.

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The Euclidean distance data indicate a partial spatial separation of the three syntopic species. Female and male barbastelles and Bechstein's bats foraged significantly closer to forest than brown long-eared bats (Table 13 and Figure 14). Female barbastelles also foraged significantly closer to edge habitat 1 (forest tracks), which were avoided by female brown long-eared bats and Bechstein's bats. Male Bechstein's bats were located close to open landscape. Male long-eared bats preferred ecotones (edge habitat 2) and open landscape. Female brown long-eared bats were also found close to open habitats that were avoided by the other two species. One male and one female brown long-eared bat regularly commuted from natural roosts in the forest (trees, see below) to foraging grounds in a nearby village (hedgerows, gardens).

Table 13. Ranking of preferences for four habitat types in three syntopic bat species; ranking is based on significant differences between the distance data sets.

landscape elements	females	males
forest	(*Mbec*, *Bbar*) < *Paur*	*Bbar* < *Mbec* < *Paur*
edg 1 (forest tracks)	*Bbar* < *Mbec* < *Paur*	*Bbar* < *Mbec* < *Paur*
edg 2 (ecotones)	*Mbec* = *Paur*, *Mbec* = *Bbar*, *Mbec* < *Bbar*	*Paur* < (*Mbec*, *Bbar*)
open landscape	*Paur* < (*Mbec*, *Bbar*)	*Paur* < *Mbec* < *Bbar*

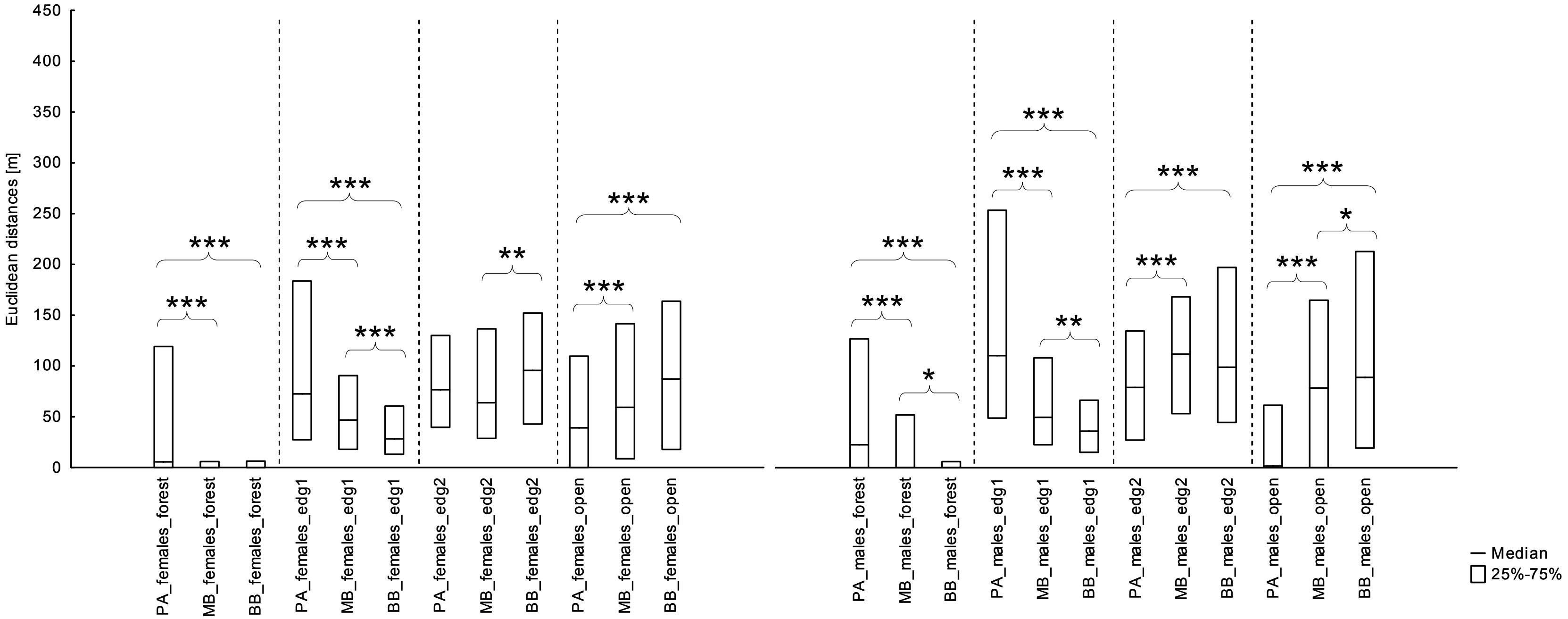

Figure 14. Box-plots showing the Euclidean distances from bat fixes to the habitat types and the results of the tests on interspecific differences in habitat selection (all species: median test; species pairs: Mann-Whitney-U-test); a) females; b) males; PA: *P. auritus*; MB: *M. bechsteinii*; BB: *B. barbastellus*; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

