

**Foraging range use by a colony of greater
horseshoe bats *Rhinolophus ferrumequinum* in
the Swiss Alps:
implications for landscape planning**

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Abstract

After having suffered a dramatic population decline, the greater horseshoe bat has been classified as highly endangered in central and western Europe. We studied seasonal foraging range use of one large colony by radio-tracking so as to get founded arguments in the face of rising land use conflicts.

The individual bats used largely overlapping foraging ranges: on average 10 bats exploited more than 80 % of the colony range estimated to be 6.7 (± 0.34) km². Altitude above sea level and distance to the roost explained 30.5 % of the variation in utilisation density. Core foraging areas enclosed 74 % of the foraging activity of the bats within 30 % of colony home range. Foraging distances were larger in spring, which is probably the critical season for greater horseshoe bats.

We conclude that conservation of the colony must be given priority (1) within distances of up to 4 km from the nursery roost, (2) especially within core foraging areas; and we suggest that (3) management measures would be more effective if implemented near to the nursery colony and would contain habitats used in spring, the season suspected to be most critical.

Introduction

In temperate regions female bats associate in large numbers during the reproduction season to benefit from communal heating to raise their young (Lyman 1970). In general, the availability of a suitable and safe place for reproduction is a key resource (Begon et al. 1990). This is particularly true for bat colonies which choose their roosting places according to complex microclimatic and structural requirements and often use these locations in strict tradition over decades. Such roosts represent therefore a limiting factor: all reproducing females of the colony join at a unique place which determines the reproductive outcome of the year.

It is therefore not surprising that so far conservation measures for endangered bat populations often have concentrated mostly on the protection of the breeding roosts (Stutz & Haffner 1984, Beck & Schelbert 1999). However, the importance of the foraging areas connected to these maternity sites have often been neglected. The location of the roost further constraints the females in their choice to find foraging areas with abundant food. This is even more important in a maternity roost, as pregnant or lactating females have to fulfil extraordinary energetic demands (Speakman & Racey 1987, Ransome 1990).

In Switzerland we were challenged by a relict and isolated nursery colony of the greater horseshoe bat *Rhinolophus ferrumequinum* (Schreber, 1774). This originally cave dwelling bat tends, particularly in the northern part of its range, to roost in buildings during the summer. Females exhibit a strong philopatric behaviour and apparently reproduce mostly in the same nursery colony where they were born themselves (Ransome 1990). This may explain the observed traditional use of a singular reproduction roost.

The greater horseshoe bat was once widely distributed through western, central and southern Europe (Schober 1998). However it has suffered a significant decline in the northern extent of its range during the second half of the 20th century (Stebbings 1988, Ohlendorf 1996). Local population declines and the loss of colonies are well documented for most

countries north of the Alpine arch (Ohlendorf 1996). This dramatic decline led to the persistence of small remnant colonies at the northern border of the European distribution area, populations which are often isolated from each other. The species is classified as in danger of extinction in most central European countries and listed in the EC Habitat Directive (Ransome & Hutson 2000), which demands priority efforts in the protection of roosts and habitat.

Although in Switzerland many colonies of greater horseshoe bats have been documented once (Baumann 1949), today only three nursery roosts are known (Beck & Schelbert 1999). Whereas two of the nursery colonies are inhabited by only 10 and 50 bats, respectively, some 150 adult bats reproduce in the third roost, which is situated in the attic of a church in an isolated alpine valley. The latter, our study site, represents the largest nursery colony of this species known in central Europe (Ohlendorf 1996).

Such remnant colonies are of special concern in conservation biology of a species because they could be starting points for a later recolonisation of abandoned area (Bellamy 1996, Bontadina et al. 2000) and represent a last chance to understand the local species specific requirements (Carroll 1992).

The nursery roost was secured by a site agreement with local authorities (Lutz & Mühlethaler 1996). However, in the direct surrounding of this vulnerable reproduction roost a reorganisation of agricultural land use and ownership was planned. This type of agricultural landscape planning is known to reduce the area of natural habitats and it often negatively affects their quality and biodiversity (Tanner & Zoller 1996, Vickery et al. 2001). Therefore the urgent need for a conservation study of this colony was given.

We investigated spatial requirements and resource exploitation of this colony in order to recognise potential utilisation conflicts, to suggest sound conservation recommendations going beyond roost protection,

and to propose the implementation of conservation measures in the re-organisation of future land use.

The detailed objectives of the study presented here, were 1) to designate the perimeter of potential land use conflict, 2) to identify representative core foraging areas and, 3) to examine whether spatial behaviour provides evidence for seasonal resource limitation.

