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Original Investigation

Impact of landscape fragmentation on a specialised woodland bat, *Rhinolophus hipposideros*Guido Reiter^{a,*}, Elisabeth Pölzer^{a,b}, Harald Mixanig^a, Fabio Bontadina^{c,d,1}, Ulrich Hüttmeir^{a,1}^a Austrian Coordination Centre for Bat Conservation and Research (KFFOE), Leonding, Austria^b University of Graz, Institute of Zoology, Graz, Austria^c SWILD, Urban Ecology & Wildlife Research, Zürich, Switzerland^d Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, Birmensdorf, Switzerland

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ABSTRACT

For habitat specialists, fragmentation has major consequences as it means less suitable habitat for the species to live in. In a fragmented landscape, we would expect larger, but spatially more clustered, foraging ranges. We studied the impact of landscape fragmentation on the foraging range and habitat exploitation of a specialised forest bat by radiotracking 16 female lesser horseshoe bats *Rhinolophus hipposideros* in a landscape with connected woodland structures and in a highly fragmented landscape in Carinthia, Austria.

Contrary to our expectations, spatial foraging behaviour was not influenced by fragmentation. No differences in the behaviour of the bats between the sites were evident for the foraging ranges (minimum convex polygon, MCP), the core foraging areas (50% kernel), nor the mean or the maximum distances from the roost. However, in the highly fragmented landscape, the foraging activity of individuals was spatially more clustered and the overall MCP of all bats of a colony was greater compared to the less fragmented landscape.

Woodland was the most important foraging habitat for the lesser horseshoe bats at both study sites. Habitat selection at the individual MCPs was evident only at the site with low fragmentation. However, in the core foraging areas, woodland was significantly selected over all other habitat types at both study sites.

We conclude that (1) conservation measures for colonies of lesser horseshoe bats should be undertaken within 2.5 km of the nursery roost, (2) woodland is the key foraging habitat particularly in the vicinity of the roost, and (3) any loss of woodland near the colonial roosts are likely to negatively influence the colony, since these bats do not seem to be able to adapt their spatial foraging behaviour in a degraded landscape. The inflexible spatial behaviour of this specialised bat highlights the need to compensate for any habitat loss within the foraging range of a bat colony.

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Introduction

The impact of humans on nature often results in habitat fragmentation, which affects communities, species and their populations (Pullin, 2002; Lindenmayer and Fischer, 2006). The process of habitat fragmentation has three recognisable components: (1) An overall loss of habitat, (2) a reduction in the size of the blocks of habitat, and (3) an increased isolation of habitats (Bennett, 1999).

Many insectivorous bat species roost and reproduce in colonial roosts and forage in specific habitats in the vicinity. For bat species which forage mainly in forests, the fragmentation of the

woodlands surrounding the roosts is likely to have major consequences for their foraging behaviour as less suitable habitat is available and woodland patches will become increasingly isolated, rendering them inaccessible for the bats.

We tested the effect of habitat fragmentation on lesser horseshoe bats *Rhinolophus hipposideros* by comparing their habitat exploitation in contrasting landscapes. Lesser horseshoe bats forage nearly exclusively in forests (Bontadina et al., 2002, 2006), but in central Europe their maternity roosts are in buildings (Reiter et al., 2004). This species varies greatly between colonies in their reproductive ecology (Reiter, 2004a), their population dynamic during summer (Frühstück, 2005), their roost selection (Reiter et al., 2004), and their emerging patterns (Duvergé et al., 2000; Reiter et al., 2008; Stone et al., 2009). We thus expected them to differ in their foraging behaviour as well.

We predicted that, in a highly fragmented landscape where suitable foraging patches are separated by unsuitable habitats: (1) the

* Corresponding author at: Fritz-Stoerk-Str. 13, 4060 Leonding, Austria.

E-mail address: Guido.Reiter@fledermausschutz.at (G. Reiter).¹ Shared senior authorship.

Table 1
Availability of habitats around the study colonies (MCPs including all radiotracking locations).