All radio-tracked bats used natural roosts in trees. We found 22 roost trees used by Bechstein's bats (12 used by females/10 used by males), 18 used by brown long-eared bats (8/10) and 14 used by western barbastelles (8/6). Some trees harboured more than one roost, so altogether we recorded roost characteristics for 21 roosts in Bechstein's bats, 17 in brown long-eared bats and 20 in barbastelle bats. Emergence counts with bat detectors revealed that with only one exception (a male brown long-eared bat which shared the same piece of loose bark of a dead pine tree with a male barbastelle bat) roosts were used by only one species.

Euclidean distances of roosts from habitat types indicated a similar preference as shown by the analysis of foraging fixes (Table 14 and Figure 15). Roosts used by the brown long-eared bat were situated close to edge habitats and open landscape. Linear landscape elements, e.g. forest tracks within the forest, seemed to have no influence on its roosting behaviour (p ('distance to edge habitat 1') = 0.368 in females and 0.674 in males), respectively.

Table 14. Roost location of three syntopic bat species; ranking is based on significant differences between the distance data sets.

landscape element	females	males
edg 1 (forest tracks)	*Bbar* = *Mbec* = *Paur*	*Bbar* = *Mbec* = *Paur*
edg 2 (ecotones)	*Paur* = *Mbec*, *Mbec* = *Bbar*, *Paur* < *Bbar*	*Paur* < (*Mbec*, *Bbar*)
open landscape	*Paur* = *Mbec*, *Mbec* = *Bbar*, *Paur* < *Bbar*	*Paur* < (*Mbec*, *Bbar*)