Colony and study area

The nursery colony roosted in the attic of the church in the centre of the small village Castrisch, in the Upper Rhine Valley, Eastern Switzerland (46°51.31' N, 8°26.14' E, 720 meters asl.). Counts of the number of animals leaving the roost in the evening, carried out since 1984, revealed constant colony size with a seasonal peak of about 150 emerging bats at the beginning of July (Lutz & Mühlethaler, unpubl. data). With “colony” we designate according to Gaisler (1963) all bats which constitute a reproductive community connected to the nursery roost. Usually only a small proportion of males join the summer group in the nursery roost. Including the males, we therefore estimate the colony to number about 200 individuals in total.

At the study site, annual precipitation is 950 mm, typical for an alpine-continental climate, with hot summers and relatively long, cold winters. The roost is situated in the river basin, 250 m from the Upper Rhine on a system of former gravel terraces only slightly higher than the river. The river valley rises on both sides steep up to 3000 m asl. There are several brooks from the sides entering the main river, which contribute with gorges and gravel deltas with treelines and bushes to a diversely structured relief.

The ground of the valley is shaped by the river with well expanded riparian vegetation. On the slopes predominate mixed broadleaf woodlands, whereas pine forests are less frequent. The productive ground in the plain is covered by intensively managed agricultural fields mostly devoted to hay production and pastures. The villages have retained some of the traditionally-managed orchards in their vicinity.

Methods

The study was conducted in 1993, one year before the landscape planning was completed. In order to compare the foraging behaviour during different seasons we studied the bats in the following three periods: spring (from 1st May to 9 June), summer (from 1st July to 6 August) and autumn (from 31st August to 12 October) corresponding to early pregnancy, lactation and post-lactation, respectively.

Radio-transmitters and tracking methods

To minimise the disturbance to the bats in the roost we caught the study animals in mist nets along flight lines when they left the roost at dusk or returned at dawn at eight different points between 10 and 500 m from the church. The bats caught were held in bags before having biometric data taken from them. Animals were sexed, the reproductive condition of the females was assessed and the individuals were banded using the official wing bands of the Museum of Geneva. Parous females were identified by the presence of large pelvic nipples (Gaisler 1963, Ransome 1990) and palpably pregnant animals were recorded. For the radio-tracking study we only tagged females as they are more bound to the maternity roost. Yet, in two cases males were radio-tracked. In order to study a representative sample of the colony we did no selection in the bats caught for tagging, except in that we omitted heavily gravid females for obvious reasons. Four individuals were tracked in two different seasons. This was due to the constraint by the limited colony size.

The bats were tagged with BD-2B transmitters from Holohil (Holohil Systems Ltd, 112 John Cavanagh Rd., Ontario KOA 1LO, Canada, www.holohil.com) with position sensors which allowed the discrimination between flying and hanging bats. The transmitters were attached to the back of the bats between the scapulae, the fur was trimmed and the tag was glued close to the skin using surgical cement (SkinBond, Smith & Nephew United Inc., Largo, Florida, USA). The transmitter batteries had a minimum lifespan between 10 to 21 days. We tracked the bats using TRX-1000 (Wildlife Materials, Inc., 1031 Autumn Ridge Road, Carbondale 62901, Illinois, USA, www.wildlifematerials.com) and

modified YEASU FT-290 receivers (adapted by Karl Wagener, Telemetrie-Material, Herwarthstrasse 22, D-5000 Köln 1, Germany) with hand-held H-aerials.

The location of the tagged bats were recorded in 15 minute intervals (interval sampling, Altmann 1974) throughout the night by triangulating the signal direction by two mobile persons. They co-ordinated their simultaneous bearings using trigger signals from Casio DB-31 watches and hand-held FM-radios were used to keep contact. If one person lost contact with the bat, the other tried to homing-in on the animal (White & Garrott, 1990). This was only possible with any reasonable accuracy when the animal was foraging in a small area. We assigned locations to one of three accuracy classes (50, 100 and 250 m) depending our confidence in the estimated location. The highest accuracy class could only be assigned when we were in close proximity to the bat, and using triangulation. The accuracy of these classes was determined during a field test at night with a transmitter being moved around in a foraging area by a colleague. A test of the deviation of the estimated locations from exactly known locations (location error method - Zimmermann & Powell, 1995) gave a location error with standard deviation (SD) of ± 9.3 degrees with the estimated locations bivariately normally distributed around the "true" transmitter position. The locations of the estimated accuracy classes of 50, 100 and 250 meters had their centre not significantly different from the "true" centre, the standard deviations of the normally distributed location errors were 44, 85 and 162 meters, respectively (Bontadina & Naef-Daenzer, in press).

Time, location of observers, bearings of the bats, accuracy data 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 subsequently calculated from the bearings and their estimated location digitised using a self-written program.

