Ann. Zool. Fennici 48: 180–190 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 June 2011

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

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Received 8 Oct. 2010, revised version received 9 Feb 2011, accepted 10 Feb. 2011

Hillen, J., Kaster, T., Pahle, J., Kiefer, A., Elle, O., Griebeler, E. M. & Veith, M. 2011: Sex-specific habitat selection in an edge habitat specialist, the western barbastelle bat. — *Ann. Zool. Fennici* 48: 180–190.

The 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 the 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.

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 an individual character (Wolf *et al*. 2007, Biro & Stamps 2008, Boon *et al*. 2008). Many 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 of insects, 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.

Material and methods

Study area and radio-tracking

Our study was carried out in the Special Area of Conservation ‘Ahringsbachtal’ near Frankfurt-Hahn Airport, Rhineland-Palatinate, Germany (Fig. 1). The area covers ca. 2000 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 the data obtained from only 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 (J. Hillen unpubl. data), whereas the males always roosted alone.

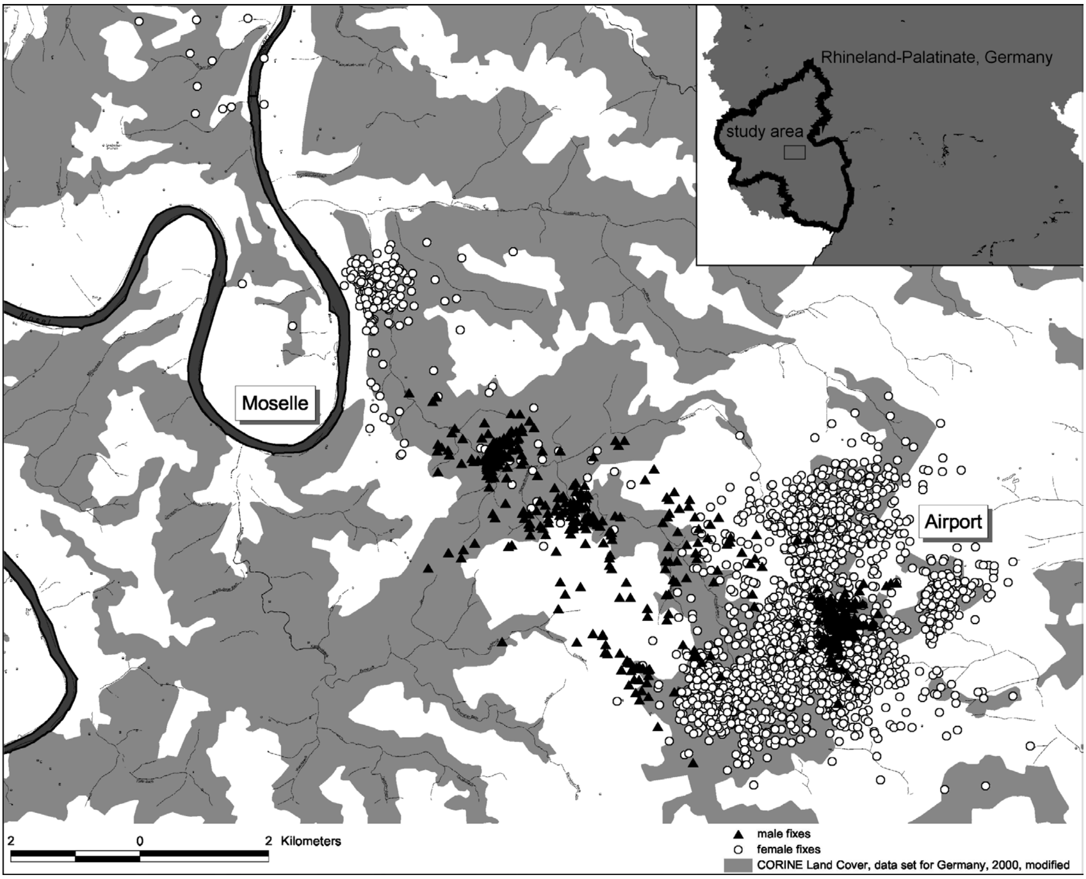

Fig. 1. Spatial distribution of bat fixes (12 female and five male western barbastelle bats radio-tracked 2004–2007); airport: Frankfurt-Hahn Airport, Rhineland-Palatinate.

Analysis of habitat selection

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 (ver. 3; Rodgers and Carr 1998). Based on digital orthophotos (resolution 0.5 m per pixel; scale 1:5000; 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 1). 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.

Method selection

According to the literature, the two most commonly used methods that had been used 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 with the Chi-square goodness-of-fit test and with 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).

Euclidean distance analysis

Here, we 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 an 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 (ver. 1.3; Jenness 2005).