Habitat type	Gallizien (%) less fragmented	Lebmach (%) highly fragmented	Classes regrouped to
Arable land	5.9	37.5	A
Pasture	7.3	19.7	A
Hedgerows and orchards	1.0	5.0	B
Broadleaf woodland	5.6	4.5	C
Mixed broadleaf woodland	37.7	7.9	C
Mixed coniferous woodland	19.4	13.2	C
Coniferous woodland	2.7	4.4	C
Riparian vegetation	13.2	0.4	C
Settlement	3.0	5.7	D
Water	2.9	0.0	D
Other	1.3	1.7	D

size of core the foraging areas would remain constant but, the colony members would spatially cluster more densely because of the limited availability of preferred foraging grounds, and (2) individual activity ranges would be larger and the bats would fly longer distances.

Material and methods

Study area, colonies and capture method

We investigated two nursery colonies in landscapes of contrasting degrees of fragmentation in Carinthia, southern Austria, from May to September 2004. The colony in the less fragmented habitat lives in a bridge in the village of Gallizien ("Annabrücke", 14.491°E, 46.573°N, 420 m a.s.l.), and the colony in the highly fragmented habitat is located in the Lebmach church (14.308°E, 46.748°N, 529 m a.s.l., about 25 km apart). Two contrasting study sites were chosen with very different levels of fragmentation and composition of the habitat types surrounding the roosts (Table 1). Woodlands dominated the less fragmented landscape in Gallizien, covering nearly 80% of the area, with only small amounts of arable land and pastures present (13%, Fig. 1). At the highly fragmented site Lebmach arable land and pastures were, in contrast, the most prominent habitat types (57%) and fragmented woodland blocks covered in total only about 30% of the area (Table 1 and Fig. 1).

In Gallizien, the bats roosted inside a hollow concrete road bridge, and in Lebmach they used the roof void and the steeple of the church. The maximum numbers of adult and subadult bats counted in the study period were 264 in Gallizien (31st May 2004) and 41 in Lebmach (26th July 2004).

Bats were captured with mist nets at roost entrances, at irregular intervals between May and September (Table 2). This procedure minimised the disturbance to the colonies and ensured a random sample of bats. Because it became difficult to capture bats in the mist nets after a few weeks in Lebmach, the last two bats were caught inside the roost during daytime. At this time of the year, almost all bats were in torpor during daytime, and hence the disturbance to the colony was negligible.

For the study, 115 lesser horseshoe bats were captured, 81 in Gallizien and 34 in Lebmach, of which 40 were males (34 in Gallizien and 6 in Lebmach). The proportion of males (42%) in Gallizien was greater compared to Lebmach (18%): $X^2 = 6.25$, $df = 1$, $p < 0.05$. Sixteen females were fitted with radio-transmitters (Table 2). To obtain comparable data, captures of animals were strictly alternated between the study sites and balanced in respect to their reproductive conditions (Table 2).

The bats caught were held in calico bags before biometric data were taken. Mass was recorded to an accuracy of 0.1 g and forearm length to 0.1 mm. Animals were sexed and the reproductive condition of the females assessed. Parous females were identified by the presence of large pelvic nipples (Gaisler, 1963), and palpably

pregnant animals were recorded. We assigned bats to one of two age classes. Yearlings, identified by their grey pelage (Gaisler, 1963), were classified as "subadult", and animals over one year as "adult". We used only females for the tracking study as sex differences in habitat selection would have been difficult to determine with a limited sample size. We tagged females with differing reproductive condition except heavily gravid females (Table 2).

Radiotracking

The bats were tagged with Titley LTM transmitters (Titley Electronics, PO Box 19, Ballina NSW 2478, Australia, www.titley.com.au), weighing between 0.38 g and 0.43 g (mean = 0.4 ± 0.02 STD). Transmitters were glued on the back of bats using surgical cement (SkinBond, Smith & Nephew United Inc., Largo, FL, USA) between the scapulae after trimming the fur. The transmitter batteries had a life span between 7 and 10 days. Transmitters fell off when the fur has grown for some days or, at most, a few weeks.

The transmitter increased the body mass of the bats by 5.7–7.4% (mean = $6.6 \pm 0.5\%$ STD), which is acceptable for short time periods with small bats (Bontadina et al., 2002). The bats were released short after the attachment of the transmitters, and flew back to the roost ($n = 5$) or hung in trees or buildings in the vicinity of the releasing site ($n = 3$) for half an hour to an hour. Six bats began to hunt immediately after release, and the two bats captured during daytime in the roost left the roost the following evening without any apparent difference in behaviour from that of the other bats in the colony.