Habitat data, spatial calculations and statistical analysis

The studied bats used not exclusively the maternity roost but inhabited occasionally other day roosts (unpubl. data). For a better comparability,

the calculated flight line distances of the location do not always refer to the maternity roost but to the day roost used the preceding day. Foraging radius (= maximum distance) and median distance of locations (= distance, which includes 50% of locations) were calculated for each bat with all data of several nights. Bootstrap calculations for the colony foraging area were computed using a self-adapted program written in Turbo Pascal (Tufto et al. 1999). We investigated the influence of spatial features by regression analysis (Norusis 1986). Linear regressions performed better than exponential decay models. We used the geographical variables DIST and ALTITUDE and five parameters which describe land cover: BROADLEAF (amount of broadleaf woodland), CONIFER (amount of conifer woodland), REST (other open land as bare, gravel), GREEN (cover by meadows & pastures) and ARABLE (cover by arable land) (Beck et al. 1994).

The spatial model was calculated based on all locations included in a 98 % minimum convex polygon ($n = 1320$) to ensure, that some unique outliers do not inflate the foraging area. We defined individual core foraging areas by the 50 % kernel contour lines.

Because of the seasonal stratified range use in bats the foraging ranges we observed do not include all places relevant to a home range. We therefore use the term activity ranges for the areas used by individual bats during the relatively short study period of some days.

There is a problem to composite core foraging areas from several individuals (Wray et al. 1992). We computed utilisation density by kernel estimations (Worton 1989) according to the procedure described in Naef-Daenzer (1994) and Bontadina & Naef-Daenzer (in press). In order to weight all individuals equally, we calculated first a matrix of utilisation density for every bat, than the matrices of all bats of a season were combined and finally the matrices of the three seasons were joined. We delimited core foraging areas of the colony by those 30 percent of the total used area with the highest utilisation density of all radio-tracked bats.

Results

In 26 radio-tracking sessions we collected 1330 locations from 22 foraging greater horseshoe bats during 99 nights (Table 1). Data collection per session lasted for 3.8 ± 1.2 (mean \pm SD) nights. Four bats were radio-tracked in two seasons. In one of these cases the foraging ranges showed a minor overlap of 13%, in the other three cases no overlap at all, pointing to spatially seasonal foraging areas. For the spatial analysis we therefore treated all tracking sessions as samples of independent members of the colony. Accordingly we studied 8 bats in spring, 11 in summer and 7 in autumn.

[Table 1]

Foraging areas

The bats foraged every night within large individual foraging areas. Mean size of activity range, revealed by 90 % kernel density contour lines, was 50.8 ± 30.3 ha ($n = 26$, range 21.9 - 162.8 ha, Table 2). The overall range use by the colony was calculated by summing up all individual foraging areas. The recorded area increased progressively with the number of bats studied. In order to estimate the total foraging range of the colony we randomly added individual foraging ranges of radio-tracked bats and calculated the cumulative foraging area (Fig. 2). This was repeated for hundred calculations while the bats included were permuted (bootstrap sampling). The individual foraging ranges overlapped to a large extent with each other: 10 bats used already more than 80 % of the total recorded foraging area. The overall foraging range of all 26 bats was 6.13 km^2 . The regression curve of the bootstrapped range data approaches an asymptote at about 6.7 km^2 , but is nearly reached by the locational data of about 15 bats from different seasons. The extrapolated foraging range of the total colony lies with confidence of 95% between 6.4 and 7.0 km^2 .

[Figure 1]

Foraging intensity

The utilisation density within the foraging range of the colony was unevenly distributed. The observed foraging was distributed over a narrow band of altitude. The lowest grounds available were at 670 m asl and no foraging was observed in areas higher than 900 m asl. In the same foraging areas we found up to 16 bats (62 % of the sample studied) in the course of the year. The foraging bats showed a selective pattern of spatial use which reflected the topographical situation of the main valley and one side valley situated towards the south (Fig. 2).

The three factors ALTITUDE (meters above sea level), DIST (distance to the roost) and BROADLEAF (broadleaf woodland cover) were found to be significant predictors in linear regression which explained 24.9 % of the variability in the observed utilisation density (Table 3). The density of use decreased with distance to the roost and altitude (Fig. 3) and increased with broadleaf woodland cover.

[Figure 2]

[Table 3]

[Figure 3]

Fifty percent of the interval sampling locations (which is equivalent to 50% of time) we found the tracked bats within 1700 m of the maternity roost whereas the maximum foraging distance was 7.4 km. If the utilisation pattern is compared to a uniform distribution, foraging areas up to 4 km from the roost are used more than expected (Fig. 4). No areas above 900 meters asl. were used for foraging.

[Figure 4]

Core areas

The size of individual core foraging areas (50 % kernel) was 7.1 ± 4.0 ha and enclosed about an area of 7 % of the overall activity areas (Table 2).

The individual core foraging areas overlapped only to a small extent, therefore the area curve increases at every step for nearly the area of the core area added (Fig. 2).

There were 15 spatially explicit core areas delimited (see Fig. 2, some of the smallest were omitted). They enclose an area of 2.1 km², according to the definition 30 % of the overall foraging area.