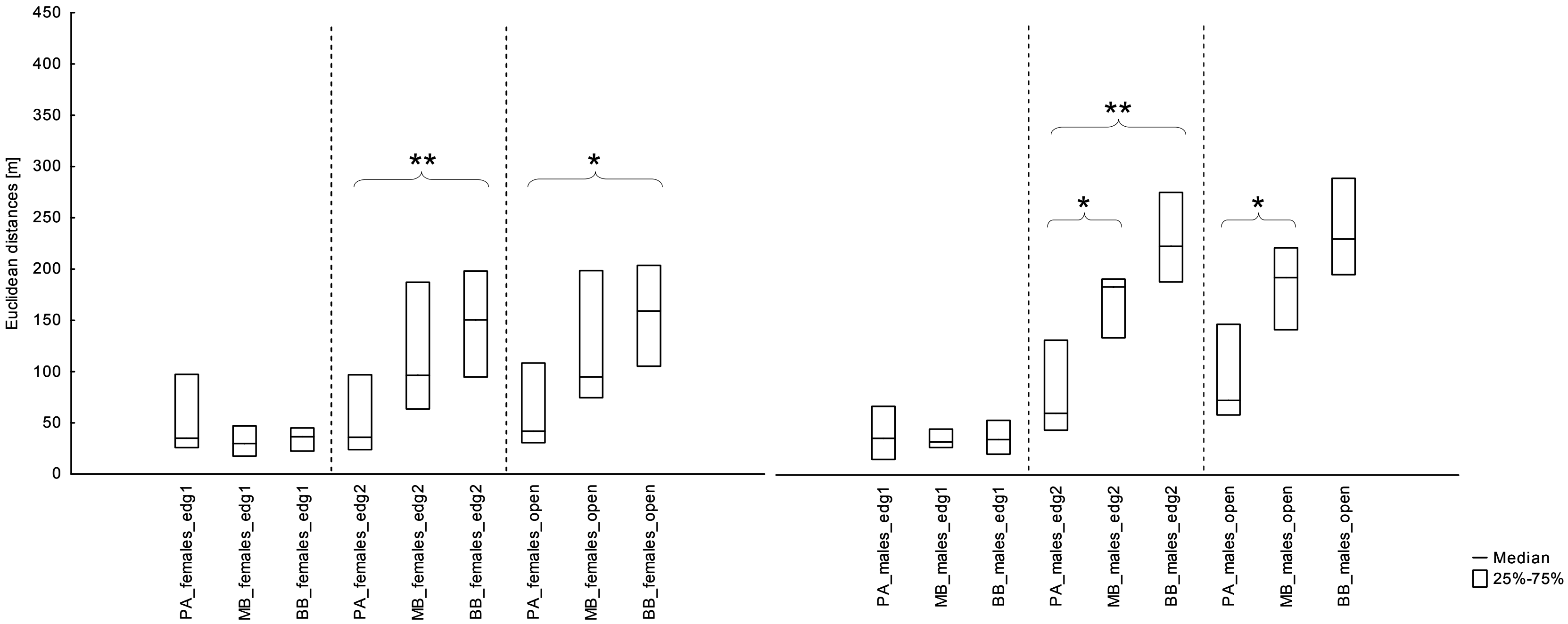

Figure 15. Box-plots showing the Euclidean distances from roosts to the habitat types and the results of the tests on interspecific differences in roost site selection (all species: median test; species pairs: Mann-Whitney-U-test); a) females; b) males; PA: *P. auritus*; MB: *M. bechsteinii*; BB: *B. barbastellus*; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

The three species differed in their selection of tree species and roost type, but not in roost height. Females appeared to be more selective than male bats with respect to tree species and roost type (significant differences between all species pairs, Table 15). Roost height ranged from 2.5 m to more than 20 m in all species. Female and male barbastelle bats roosted in dead oaks (N = 9) and dead pine trees (N = 3) with loose bark. Bechstein's and brown long-eared bats, both cavity-dwelling species, showed some overlap in roost utilisation, but also some significant differences (Table 15). Roosts of Bechstein's and brown long-eared bats were found in live Douglas fir and beech, but most roosts of brown long-eared bats were found in live beeches (N = 10). Most roosts of Bechstein's bats were found in live oaks (N = 13). Woodpecker holes (N = 5) and natural cavities (N = 5) appeared to be the preferred roost structures of Bechstein's bats, while crevices (N = 9) and basal hollows (N = 2) were preferred by brown long-eared bats.

Pianka's index for pair wise comparison of species also indicates high niche overlap in terms of roost height (both females and males, 52-91% overlap, Table 16), but low overlap in terms of roost type and tree species. Female bats appeared to be much more specialised than male bats (0-16% (females) versus 0-79% (males) overlap in terms of roost type and tree species).

Table 15. Results (p-values) of the tests on interspecific differences in roost selection of female and male western barbastelles, Bechstein's bats and brown long-eared bats bats near Frankfurt-Hahn airport, Rhineland-Palatinate; CF- χ^2: Craddock-Flood-Chi^2; HD-U: Haldane-Dawson-U.

test	roost height		tree species		roost type	
females:						
all species	< 0.05	CF-χ^2 = 16.1838 (df = 8, n = 37)	< 0.001	CF-χ^2 = 43.7500 (df = 8, n = 28)	< 0.001	CF-χ^2 = 41.0714 (df = 8, n = 23)
B. barbastellus - M.bechsteinii	0.153	CF-χ^2 = 5.2765 (df = 3, n = 28)	< 0.01	CF-χ^2 = 16.2500 (df = 3, n = 20)	< 0.01	CF-χ^2 = 16.0000 (df = 2, n = 16)
B. barbastellus - P. auritus	0.053	CF-χ^2 = 9.3440 (df = 4, n = 25)	< 0.01	CF-χ^2 = 16.0000 (df = 3, n = 16)	< 0.01	CF-χ^2 = 15.0000 (df = 3, n = 15)
M. bechsteinii - P. auritus	0.118	CF-χ^2 = 7.3662 (df = 4, n = 21)	< 0.01	CF-χ^2 = 15.0000 (df = 3, n = 20)	< 0.01	CF-χ^2 = 11.7857 (df = 3, n = 15)
males:						
all species	0.466	CF-χ^2 = 3.5815 (df = 4, n = 21)	< 0.01	HD-U = 2.8830	< 0.05	CF-χ^2 = 19.5370 (df = 8, n = 20)
B. barbastellus - M.bechsteinii	0.402	CF-χ^2 = 1.8228 (df = 2, n = 13)	< 0.01	HD-U = 3.4694	< 0.05	CF-χ^2 = 11.0000 (df = 4, n = 11)
B. barbastellus - P. auritus	0.165	CF-χ^2 = 3.6000 (df = 2, n = 12)	0.070	CF-χ^2 = 7.0603 (df = 3, n = 16)	< 0.05	CF-χ^2 = 10.3704 (df = 3, n = 14)
M. bechsteinii - P. auritus	0.686	CF-χ^2 = 0.7533 (df = 2, n = 17)	0.146	HD-U = 1.0525	0.471	CF-χ^2 = 3.5417 (df = 4, n = 15)

Table 16. Pianka's index of niche overlap for females and males of syntopic western barbastelles, Bechstein's bats and brown long-eared bats.