We tracked the bats using a TRX-2000S receiver (Wildlife Materials, Inc., 1031 Autumn Ridge Road, Carbondale 62901, IL, USA, www.wildlifematerials.com) and modified stabo XR100 communication receivers (stabo Elektronik GmbH, Hildesheim, Germany) with hand-held three-element Yagi aerials (model AY/C, Titley Electronics, Australia) or, occasionally, H-aerials. The location of the tagged bats was recorded at 5 min intervals throughout the night by triangulating the signal direction. The chosen interval of 5 min does allow bats to reach all habitats available, therefore avoiding the problem of spatial autocorrelation. Two field-workers approached the bat to a distance of less than 500 m to the bat and coordinated their simultaneous bearings using trigger signals from synchronised Casio G-Shock watches. Hand-held FM-radios were used to remain in contact.

The time, location of observers, bearings on the bats, estimated accuracy of locations (according to Bontadina and Naef-Daenzer, 1996) and general observations were recorded in the field on a dictaphone and later transcribed onto data sheets. The positions of the bats in the field were calculated from the bearings and their estimated location written into a Geographical Information System (GIS) ArcView 3.2a (ESRI, Environmental Systems Research Institute Inc., California, USA, www.esri.com).

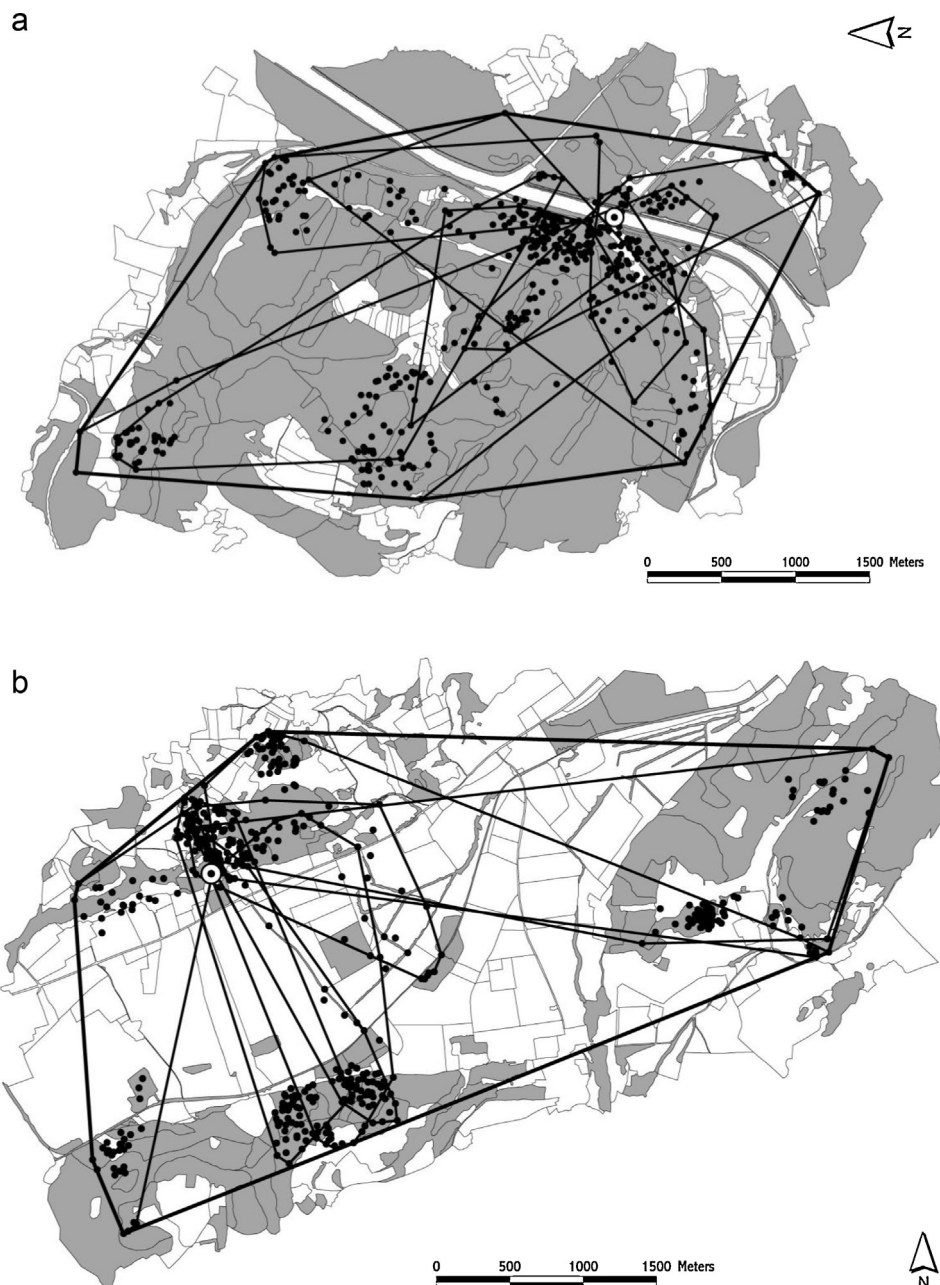


Fig. 1. Study areas in contrasting landscapes: (a) less fragmented woodlands in Gallizien and (b) highly fragmented woodlands in Lebmach. Vegetation structures (woodlands, orchards, hedgerows, tree lines and parks) are marked in grey. Nursery roosts (white dot), tracking locations (black dots), individual activity ranges (minimum convex polygon (MCP) encompassing these locations) and the colony range (MCP around all locations) are given.

Data analysis