Indication for critical season

The body weight of 51 bats caught when emerging from the roost was 21.0 ± 2.8 g and showed no seasonal differences (ANOVA, $F_{2,48} = 1.40$, $p > 0.25$). The foraging distance of the bats differed in the three seasons (Median distance of individuals tested by season with Kruskal-Wallis test, $\text{Chi}^2 = 7.04$, $df = 2$, $p < 0.05$). In spring the bats foraged half of the time exterior to a distance of 2523 m from the roost. In summer, however, the distance was only 1524 m and decreased to 1005 m in autumn (Table 2). This difference in mean foraging distance was reflected by the amount of time they foraged in immediate vicinity of the roost. Whereas in spring the bats stayed for only 17.7 % of the time within 1.2 km of the roost but for 52.2 % further away than 2.4 km, this proportion was 66.1 % and 13.4 %, respectively, in autumn (Fig. 5).

[Figure 5]

The number of locations collected showed no influence on individual activity range size (linear regression, $n = 26$, $r = 0.04$, $p = 0.85$). We therefore compared seasonal activity ranges without correction for sample size. Mean activity ranges by 90 % kernel density estimates showed no significant seasonal differences (ANOVA, $F_{2,23} = 1.42$, $p = 0.26$) (Table 2).

Discussion

Foraging area of the colony

Greater horseshoe bats usually forage in short distance to their nursery roost, as the results of this study demonstrate. This finding could only be revealed by radio-tracking, as former attempts to find foraging areas by the use of an ultrasound detector in the field were only successful near to the nursery roost (Zahner 1997). Since the availability of transmitters, light enough to study greater horseshoe bats, there are several investigations which explored foraging behaviour in greater horseshoe bats in UK (Stebbing 1982, Jones & Morton 1992, Jones et al. 1996, Duvergé 1996), in Luxembourg (Pir 1994), Germany (Geiger et al. 1993), Italy (Bontadina et al. 1999) and Switzerland (Beck et al. 1994, Bontadina et al. 1995, Lugon 1996).

Lugon (1996) found median foraging radii of 1 km in an Alpine Valley. Jones & Morton (1992) calculated mean foraging radii between 2 and 4 km, and Duvergé (1996) found values between 1.6 and 2.8 km in his extensive study. Our results are consistent with these findings and confirm that in different habitats and regions the mean distances used by greater horseshoe bats are very limited, mainly in the range of 1-4 km, although this sometimes may include foraging in peak distances of up to 7 km, as we observed in our study. The relatively small range used for foraging by greater horseshoe bats gets even more obvious when it is compared with ranges of other European bat species of similar size. Greater mouse eared bats *Myotis myotis* were observed to commute much larger distances of up to 25 km for foraging (Güttinger 1997, Arlettaz 1999) and noctule bats *Nyctalus noctula* went at least 16 km (Kronwitter 1988).

An estimation of the foraging range of all members of the colony based on an extrapolation of spatially overlapping individual activity ranges revealed a foraging area of 7 km², an area significantly smaller than expected by the maximal ranges (at radius = 3.5 km: 39 km²). This was mainly contributed to a limitation by topography. Although this restriction, there was no indication for exceptionally enlarged foraging distances, if compared to other studies. This supports the hypothesis of Jones et al. (1995), which postulated that the foraging radius of a species is mainly limited by its wing morphology.

Identification of core foraging areas

Our results suggest that the cumulative foraging ranges of 15 bats from different seasons are sufficient to describe the overall foraging range of a colony as a whole. This is, however, not the case for the core foraging areas, those areas used most intensively for feeding and therefore judged to be the most important ones. The overlap of individual core areas was relatively small. Even the study of 26 bats, which represents about one sixth of the colony, could detect only a small amount of those core foraging ranges presumably used by all members of the colony. The steady increase of the core area curve depending on individuals included indicates, that colony core foraging areas, in difference to the small individual core ranges, are large and may even enclose a main part of the foraging area of the colony.

This pattern with small individual core foraging areas with minor overlaps with each other, and dispersed over a large area, could represent territorial defence of foraging areas or avoidance of interspecific competition. In accordance with Duvergé (1996) we had no indication of any territorial behaviour in the foraging area, except of two observations where a bat was chased away from a perch by another greater horseshoe bat.

Core areas are object of dispute in ecology (Wray et al. 1992), because their boundaries can not objectively be determined. In order to provide

priorities for conservation within the foraging area we stratified the colony area by the designation of those 30 % of the area with highest utilisation density (key feeding areas). This allowed the spatially explicit indication of areas of highest importance as required by landscape planning (e.g. Marzluff & Ewing 2001).

Factors explaining foraging intensity

Habitat selection may be examined at several spatial levels. After having identified a hierarchical order of selection processes, from selection of geographical range to selection of food items (Owen 1972), it is a fundamental concept to exercise resource exploitation studies at different scales (Wiens & Milne 1989). Thereby the components available depend upon the order of selection considered (Johnson 1980).

