# Reproductive and age classes do not change spatial dynamics of foraging long-fingered bats ()

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# Reproductive and age classes do not change spatial dynamics of foraging long-fingered bats (*Myotis capaccinii*)

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Egoitz Salsamendi · Inazio Garin**

**Abstract** Spatial dynamics of foraging long-fingered bats
(*Myotis capaccinii*) were studied in the Eastern Iberian
Peninsula. We analysed the locations of 45 radio-tracked
individuals during three discrete periods through the
breeding season and measured the spatial parameters
related to their foraging behaviour in order to test whether
variations in spatial use occur. Colony range, measured as
the minimum convex polygon through all the radioloca-
tions, was 345 km$^2$, but the area used during each period
was smaller. During pre-breeding, foraging bats gathered at
two stretches of different tributary rivers; during lactation,
they scattered throughout the river system; and during
weaning, they aggregated at a stretch of the main river.
Individuals on average flew 5.7 km from roosts to foraging
areas, with a maximum absolute distance of 22.7 km.
Individual foraging ranges were measured linearly, because
the bats foraged mostly along rivers; their values averaged
1.3 km/night and overlapped extensively between neigh-
bouring bats (>65% on average). The sampling period,
rather than the bats' reproductive status, age, or sex,
explained the observed variability in spatial distribution
and size of hunting sites. We did not find differences in
spatial parameters between lactating females and non-
lactating bats, nor between juveniles and adults. This is
the first study to split the independent effects of season and
population class in order to enable unconfounded interpre-
tations of the spatial dynamics of foraging reproductive
females and juveniles. We speculate that the relationship
between colony size and prey availability ruled the
observed changes in foraging area through seasons. The
considerable overlap in individual foraging ranges may be a
necessary adaption to large colonies forced by the specific
roost requirements of the long-fingered bat and the narrow
foraging niche they appear to occupy.

## Introduction

The lack of empirical evidence about size of foraging
ranges used by bats hampers effective conservation meas-
ures around roosts, as wildlife managers may be unable to
define areas for protection based on sound biological
criteria (Racey and Entwistle 2003). In addition, the spatial
distribution of bats' foraging areas is difficult to predict,
because patterns of spatial use among species and pop-
ulations are extremely variable (e.g., Fenton 1997; Racey
and Entwistle 2003). It has been suggested that features
governing bats' aerodynamic abilities, such as size and
wing morphology, constrain the distances that individuals
can travel from roosts to foraging areas and thus, their
distribution around the colony roost. Norberg and Rayner
(1987) predicted that heavier bats and/or those with long
and narrow wings would be favoured to travel long
distances. In support of this hypothesis, Jones et al.
(1995) found positive significant correlation between wing
shape and distance travelled to foraging areas in 17 bat
species, and Fenton (1997) found that heavier bats covered
or flew longer distances.

Nevertheless, along with the advent of miniaturized radio
transmitters, numerous studies have revealed that the dis-
tances flown by bats to hunting sites do not always fit the

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expectations derived from their wing morphology and size (e.g., *Myotis moluccarum*, Barclay et al. 2000; *Chalinolobus tuberculatus*, O'Donnell 2001; *Macrophyllum macrophyllum*, Meyer et al. 2005; *Rhinolophus euryale* and *Rhinolophus mehelyi*, Russo et al. 2005; Goiti et al. 2006). Moreover, it has been asserted that, because bat wings do not behave as a simple air foil, bats' flight performance cannot be fully explained by traditional aerodynamic models (Swartz et al. 2006), which limits our ability to predict the constraints of bats in flight. The abundance and distribution of preferred foraging resources around roosts, rather than wing morphology and size, have been proposed to explain differences in hunting space parameters between colonies of the same species (Goiti et al. 2003).