	Pianka's indices		
Roost niche overlap	roost height	roost type	tree species
females:			
B. barbastellus - M.bechsteinii	0.737	0.000	0.161
B. barbastellus - P. auritus	0.683	0.000	0.000
M. bechsteinii - P. auritus	0.469	0.136	0.056
males:			
B. barbastellus - M.bechsteinii	0.822	0.000	0.151
B. barbastellus - P. auritus	0.516	0.192	0.183
M. bechsteinii - P. auritus	0.910	0.791	0.519

4. Discussion.

Our radio-tracking study clearly shows that in syntopy the western barbastelle bat, Bechstein's bat and the brown long-eared bat use overlapping home ranges and core areas. Within these areas they segregate through foraging in different habitat types and through differential roost site selection. Niche segregation between Bechstein's bat and the western barbastelle appears to be less pronounced than that between the two species and the brown long-eared bat. Male and female brown long-eared bats prefer roosts close to forest edges and open landscape, while roosts used by barbastelle bats and Bechstein's bats were located inside forest stands and close to forest tracks. Western barbastelles and Bechstein's bats foraged predominantly in or near forests and along forest tracks (= edge habitats within forest) while the brown long-eared bats spent comparatively more time outside the forest.

The three focal species clearly differ in their use of linear elements within forests. This is the most important habitat type for the western barbastelle, an edge habitat specialist (Greenaway & Hill, 2005; Hillen *et al*., 2011). *Myotis bechsteinii*, an aerial hawking and gleaning species, uses corridors within forests which facilitate the detection of flying and non-flying prey. *Plecotus auritus* uses the same foraging strategies and is also described as a typical forest species. However, it is known to use a variety of habitats and in this respect seems to be more opportunistic than the other two species. It therefore comes not as a surprise that our radio-tracked brown long-eared bats also foraged outside the forest. In Germany, Fuhrmann and Seitz (1992) observed brown long-eared bats foraging in orchards. Also in Ireland the species uses open landscapes, e.g. meadows, as foraging habitat (Howard, 1995). This may be explained by the high flexibility in prey selection of brown long-eared bats. Although they frequently prey on moths (Beck, 1995), their diet also regularly contains other arthropods such as blow-flies, harvestmen and especially crane-flies (*Tipula* spec., Rydell, 1989). The latter are large dipterans which are commonly found sitting in grassland or flying above the ground in meadows and forests. For brown long-eared bats these habitat types may serve as a ‘horizontal edge’.

Meadows (used for hay production), grain fields with hedgerows and woodland form a complex habitat mosaic in our study area and may facilitate the opportunistic foraging behaviour of brown long-eared bats in order to avoid exploitative competition. Two of the tracked *P. auritus* even commuted from roosts inside the forests to forging grounds in open or semi-open habitats (gardens, hedgerows). In this context it is interesting that this slow-flying species, which is even more specialised (very broad wings, hovering flight, long ears for detection of prey-generated sounds in a cluttered habitat) than the Bechstein's bat, uses such a variety of habitats. This may also explain why Meschede and Heller (2000) consider it to be a pioneer species.

The western barbastelle and Bechstein's bat obviously avoided meadows, orchards and other open or semi-open habitats. Only male barbastelles foraged in open habitats (see also Hillen *et al.*, 2011). Although both species have already been observed foraging in open habitats, such as traditional orchards and even suburban areas (*M. bechsteinii*; Dietz, 2009; Hillen *et al.*, 2010 b) and grassland (*B. barbastellus*: Greenaway & Hill, 2005), our observations are in line with the majority of previous studies (Boye & Dietz, 2005; Dietz *et al.*, 2007).

Roosts are another important resource, especially for reproducing bats. Forest dwelling colonies need numerous roosts with specific but different microclimatic attributes to successfully establish maternity colonies (Kurta *et al.*, 2003). Most bats prefer warmer roosts, i.e. roosts exposed to more solar radiation (Entwistle *et al.*, 1997) or roosts with a better insulation (e.g. tree holes with thicker walls; Lewis, 1995). Short distances to foraging habitats are an additional factor that may influences roost site selection (Entwistle *et al.*, 1996).