The differences in utilisation densities of the colony may partly be explained by altitude, broadleaf woodland cover and flight distance to the roost. Greater horseshoe bats forage mostly in areas of low altitude of their colony range. We suppose altitude represents the known dependency of nocturnal insect availability on temperature (Lewis & Taylor 1964, Duvergé 1996). Duvergé (1996) found insect, especially moth, availability to increase about twofold by an increase of two degrees of the initial nightly temperature within a range of 5 to 15 degrees. On the other hand the temperature drops about 0.65 degrees per 100 m as altitude increases (Pfister 2000). In particular in the alpine range greater horseshoe bats might benefit from this effect by looking for the lowest located suitable areas. In contrast they seemed to avoid altitudes more than 900 m asl. at all, although habitats did not change abruptly at this altitude. The second factor with influence on foraging was DISTANCE to the roost. The smaller the distance to the roost, the more bats were observed foraging. Therefore we suggest that the value of conservation measures increases with decreasing distance to the roost. This could be of particular interest for subadult bats, which only slowly enlarge their foraging ranges (Duvergé 1996) and therefore are restricted to suitable habitats in the ultimate vicinity to their roost. The only factor of cover

which contributed to the model was cover of broadleaf woodland. However, only 25 % of the variability in utilisation density could be explained by spatial and geographical factors at the colony level. A first evaluation of the individual's selection of their activity ranges revealed a selective use of woodlands in spring (Bontadina et al. 1995). Other studies found specific habitat types selected for, too (Pir 1994, Duvergé 1996, Lugon 1996). We suppose therefore that habitat selection, carried out by individuals within their activity ranges, is responsible for a large part of the remaining variability in utilisation density.

Indication for critical season

In the circadian rhythm of hibernating bats, spring usually represents the season with their lowest weight of the year (Beasley et al. 1984). In captive pallid bats *Antrozous pallidus* peak levels of food intake occurred at times of the year when body weight was low (Beasley 1986). Ransome (1990) observed in greater horseshoe bats a body weight reduction of about one third during hibernation. The bats have to restore their condition after hibernation which signifies an increased energy demand. This is especially the case for female bats, which only shortly afterwards enter pregnancy and it is probably more severe in the continental climate of the Alps with long, cold winters. Moreover in early spring the insect abundance is very low (Ransome 1990, Duvergé 1996, own unpublished data) which requires an additional effort to replenish their resources. It was in spring, when we found larger foraging radii of female greater horseshoe bats. This means not only additional travel expenses, but also that the bats dispersed over more than twice the area used by the colony in summer (area with radius 1.5 km = 7 km² vs. 19.6 km² at radius of 2.5 km). We interpret the increase in foraging distance as an indication for food being a limiting resource in this season. This is in accordance with the findings from Ransome (1978), that reproduction success (in term of an early date of birth) was mostly related with the mean temperature, and hence insect availability, in spring. Racey & Swift (1985) found foraging areas contracting in lactating female Pipistrelle bats in summer, but Barclay (1989) found no correlation of foraging behaviour with sea-

son in pipistrelle bats *Pipistrellus pipistrellus*. Significant differences can be interpreted as a seasonal or reproductive effect (Duvergé 1996). This plays a minor role in our interpretation, as we use the result as indication of an increased effort necessary, independent whether this derives from increased energetic demand by the reproduction state and/or a seasonal shortage of food.

Species that have low fecundity but are long-lived, as this is the case in greater horseshoe bats (Ransome 1990), are most sensitive to seasonal resource bottlenecks (Payne & Wilson 1999). We therefore suggest to pay special attention to critical seasons in greater horseshoe bats. If the requirements of a highly endangered species has to be included into a conservation scheme in densely populated area, utilisation conflicts are inevitable. This is even more the case in synanthropic bat species which often have their roost within a human settlement and use large foraging areas in the vicinity. It was generally recognised in mammals, that viable populations often would require the preservation of areas of a size of some magnitudes larger than any existing natural reserves (Shaffer 1987). If therefore compromises between different utilisation interests are drawn, areas and habitats used in such a critical season should gain priority in a conservation scheme.

Implications for conservation

Mitchell-Jones (1995, 1999) outlined the importance of the identification of critical feeding areas around the breeding roosts. The spatial demands of this large relict colony of greater horseshoe bats, as revealed by radio-tracking, extends the perception of the conservation needs of this colony beyond the roost. For a successful conservation of the colony their spatial requirements for foraging must be considered (Bontadina et al. 1996). First, we suggest that with regard to possible utilisation conflicts the presence of greater horseshoe bats and their requirements must be considered within a distance of up to 10 km around all roosts used by several greater horseshoe bats. However, the requirements of greater horseshoe

bats must be given priority within a distances of 4 km to the nursery roost. **Second**, conservation of key feeding areas should earn highest priority. They concentrate a major amount of foraging activity of a significant proportion of the colony on a relatively small area. Further analysis should investigate fine grained habitat use within individual activity areas, in order to be able to extrapolated sufficiently the essential foraging areas. **Third**, we suggest that management measures are more effective, when they are implemented near to the nursery colony and enclose habitats used in spring, the season suspected to be critical.