Based on the results of previous studies (Bontadina et al., 2002, 2006) and taking into account the local situation, the habitat in the area was divided into eleven categories: Arable Land, Pasture, Hedgerows and Orchards (including Treelines, Parks), Broadleaf Woodland (<10% coniferous trees), Mixed Broadleaf Woodland (10–50% coniferous trees), Mixed Coniferous Woodland (50–90% coniferous trees), Conifer Woodland (>90% coniferous trees), Riparian Vegetation, Settlement (including roads), Water, and Other (e.g. wall of rock, clear-cutting). These habitats were mapped in the GIS using 1:50,000 maps and aerial photographs.

For all bats we visually checked whether the individual foraging areas were completely recorded by plotting the cumulative area of the minimum convex polygon (MCP) against the number of nights.

If the resulting curves reached an asymptote, the maximum area covered by the bats is reached. This was the case for all individuals with the exception of bat 3.03 because the contact time was short, and with bat 3.10 the transmitter fell off after two days (Table 2). We subsequently excluded both bats from most of the further analysis.

The foraging ranges of the tagged bats were determined using a MCP, including all locations of an individual. The areas covered by the MCP and individual foraging distances were determined in the GIS. The relationship between the number of locations and foraging range was computed using the “animal movement” extension in ArcView 3.3 (Hooge and Eichenlaub, 1997).

We investigated habitat selection on two levels (Johnson, 1980; Bontadina et al., 2002). (1) At the landscape scale, we analysed the selection of foraging ranges compared to the habitat available for the colony. The available foraging area was assessed as the

Table 2
Morphological measurements, reproductive status and basic radiotracking data of 16 female *Rhinolophus hipposideros* bats. Two bats with insufficient data (marked in *italic*) were excluded from the analysis. LF, less fragmented; F, highly fragmented.