Interspecific differences in roost selection were detected in roost structure and tree species, but not in roost height. It is well-known that the western barbastelle occupies a comparatively narrow roost niche with a clear preference for crevice-like roosts, mainly under the loose bark of dead trees (Russo *et al.*, 2005 b; Russo *et al.*, 2010). Therefore, we expected a stronger competition for roost sites between the two cavity-dwelling species *P. auritus* and *M. bechsteinii*. Due to the comparatively small size of their maternity colonies, brown long-eared bats may be much more flexible than Bechstein's bats in selecting roost sites. Accession of small cavities and crevices may be much easier for them than for large colonies, such as in *M. bechsteinii* (Dietz *et al.*, 2007). By using these small cavities they also avoid competition with the larger Bechstein's bat.

Different social behaviour and anti-predator strategies may also contribute to roost partitioning in bats. Syntopic noctule bats, *Nyctalus noctula* and *N. leisleri*, show fine-scale roost partitioning due to different anti-predator strategies (Ruczynski & Bogdanowicz, 2005, 2009). While *N. noctula* mainly used woodpecker holes, *N. leisleri* preferred other cavities with more than one entrance. This difference may be explained by the pronounced aggressive behaviour of *N. noctula*, whereas the smaller and less aggressive *N. leisleri* hides in less accessible cavities with extra exits to escape from potential predators. A similar strategy of competition avoidance may also explain differential roost site selection of *P. auritus* and *M. bechsteinii*. Future research will have to assess the importance of such special mechanisms of resource partitioning, e.g. anti-predator strategies. They should consider interactions between factors, such as predator avoidance strategies, different roost characteristics and species interactions. This will help to explain the small-scale spatial distribution of syntopic bat colonies and thus enhance a better understanding of factors that allow for existence of endangered bat species and the evaluation of bat habitats.

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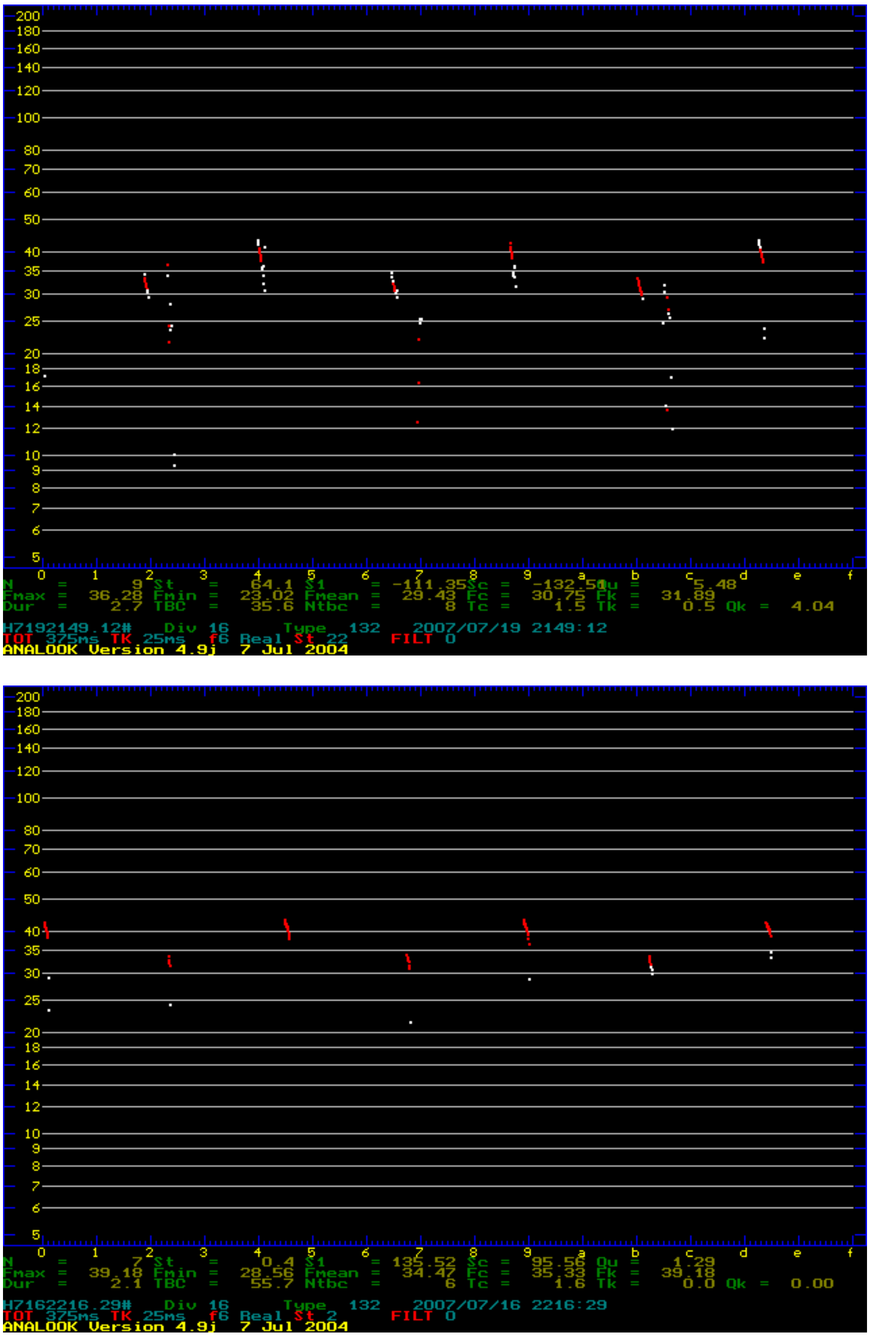
Appendix.