We applied a distance-based approach to test for non-random habitat use. We adopted the method of Conner and 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, we applied non-parametric statistics (Kolmogorov-Smirnov test) (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 using a Mann-Whitney U-test for a significant difference from a vector of 1 which represents random use of a specific

Table 1. 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

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 using a 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 $\alpha = 0.05$.

Results

We analysed a total of 12 successfully tracked females, altogether comprising 2737 fixes (Hillen *et al*. 2009), 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 2551 ha (Table 2). 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 2). 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*. 2010).

Habitat composition within home ranges

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

Table 2. 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).

	Number of 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	2551	–	–	160
BF3	98	42	–	398	539	207	–	583
BF4	135	–	–	183	343	–	–	403
BF5	–	32	96	–	–	922	198	–
BF7	–	x	x	132	–	–	–	2097
BF8	–	181	x	–	–	125	–	–
BF9	–	–	151	–	–	–	399	–
BF10	–	–	–	167	–	–	–	258
BF11	–	–	–	192	–	–	–	352
BF12	–	–	–	207	–	–	–	1622
BF13	–	–	–	206	–	–	–	1835
Males								
BM1	91	–	–	–	558	–	–	–
BM2	78	–	–	–	344	–	–	–
BM3	–	90	–	–	–	–	93	–
BM5	–	–	167	–	–	–	88	–
BM6	–	–	58	–	–	–	864	–

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 3).

Habitat selection

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 (pairwise test).

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 4).

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 5). The males' preferences appeared to be the opposite of the females' (Fig. 2), even though habitat availability within the home ranges of both sexes was similar.

Discussion

Habitat use of western barbastelle bats

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 as compared with other bat species' food ranges. Barbastelle bats mainly feed on small to medium-sized moths, but they do not rely on certain prey species. A recent study conducted by Andras *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.*

Table 3. Mean habitat availability (% home range area) within home ranges of 17 western barbastelle bats (12 females, five males); * mean of four male home ranges).

Habitat type	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

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 a 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

Table 4. Annual individual habitat distance ratios d of tracked western barbastelle bats including annual data for five repeatedly tracked females ($d < 1$ indicates preference, $d > 1$ indicates 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 5. Mean habitat distance ratios Δ (= d_{mean}) of 17 western barbastelle bats (12 females, five males) ($\Delta < 1$ indicates preference, $\Delta > 1$ indicates 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

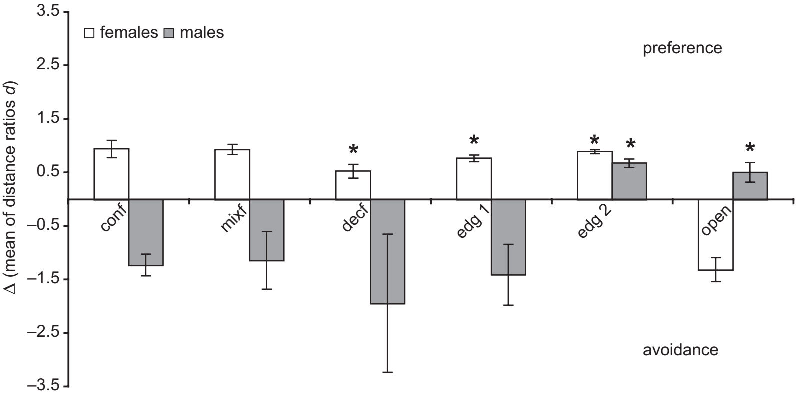

Fig. 2. Mean distance ratios (Δ) and standard errors of 12 female and four male western barbastelle bats (Δ < 1 indicates preference, Δ > 1 indicates avoidance); original Δ values and SEs > 0. Mean distance ratios and standard errors were multiplied by −1 to facilitate the differentiation of preferred 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.

observed behaviour, but it does not 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).

Sexual segregation in habitat use

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.* 2010) 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 and 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 particoloured 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 interannual site fidelity to their home ranges, but competition between sexes still remains to be examined in more detail.

Conclusions

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.

Acknowledgements

We thank all colleagues who helped in field work and data analysis. Radio-tracking of *Barbastella barbastellus* was carried out under licence no. 425-107-0502 from the ‘Struktur- und Genehmigungsdirektion Nord, Koblenz’. This study was funded by the ‘Flughafen Frankfurt-Hahn GmbH’. Personal grants to JH were provided by the the ‘Deutsche Bundesstiftung Umwelt’ and the Federal Ministry for the Environment, Forestry and Consumer protection (‘Ministerium für Umwelt, Forsten und Verbraucherschutz Rheinland-Pfalz’). We thank K. Witzenberger for lingual improvement of our manuscript.

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