Animal ID	Date of capture	Study site	Forearm (mm)	Mass (g)	Breeding status	Age class	Number of nights	Number of locations	Mean contact time (%)
3.01	17 May 04	LF	40	5.8	Pregnant	Adult	5	36	92
3.02	24 May 04	F	41.9	6.1	Pregnant	Adult	6.5	99	84
3.03	01 Jun 04	LF	41.1	6.5	~Pregnant ^a	Adult	3.5	14	45
3.04	07 Jun 04	F	38.9	6.8	Pregnant	Adult	4.5	54	94
3.05	27 Jun 04	LF	39.7	5.4	Non breeding	Subadult	5	103	86
3.06	04 Jul 04	F	39.7	5.7	Non breeding	Subadult	4.5	69	100
3.07	09 Jul 04	LF	40.3	6.2	Lactating	Adult	5.5	42	77
3.08	16 Jul 04	F	40.1	6.3	Lactating	Adult	5	58	95
3.09	24 Jul 04	LF	40.8	6.7	Lactating	Adult	4.5	67	90
3.10	31 Jul 04	F	40.2	6	Lactating	Adult	2	36	96
3.11	03 Aug 04	LF	38.5	5.6	Lactating	Adult	4	78	98
3.12	09 Aug 04	F	39.2	6.4	Lactating	Adult	4.5	83	94
3.13	14 Aug 04	LF	39.1	6.3	Post lactating	Adult	4.5	72	66
3.14	23 Aug 04	F	39.1	6.4	Post lactating	Adult	4	61	72
3.15	01 Sep 04	LF	39.2	5.8	Post lactating	Adult	3.5	75	78
3.16	16 Sep 04	F	38.9	6.5	Post lactating	Adult	4	44	95
Mean ± STD	–	–	39.8 ± 0.92	6.2 ± 0.4	–	–	4.4 ± 1.0	61.9 ± 23.9	85.1 ± 14.6
Total							70.5	991	

^a Classification uncertain.

area inside the MCP around all tracking locations of the animals of a colony (colony range). The habitat within this available area was compared with the habitat within the MCPs of the individual bats. (2) At the home range scale, we analysed the habitat selected by individual bats within their foraging range. This was done by comparing the core foraging areas used by each animal with the habitat available within the individual MCPs. Core foraging areas were defined by the 50% contour lines of the fixed kernel estimation (Worton, 1989) on the GIS ArcView (Hooge and Eichenlaub, 1997). We used the same smoothing factors for all animals to allow comparisons.

To overcome the problem of inverse correlation of area of a specific habitat class with the area of the other classes (Otis and White, 1999), we used compositional analysis to investigate habitat selection (Aebischer and Robertson, 1992; Aebischer et al., 1993). This non-parametric technique uses the single animal as the sample unit instead of the locations. We computed the statistics with the Excel macro Compos Analysis 5.1 (P. Smith, 1, Bettws Cottage, Bettws, Abergavenny, Monmouthshire, NP7 7LG, Wales, UK, www.smithecolony.com; Smith, 2004), which also carried out the randomisation procedure (randomised $p = p_r$, 10,000 iterations) as recommended by Aebischer and Robertson (1992).

To overcome limitations in compositional analysis regarding the number of habitat classes and to focus on general results, we merged the habitat classes into four main groups.

Results

We collected a total of 472 locations in Gallizien (less fragmented, $n = 7$ bats) and 468 locations in Lebmach (highly fragmented, $n = 7$ bats), in the tracking sessions, which each lasted between 2 and 6.5 days (mean = 4.4 ± 1.0 STD). The bats were tracked for the complete night ($n = 66$), or until midnight in nine nights. Both study sites were covered with the same effort, with equivalent numbers of tracking locations (Mann–Whitney test: $U = 23.0$, $p = 0.9$) and nights per bats ($U = 24.0$, $p = 1.0$), as well as the same contact time ($U = 14.0$, $p = 0.21$).

Impact of fragmentation

The distribution of the radio-tracking fixes was spatially less clustered in the less fragmented habitat (all fixes located in 75%

of 500 m squares) than in the highly fragmented one (55%, Fig. 1a and b). The recorded locations at the highly fragmented site were grouped into three main fractions divided by arable land and pastures (Fig. 1b).

Fifty percent of the time (comparable to this amount of fixes) the bats were located within a mean of 1172 m (± 1031 STD) around the roost at the less fragmented site and within 1241 m (± 1048) at the highly fragmented site. If the overall utilisation pattern is compared to a uniform distribution, foraging distances up to 2.5 km at the less fragmented site and 2.3 km at the highly fragmented site were used more than expected, with a notable peak within 600 m to the roosts (Fig. 2a and b). However, at both study sites, we also found less-used areas within these distances. At the highly fragmented site these areas are often comprised by arable habitat.