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ANALOOK Version 4.9j  7 Jul 2004
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Dur  =    2.1 TBC  =    55.7 Ntbc  =       6 Tc =      1.6 Tk =     0.0 Qk =  0.00

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Figure A-1. Two example call sequences of western barbastelle bats recorded at flight corridors (forest tracks) in the SAC 'Ahringsbachtal'. Calls were recorded with the ANABAT detector system and analysed in Analook 4.9j for Windows (Corben, 2004); x-axis: time (time per step: 25 ms); y-axis: frequency (kHz).

Figure A-2. Western barbastelles (a) and the two most frequent roost structures: b) dead oaks with loose bark, here showing tagged and ringed western barbastelle females, and c) dead pines with loose bark.

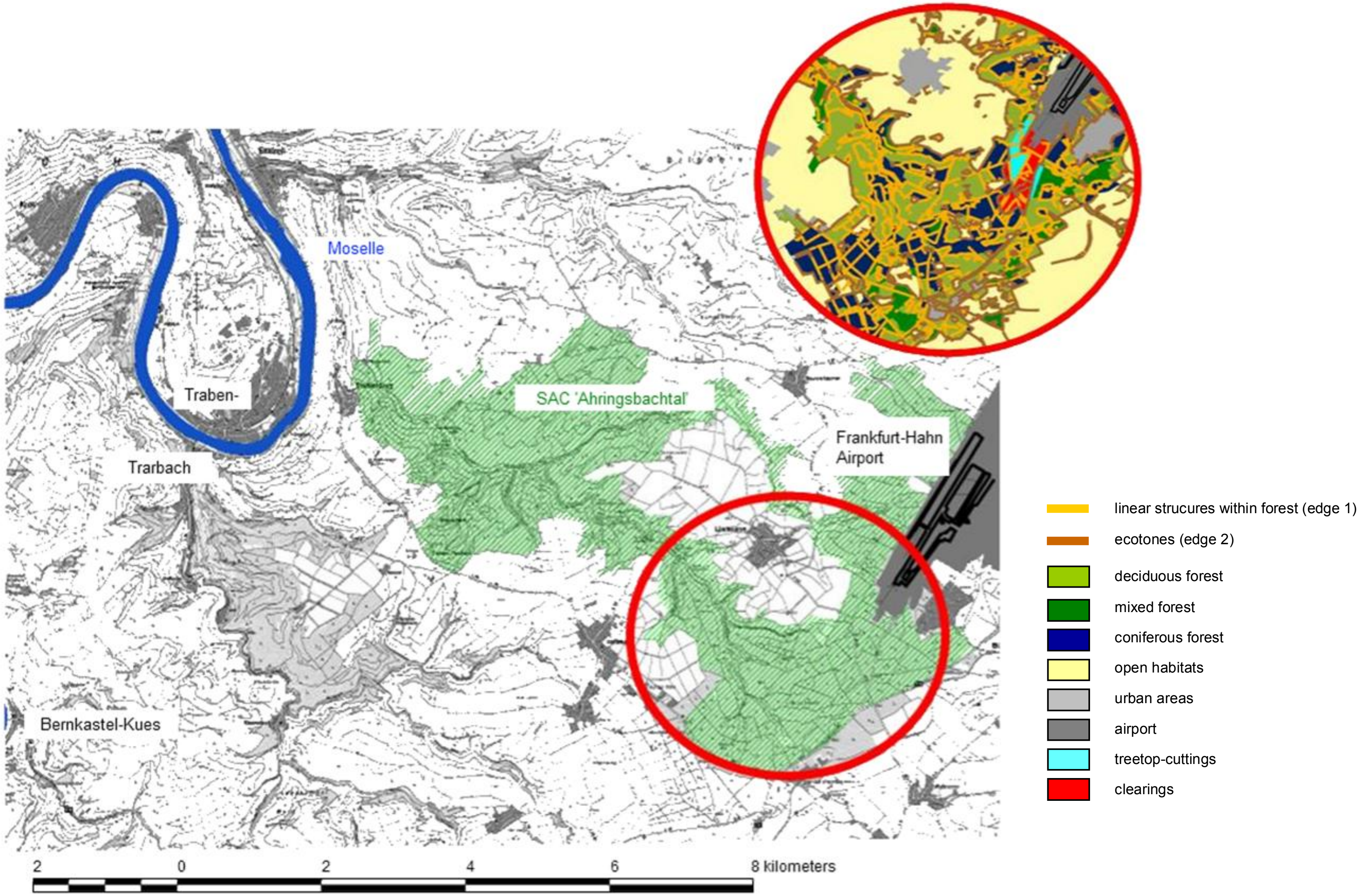

Figure A-3. The study area; ellipse showing an example section of the habitat map including the transformed areas around the Frankfurt-Hahn airport (clearings). Habitat types were defined for all areas covered by home ranges of radio-tracked bats.

a) b) c) d)

Figure A-4. Habitat features in the central SAC 'Ahringsbachtal'; a) oak-dominated forest patches, with dense understorey; b) forest tracks = linear foraging habitat and commuting corridor; c) forest edge and scattered trees; d) beech-dominated forest patches.

Table TA-1. P-values of the tests on interspecific differences in habitat selection (Chapter IV) using Euclidean distances from bat fixes to four landscape elements (all species: median test; species pairs: Mann-Whitney-U-test); open: open landscape; edg1: edge habitat 1 (forest tracks); edg 2: edge habitat 2 (ecotones).

test	forest	edg 1	edg 2	open
females:				
all species	< 0.001	< 0.001	< 0.01	< 0.001
B. barbastellus - M.bechsteinii	0.906	< 0.001	< 0.01	0.232
B. barbastellus - P. auritus	< 0.001	< 0.001	0.102	< 0.001
M. bechsteinii - P. auritus	< 0.001	< 0.001	0.221	< 0.001
males:				