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- Table 1:** Summary of 26 telemetry sessions of *Rhinolophus ferrumequinum* carried out in 1993: animal code with sex, wing band number, age and reproduction state, period of tracking session, number of nights with observations and number of sampling locations (five minutes intervals) are given and summarised for the three seasons spring, summer and autumn, which correspond to early pregnancy, lactation and post-lactation.

animal code (W = female, M = male)	wing band number	reprod. state, age class	date of tracking session	nights with observations	locations n
W1	H967	ad., 2	30.4.-2.5.	3	9
W7	H968	ad., 2	7.5.-12.5.	5	28
W17	H970	ad., 2	13.5.-17.5.	3	44
W27	H971	ad., 2	18.5.-25.5.	5	27
W8	H969	ad., 2	22.5.-30.5.	5	115
W9	H972	ad., 2	27.5.-3.6.	5	45
W18	H973	ad., 2	1.6.-6.6.	4	56
W19	H974	ad., 2	6.6.-11.6.	4	110
spring				34	434
M8	H979	ad., 2	25.7.-31.7.	3	35
W37	I526	ad., 3	1.7.-2.7.	3	59
W47	H978	ad., 3	4.7.-7.7.	3	32
W57	H975	ad., 3	9.7.-12.7.	2	3
W28 (former W1)	H967	ad., 3	12.7.-22.7.	5	79
W29	H976	ad., 3	13.7.-24.7.	4	49
W3	I517	ad., 3	17.7.-26.7.	4	54
W11	H977	ad., 3	21.7.-30.7.	4	51
W2 (former W9)	H972	ad., 3	25.7.-31.7.	4	130
W13	H980	ad., 3	30.7.-1.8.	2	9
W23	H981	ad., 3	2.8.-?	4	104
summer				38	570
M0	plastic ring #75	ad., 5	30.8.-24.9.	2	8
W3_h (former W3)	I517	ad., 2	30.8.-?	3	10
W22 (former W7)	H968	ad. (post lac.)	30.8.-21.9.	4	45
W38	H982	subad., 1	2.9.-?	4	67
W21	H983	ad., (non lac.)	1.9.-21.9.	4	63
W32	no ring	ad., 2	29.9.-?	4	58
W31	H986	ad., 1	29.9.-?	7	40
autumn				27	283
year			26 sessions	99	1330

Table 2: Maximum foraging radius and Median distances (IQR = inter-quartile range) the bats went foraging from the roost.

animal code	maximum foraging radius	Median distance (IQR)	50 % kernel core area size [ha]	90 % kernel activity range size [ha]
W1	1917	1733 (1700 - 1785)	5	26.98
W17	2460	1950 (1589 - 2056)	10.3	61.04
W18	3262	2439 (627 - 2997)	6.1	56.85
W19	4174	3171 (2743 - 3608)	2.5	70.78
W27	7372	5941 (2347 - 6842)	4.4	48.12
W7	2333	1969 (1649 - 2069)	4.7	34.04
W8	4565	2448 (2295 - 2628)	5.4	27.39
W9	1702	535 (431 - 1143)	4.2	35.07
mean spring	3473	2523 (1672 - 2891)	5.3 ± 2.7	45.03 ± 16.59
W13	3457	536 (261 - 3332)	1.8	43.78
M8	3918	2928 (1982 - 2948)	5.2	23.76
W11	4744	1417 (1032 - 1527)	4.4	65.87
W2	4369	1876 (1763 - 3071)	4.2	35.51
W23	3789	1041 (951 - 1164)	5.6	40.97
W28	3251	1877 (1030 - 2151)	10	74.88
W29	2726	893 (258 - 1377)	7	59.87
W3	3448	1257 (951 - 1853)	18.7	162.80
W37	3290	2794 (2672 - 2995)	11.1	56.33
W47	2453	1010 (637 - 1575)	14.1	93.37
W57	2841	1129 (792 - 1985)	10.9	25.58
mean summer	3448	1524 (1121 - 2180)	8.5 ± 5.0	62.07 ± 39.53
M0	728	275 (205 - 544)	5.1	38.19
W21	5540	2411 (1175 - 2804)	5.1	27.35
W22	2118	1194 (950 - 1397)	5.4	28.05
W3_h	3282	617 (201 - 1519)	6.8	51.96
W31	1839	746 (456 - 1386)	13.9	83.64
W32	1235	787 (714 - 862)	4.9	21.87
W38	1472	1003 (685 - 1087)	10.8	27.02
mean autumn	1839	1005 (627 - 1371)	7.4 ± 3.5	39.73 ± 21.80
mean year	2743	1691	7.1 ± 1.6	50.81 ± 30.28