The mean foraging distance to the roost of all bats was 1.3 (± 0.6 km STD) and the maximum distances reached up to 4.7 km to the day roost (mean for all bats = 2.7 ± 1.1 km). There were no differences in the distances travelled by the bats at both study sites (all $p > 0.1$, Table 3). However, the overall MCP for all radio-tracked bats was 27% greater at the site with a high degree of fragmentation (12.2 km^2) than at the site with less fragmentation (9.6 km^2).

Habitat use and selection

Woodland was the most important foraging habitat for the bats at both study sites, and only 9% of the locations at the less fragmented site and 28% at the highly fragmented site were in a different habitat type. The proportion of woodland within individual MCPs were greater at the study site with low fragmentation than at the fragmented one (Mann–Whitney test: $U = 5.0$, $p = 0.01$).

Habitat selection of the aggregated habitat types was investigated in two steps. The first step gives an insight into which habitats the bats selected by choosing their foraging ranges (see the individual foraging ranges in Fig. 1). The foraging ranges of the bats was compared with the colony range available by a compositional analysis, which revealed a significant habitat selection pattern at the less fragmented study site ($X^2 = 26.61$, $df = 3$, $p_r = 0.029$), but no detectable selection pattern at the highly fragmented study site ($X^2 = 2.56$, $df = 3$, $p_r = 0.65$).

In the second step we looked at which foraging areas the bats selected most frequently (core foraging areas). A significant

Table 3

Radio-tracking data of 14 successfully tracked *R. hipposideros*. The size of the foraging areas is given by the minimum convex polygon (MCP) and that of the core foraging area by the 50% contour lines of the kernel estimation. LF, Less fragmented, F, highly fragmented.

Animal ID	Study site	Foraging area (MCP, ha)	Core foraging area (50% kernel, ha)	Mean distance from day roost (km)	Maximum distance from day roost (km)
3.01	LF	264	22	1.4	3
3.02	F	430	4	1.9	4.7
3.04	F	127	11	0.6	1.7
3.05	LF	110	8	0.6	1.9
3.06	F	68	7	1	2.1
3.07	LF	140	13	1.8	2.4
3.08	F	250	7	1.3	4.3
3.09	LF	117	10	0.7	1.4
3.11	LF	57	9	0.4	1.2
3.12	F	122	12	1.2	2.1
3.13	LF	441	8	1.7	4
3.14	F	161	5	1.3	2.5
3.15	LF	287	11	2.4	3.7
3.16	F	170	12	1.5	2.1
LF site Mean ± STD	–	202 ± 135	12 ± 5	1.3 ± 0.7	2.5 ± 1.1
F site Mean ± STD	–	190 ± 120	8 ± 3	1.3 ± 0.4	2.8 ± 1.2
Both study sites Mean ± STD	–	196 ± 123	10 ± 4	1.3 ± 0.6	2.7 ± 1.1
Mann-Whitney test	–	$U = 24.0$ $p = 1.0$	$U = 14.0$ $p = 0.21$	$U = 24.0$ $p = 1.0$	$U = 20.0$ $p = 0.62$

habitat selection pattern was noticeable at both study sites (less fragmented: $X^2 = 12.05$, $df = 3$, $p_r = 0.029$; highly fragmented: $X^2 = 14.21$, $df = 3$, $p_r = 0.05$; Fig. 3). Woodland was selected significantly over all other habitat types (Fig. 3a and b).