all species	< 0.001	< 0.001	< 0.001	< 0.001
B. barbastellus - M.bechsteinii	< 0.05	< 0.01	0.699	< 0.05
B. barbastellus - P. auritus	< 0.001	< 0.001	< 0.001	< 0.001
M. bechsteinii - P. auritus	< 0.001	< 0.001	< 0.001	< 0.001

Table TA-2. P-values of the tests on interspecific differences in roosting habitat selection (Chapter IV) using Euclidean distances from bat roosts to three landscape elements (all species: median test; species pairs: Mann-Whitney-U-test); open: open landscape; edg1: edge habitat 1 (forest tracks); edg 2: edge habitat 2 (ecotones).

test	edg 1	edg 2	open
females:			
all species	0.368	0.264	0.092
B. barbastellus - M.bechsteinii	0.382	0.277	0.310
B. barbastellus - P. auritus	0.743	0.008	0.015
M. bechsteinii - P. auritus	0.384	0.057	0.098
males:			
all species	0.674	0.003	0.003
B. barbastellus - M.bechsteinii	0.859	0.075	0.165
B. barbastellus - P. auritus	0.310	0.001	0.001
M. bechsteinii - P. auritus	0.165	0.019	0.043

Zusammenfassung.

Im Rahmen meiner Dissertation habe ich die individuellen und geschlechtsspezifischen Habitatnutzungsmuster sowie die Standorttreue der Westlichen Mopsfledermaus, *Barbastella barbastellus*, untersucht. Die Datengrundlage für die vorliegende Arbeit bilden Telemetriedaten aus einem vierjährigen Monitoringprogramm in einem FFH-Gebiet in Rheinland-Pfalz, Deutschland. Die Westliche Mopsfledermaus ist in Mittel- und Südeuropa von Portugal bis zum Kaukasus weit verbreitet, doch gilt sie in vielen Teilen ihres Verbreitungsgebietes als seltene Art. Dennoch, oder möglicherweise gerade aufgrund ihrer Seltenheit, fehlen Langzeitstudien zur Untersuchung der Standorttreue in den Jagd- und Quartiergebieten und möglicher Einflüsse von intra- und interspezifischer Konkurrenz auf die Habitatnutzung dieser Art. Solche Daten bilden jedoch eine wichtige Ergänzung zu bereits bestehenden Schutzmaßnahmen und ermöglichen eine bessere Abschätzung der räumlichen und qualitativen Ansprüche von Populationen dieser Art.