[Table 3]

Table 3. Utilisation density (UTILD) in the foraging area of the colony explained by the independent factors ALTITUDE (meters above sea level), DIST (distance to the colony), BROADLEAF (amount of broad-leaf woodland cover), CONIFER (amount of conifer woodland cover), REST (other open land as bare, gravel), GREEN (meadows & pastures) and ARABLE (arable land) in linear regression (n = 743 ha squares with \geq one location). The dependent variable utilisation density was $\log_{10}(\text{UTILD}+1)$ transformed to achieve normality.

	std correlation coef.	T	p
constant	856	1.681	.093
ALTITUDE	-.174	-4.638	<0.001
DIST	-.257	-7.160	<0.001
BROADLEAF	.703	2.143	.032
CONIFER	.620	1.781	.075
REST	.595	1.449	.148
GREEN	.498	1.238	.216
ARABLE	.035	.235	.814

[Figure 1]

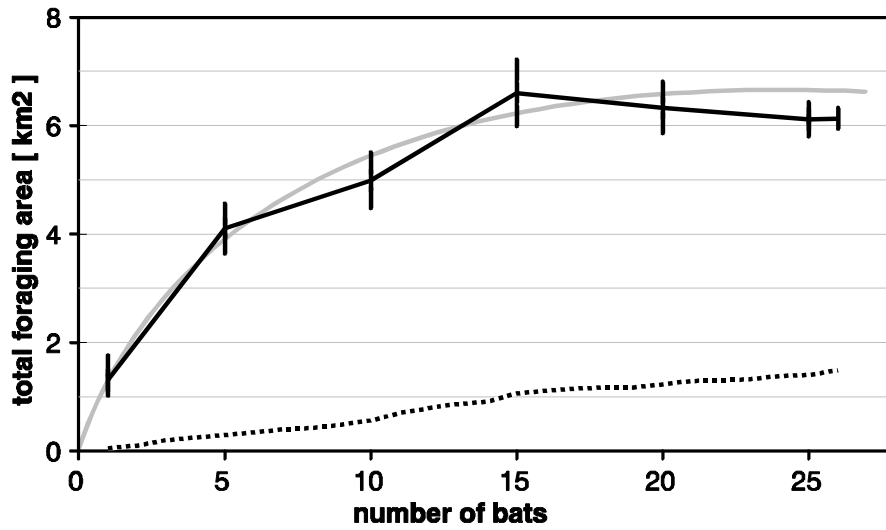


Fig. 1: Relation of area depending on number of individuals included. Black line: 90 % kernel contour colony foraging area size computed as cumulated foraging areas of individual bats (mean \pm 95 % confidence intervals of 100 bootstrap resamples). Grey curve: logistic regression line. Black dotted line: core area size computed as cumulated foraging areas of individual bats.

[Figure 2]