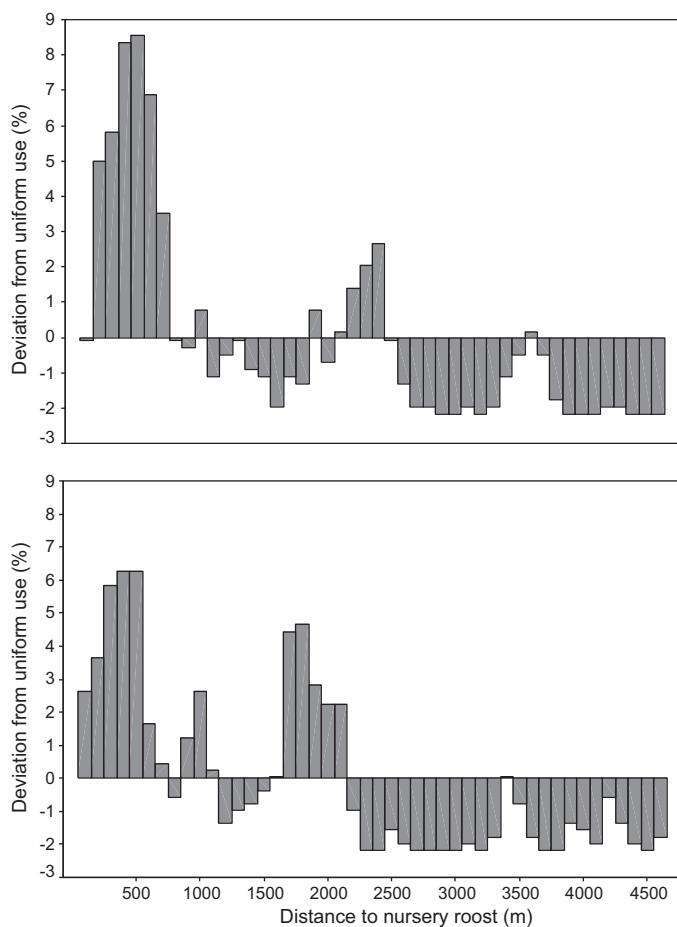


Fig. 2. Deviation of the observed frequency of locations compared with a model of uniform spatial use at the (a) less fragmented ($n = 472$) and (b) highly fragmented ($n = 468$) sites.

Discussion

Surprisingly, the general foraging behaviour of the lesser horse-shoe bats did not appear to be influenced by fragmentation. However, the individual foraging areas were more clustered in the highly fragmented landscape and the overall MCP of all bats was greater. Furthermore, our findings emphasise the importance of woodland as the most important foraging habitat for the species.

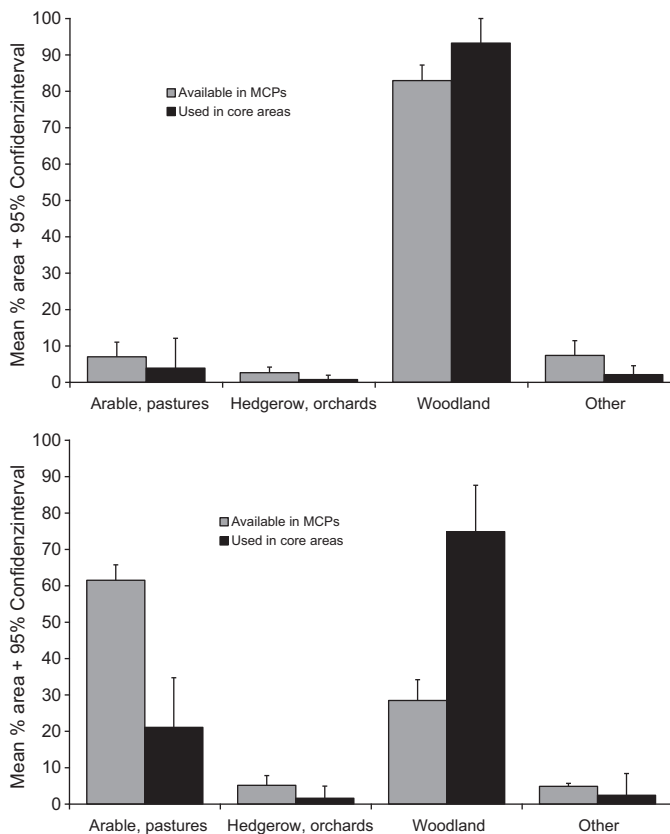


Fig. 3. Selection of core foraging areas by *Rhinolophus hipposideros*: comparison of the individual foraging ranges (available area, MCP) with individual core foraging areas (50% kernels) at the (a) less fragmented and (b) highly fragmented site.

Impact of fragmentation

Contrary to our predictions, we found no differences between the highly fragmented and less fragmented landscapes in the size of the individual foraging areas, the size of the core foraging areas and the maximum distance travelled by the lesser horseshoe bats. This suggests that the behavioural or ecomorphological constraints probably limit how well this species can adapt its foraging behaviour in degraded landscapes.