Ich habe radiotelemetrische Techniken, Home range-Analysen und automatisierte Detektoraufnahmen verwendet, um die funktionalen Zusammenhänge zwischen bestimmten Landschaftselementen und der Westlichen Mopsfledermaus bzw. ihrer Quartiere zu untersuchen und die Nischenüberlappung mit zwei ausgewählten waldbewohnenden Fledermausarten, der Bechsteinfledermaus (*Myotis bechsteinii*) und dem Braunen Langohr (*Plecotus auritus*), abzuschätzen.

Individuenbasierte Analysen der intra- und interannuellen Home range-Überlappungen weiblicher *B. barbastellus* belegten die ausgeprägte Standorttreue dieser Tiere zu ihren individuellen Jagdgebieten. Diese Teilstudie zeigte, dass es innerhalb einer Kolonie eine traditionelle Nutzung bestimmter Jagdgebiete gibt, die einen größeren Einfluss auf die lokale Raumteilung der Koloniemitglieder hat als intraspezifische Konkurrenz.

Die Auswertung der jährlich aufgesuchten Wochenstubenquartiere und Aktivitätsdichten, die an Flugkorridoren im Quartiergebiet aufgezeichnet wurden, zeigten deutlich, dass Wochenstubenkolonien ganze Quartierkomplexe über mehrere Jahre nutzen und eine ebenso starke Bindung an traditionell genutzte Flugwege aufweisen. Ein effektiver Quartierschutz muss daher den gesamten Quartierverbund inklusive der zugehörigen Flugkorridore, beispielsweise Waldwege, berücksichtigen.

Weiterhin wurden mit einem Verfahren, das auf den Euklidischen Distanzen der Aufenthaltsorte der Mopsfledermäuse zu verschiedenen Flächentypen und linearen Landschaftselementen basiert, die geschlechtsspezifischen Habitatpräferenzen von *B. barbastellu*s untersucht. Diese so gewonnenen Daten deuten auf eine partielle Nischentrennung zwischen den beiden Geschlechtern in ihren Sommerhabitaten. Die Weibchen bevorzugten Laubwaldflächen und besonders lineare Landschaftselemente innerhalb der Waldflächen, während die Männchen häufiger an Waldrändern und sogar über offenen Flächen jagten.

Schließlich habe ich auch die Jagdhabitat- und Quartiernutzung der Westlichen Mopsfledermaus mit zwei syntop vorkommenden Arten, der Bechsteinfledermaus und dem Braunen Langohr, verglichen um mögliche Nischenüberlappungen bzw. Raumteilung zwischen diesen Arten zu quantifizieren. Hier wurden jeweils unterschiedliche Artenpaare simultan telemetriert, um optimal vergleichbare Datensätze zu erhalten. Offensichtlich existiert zumindest eine teilweise räumliche Trennung dieser Arten im untersuchten Gebiet, die sich in einer Verteilung der Aktivitäten der einzelnen Arten entlang eines Gradienten von Waldkernzonen über den Waldrand bis zu offenen Flächen zeigte. Die untersuchten Langohren hielten sich häufiger am Waldrand und in eher offenen Flächen auf, die von *B. barbastellus* und *M. bechsteinii* eher gemieden wurden. Die beiden zuletzt genannten Arten bevorzugten Waldflächen bzw. lineare Landschaftselemente im Wald. Die Betrachtung der Quartiernutzung ergab einige Unterschiede bezüglich genutzter Hohlräume, insbesondere auch bei den höhlenbewohnenden Arten *M. bechsteinii* und *P. auritus* (Spechthöhlen in Eichen bevorzugt von *M. bechsteinii*, Spalten und Stammfußhöhlen von *P. auritus*).

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Hiermit erkläre ich, dass ich die vorgelegte Dissertation selbständig, ohne unerlaubte fremde Hilfe und nur mit den Hilfen angefertigt habe, die ich in dieser Arbeit angegeben habe.
In meinen Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, niedergelegt in der Ordnung zur Sicherung guter wissenschaftlicher Praxis der Johannes Gutenberg-Universität Mainz, eingehalten.
Beiträge Dritter zu den einzelnen Kapiteln (Co-Autorenschaft der Publikationen) sind als solche kenntlich gemacht worden. Alle Textstellen, die wörtlich oder sinngemäß aus Veröffentlichungen oder anderen schriftlichen Quellen oder mündlichen Angaben stammen, sind ebenfalls entsprechend kenntlich gemacht worden.