Differences in energy demands have been proposed as responsible for intraspecific variation in foraging behaviour among individuals within a population. Some stages in the bat's life cycle (typically lactation or spermatogenesis) require a higher energetic intake (Kurta et al. 1989; Kurta et al. 1990; Speakman and Thomas 2003; Encarnação and Dietz 2006). Accordingly, lactating females and spermatogenic males have usually been found to spend more time foraging compared with other individuals (Rydell 1993; Shiel et al. 1999; Barclay et al. 2000; Encarnação and Dietz 2006; but see Dietz and Kalko 2007). During the spermatogenic phase, male *Myotis daubentonii* use larger foraging ranges compared with other classes (Encarnação and Dietz 2006; Dietz and Kalko 2007). Contrasting results on relative size of foraging range in lactating females have been observed across studies, and specific lactation behaviour and surveyed colony size were suggested to be responsible for that variability (Shiel et al. 1999; O'Donnell 2001; Fellers and Pierson 2002; Henry et al. 2002; Goiti et al. 2006). Furthermore, spatial use shown by young individuals (2–4 months old) has been attributed to exploratory behaviour, presumed to be typical at this stage (Audet 1990; Jones et al. 1995; Shiel et al. 1999; O'Donnell 2001; Goiti et al. 2006).

Given those observations, we anticipate variation in individual foraging dynamics with changing seasons, as the physiology of adults varies and as juveniles begin to fly. The effect of time—that is, periods or seasons of different biological meaning—and animal classes on spatial behaviour have not been separately studied in most investigations dealing with the spatial ecology of foraging bats (e.g., Racey and Swift 1985; Audet 1990; Shiel et al. 1999; Henry et al. 2002). This means, for instance, that differences in home range or foraging time between pregnant and lactating females will not necessarily correspond to differences in energetic requirements, unless environmental features are similar during the two periods. Previous studies have failed to separate the effect of changing seasons on the differences in spatial dynamics seen between individuals or classes of bats.

Our aim was to investigate the foraging range of the long-fingered bat (*Myotis capaccinii*, Bonaparte 1837), a species that shows a high degree of specialisation in habitat requirements for both roosting and foraging. *M. capaccinii* is strictly cave-dwelling and may form large colonies (up to several thousands), especially during the lactation period (Chytil and Vlašín 1994; Spitzenberger and von Helversen 2001; Papadatou et al. 2008). Several studies have highlighted the type of foraging habitat used by this species during the breeding season, although none focused specifically on the spatial metrics of foraging behaviour (Almenar et al. 2006; Papadatou 2006; Biscardi et al. 2007; Némoz and Brisorgueil 2008): *M. capaccinii* forages almost exclusively on aquatic environments, preferring rivers with calm water surfaces, and distances flown by breeding females from roosts to hunting sites may reach up to 31 km.

We tested whether intraspecific variation in spatial foraging pattern is influenced by bats' age, sex, or reproductive condition, or alternatively, whether the period of the year determines the behavioural differences between the classes. Firstly, we calculated the size of the colony foraging range and its seasonal variation, the size of individual foraging ranges, the distances travelled between roost and foraging sites, and the degree of overlap between individual foraging ranges. Secondly, we assessed the spatial foraging behaviour of individuals in relation to age, sex, and/or reproductive class.

## Materials and methods

### Study area, study population, and roosts

The study area, more fully described in Almenar et al. (2009), is located in the eastern Iberian Peninsula (39°04′ N–0°35′ W) and spreads over 3,850 km² of the lower basin of the Xúquer River. This area includes several tributaries, amongst which the Albaida and Sellent rivers are the most important. The water flow shows Mediterranean seasonality, with lower levels during summer. Rivers are managed via a large dam (called Presa de Tous), many weirs (locally known as "assuts"), and a vast network of irrigation canals. There are also many ponds (about 3/km²). Aquatic habitats cover 1.2% of the study area; of these, the calm smooth-surfaced waters that are the preferred foraging habitat of long-fingered bats account for 72% (Almenar 2008). A large floodplain (20–50 m a.s.l.) mainly covered by orange groves comprises approximately two-thirds of the study area. The remaining area is hilly (max. altitude 600 m a.s.l.) and covered by Mediterranean vegetation.

Two roosts in the area are inhabited permanently by large groups of *M. capaccinii* during the breeding season. The main roost is a limestone cave with a variable

population up to 500 individuals during spring and summer. More than a hundred individuals inhabit the second roost, located 8.4 km from the first. Both roosts are shared with other bat species (*R. euryale*, *R. mehelyi*, *Myotis blythii*, *Myotis myotis*, *Myotis emarginatus*, *Myotis nattereri,* and *Miniopterus schreibersii*). *M. daubentonii*, a species with similar foraging habits to *M. capaccinii*, is not known in the area.