However, as a consequence of the limited woodland available at the highly fragmented site, the foraging areas of the bats appeared to be more spatially clustered and it seems that they selected woodland more intensely than in the less fragmented landscape. This pattern was found even though the size of the colony at the less fragmented site (260 bats) was much higher than that at the highly fragmented site (40 bats), which was the single major difference between the two colonies. According to Reiter (2004b) the colony size of lesser horseshoe bats in Austria is in general linked to the size of the area covered with woodland in their surroundings. Roosts in densely forested areas therefore tend to consist of larger colonies. Our findings may help to explain this relationship, as they demonstrate that lesser horseshoe bats in a highly fragmented landscape forage in the same manner spatially as bats in a less fragmented landscape. It therefore seems that these bats are not able to compensate for the consequences of fragmentation, e.g. for the loss of foraging habitat, by extending their foraging flights. Hence, the observed differences in colony size could be explained by less favourable landscapes supporting only smaller colonies.

Habitat fragmentation is known to alter the use of space by animals in other ways (Lindenmayer and Fischer, 2006). For example, animals may move greater distances to find food or mates compared to conspecifics in unmodified areas (Fraser and Stutchbury, 2004). Alternatively, the home range size may even decrease if the patch size decreases (Pope et al., 2004). Another possible explanation for the observed patterns in foraging behaviour of lesser horseshoe bats could be an indirect effect of landscape structure on the availability and distribution of their preferred prey.

Habitat use and selection

Our results from Austria are in accordance with those of previous radio-tracking studies of lesser horseshoe bats in Wales, UK (Bontadina et al., 2002; Schofield et al., 2002), the Grisons, Switzerland (Bontadina et al., 2006) and Bavaria, Germany (Zahn et al., 2008). We found that bats seemed to be selective in choosing their individual foraging ranges at the less fragmented site, but not at the highly fragmented site. This suggests that the bats at the highly fragmented site were forced to exploit all potential foraging areas in the vicinity of their roost, and that the selection of the roost site is decisive to ensure all colony members have foraging opportunities and good potential food sources. Support for this claim comes from Boughey et al. (2011), who found a strong correlation for lesser horseshoe bats to locate their roosts in the vicinity of broadleaved forests. It is therefore likely that the pivotal criteria for the selection of a colonial roost are not only its microclimate, but also the foraging quality in its surroundings. However, a comparison of the core foraging areas of the bats with their MCPs revealed a significant habitat selection at both sites. Thus, the bats seem able to assess the foraging quality of different areas within their home range and probably prioritise their foraging behaviour according to which patches are the most profitable (Jones, 1990). It would be interesting to see more studies on the foraging behaviour of bats as well as food availability and selection at sites that vary in the degree of fragmentation.

Implications for conservation and management

According to our findings high fragmentation had clear consequences on the spatial foraging behaviour of lesser horseshoe bats. Thus, we may expect that every loss of woodland in the surroundings of a colonial roost will negatively affect the individuals of the colony. Moreover, the life cycle of this species is adapted to a continuous environment and its reproduction rate is very low, so that the negative effects of habitat fragmentation and habitat loss might only become evident after many years. Management and mitigation measures, as well as their monitoring, will therefore need to take into account the long-term effects of habitat loss and fragmentation. Furthermore, the conservation recommendations for this species of Bontadina et al. (2002), which are based on research in Wales, are supported by our findings from a different region in Europe. Hence, the following recommendations should therefore strongly be considered when conservation measures for this species are required, designed and put into action:

- (i) Since lesser horseshoe bats seem not able to adopt their spatial foraging behaviour in a degraded landscape, we conclude that any loss of woodland within foraging distance of their colonial roosts can be expected to have negative influences on the colony.
- (ii) Conservation measures for lesser horseshoe bats should be undertaken near to the roost, particularly within 2.5 km to the nursery roosts. This recommendation is in accordance with the conclusions of Bontadina et al. (2002).
- (iii) The quantity of woodland within these areas should be maintained and where possible enhanced, especially within 600 m of the roosts, recommended also by Bontadina et al. (2002).
- (iv) Fragmented woodlands and patches of bushes and trees in the surroundings of colonies should be connected by hedgerows or tree lines to resume function as steppingstones or connecting linear landscape elements to overcome habitat fragmentation, as also pointed out by Frey-Ehrenbold et al. (2012) for all short-range echolocating bats.

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