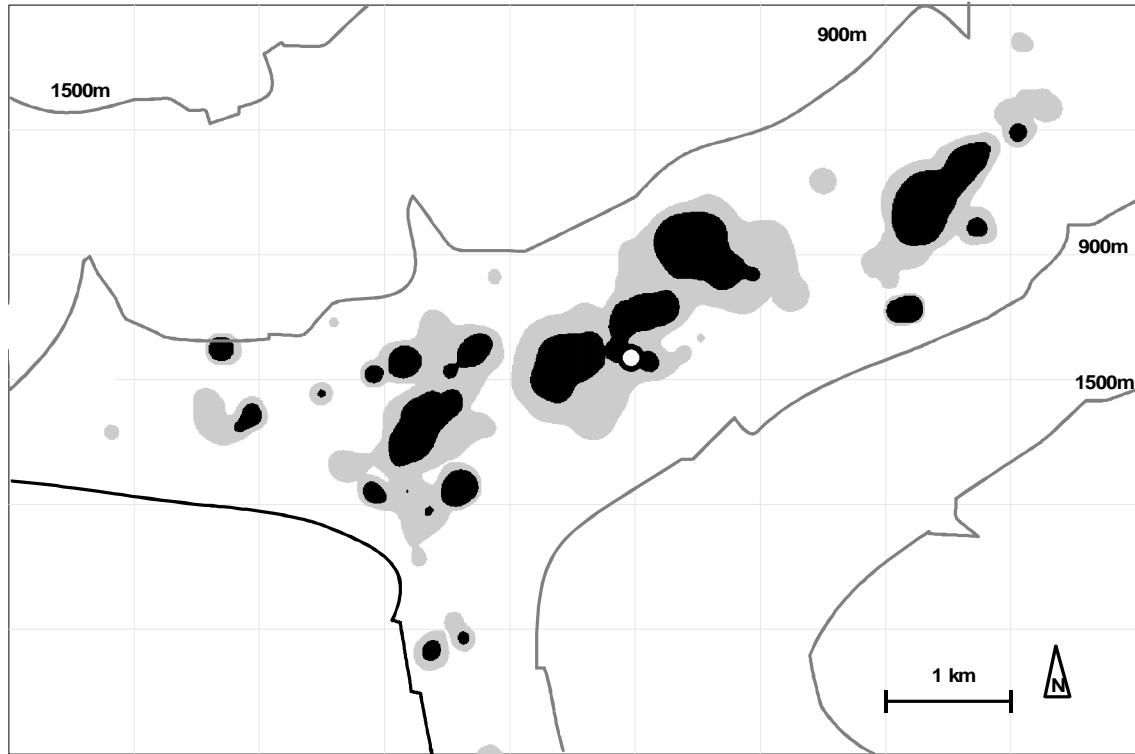


Fig. 2: Mean utilisation density (with 95 % confidence intervals) depending on classes of altitude above sea level.

[Figure 3]

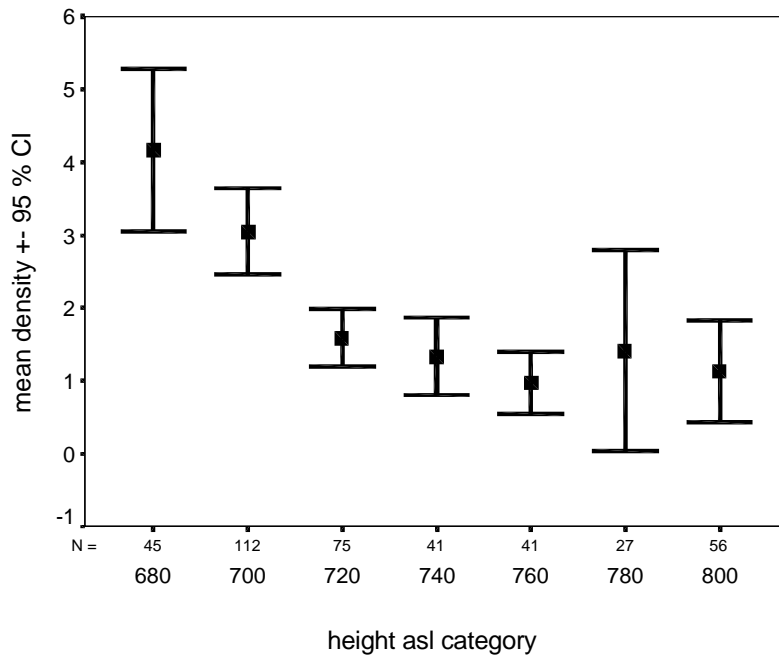


Fig. 3: Mean utilisation density (with 95 % confidence intervals) depending on classes of altitude above sea level.

[Figure 4]

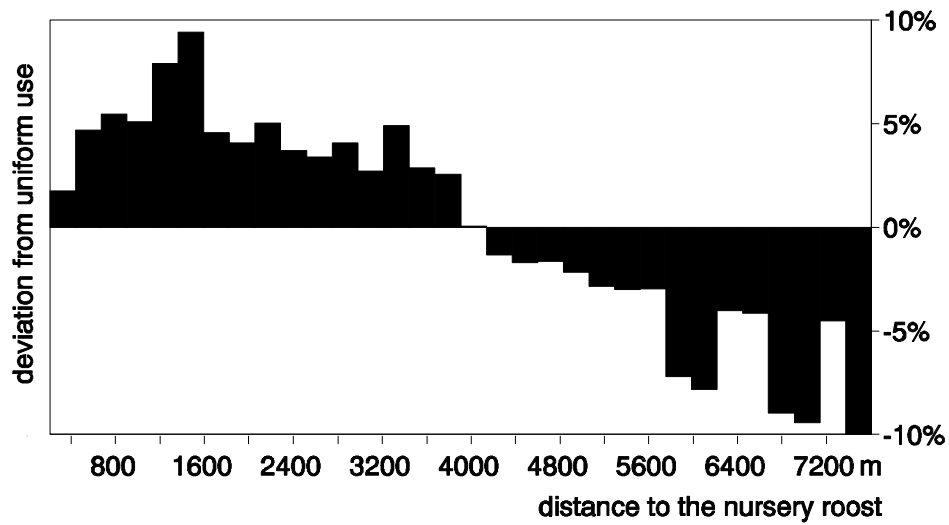


Fig. 4: Deviation of the observed frequency of locations (n = 1330) when compared with a model of uniform spatial use. If the bats would have used all areas within 7400 m (maximal range) to the nursery roost equally, no deviation from the baseline would be observed. Distances near to the roost up to about 4 km were used more often for foraging than expected by the uniform model.

[Figure 5]