### Trapping, tagging, and data collection

Bats from the main roost were captured and radio-tracked in 2004 during three periods: pre-breeding (9–30 April), lactation (24 May–11 June), and weaning (1–17 July). We captured bats twice per period when they returned to the main roost after their nightly foraging, using a harp trap (modified from Tuttle 1974). In total, 62 bats were sexed, aged, and weighed. After clipping the fur between their shoulder blades, we equipped the bats with a 0.45-g PIP II radio-transmitter (Biotrack Ltd., Dorset, UK) by means of Skinbond surgical adhesive (Smith and Nephew, Largo, Florida, USA). The transmitter represented a load of less than 5% of the bat's weight (Aldridge and Brigham 1988), except for 11 cases, mostly juveniles, in which it reached 6.3%, although no abnormal behaviour was observed in these individuals. Capture, manipulation, and tagging were performed with permission from the Valencian Government.

Bats were (as much as possible) continuously tracked from emergence to return. Up to six tracking teams searched for bats simultaneously, using either 1000-XRS radio-receivers (Wildlife Materials, Carbondale, Illinois, USA) or FT-290RII units (A. Wagener Telemetrieanlagen, Köln, Germany) and three-element Yagi antennae. Mobile teams tracked bats by car or on foot and were guided to foraging sites by up to three observers located at stationary vantage points. The stationary observers received radio signals from additional locations, and their searching scope encompassed both aquatic and terrestrial habitats. Two or three bats were tracked each night, and we analysed only fixes obtained through homing-in by the mobile teams (White and Garrot 1990).

Each period the 15 bats with the most foraging locations were selected for analyses among tracked individuals (12–140 fixes/bat). The individuals were classified as females ($n=7$) and males ($n=8$) during pre-breeding, as lactating females ($n=10$) and other adults ($n=5$) during lactation, and as juveniles ($n=10$) and adult females ($n=5$) during weaning. When bats flew directly and quickly between the roost and a foraging site or between two separate foraging sites, we considered them to be commuting. Continuous movements to and fro over a location were considered to represent foraging activity. Because bats were able to commute to distant foraging sites in 10 min (personal observation), we used a

time interval of 10 min between consecutive fixes to avoid spatial autocorrelation. Fixes were mapped in the field on orthoimages or 1:10,000 topographic maps and then transferred into a Geographical Information System (GIS, ArcView 3.2, ESRI, California, USA).

### Spatial variables

Colony home range was defined as the minimum convex polygon (MCP; White and Garrot 1990) that enclosed all radiolocations (foraging, commuting, or resting in roosts) of the bats chosen for analysis. Home range was estimated for the entire study and for each period.

Range measurements (e.g., MCPs and kernels) are usually based on bidimensional geometry (see White and Garrot 1990; Kernohan et al. 2001). However, all radio-tracking surveys to date on foraging of the long-fingered bat have found it on linear-like habitats (Almenar et al. 2006; Biscardi et al. 2007; Némoz and Brisorgueil 2008), so we considered linear representations to be more appropriate. This approach has frequently been used in other animals that forage on rivers or shores (Bowyer et al. 1995; Garin et al. 2002; Meyer et al. 2005). Accordingly, sizes of individual foraging ranges were calculated as linear measurements. Thus, we measured the length of the river or canal stretch between the two farthest foraging locations for each bat. When bats hunted in more than one river or canal, we summed the lengths of discrete stretches used. For bats that hunted at isolated pools, the pool's maximum diameter was taken. Additionally, we calculated the geometrical mean of this measurement rather than the arithmetical mean because it showed a lognormal distribution (Quinn and Keough 2002).

For each tracking night, we also measured the straight distance from each foraging location to the last known roost, in order to calculate the average and maximum distances travelled between day-roosts and foraging locations per individual. We found that during pre-breeding, some tagged bats (three males and four females) shifted temporarily to two previously unknown roosts in an underground section of an irrigation canal and a chalky tuff. During weaning, four adults and four juveniles shifted progressively to the second known roost. Percentage overlap was calculated as the percent of the individual foraging range overlapping that of other individuals during the same period. Finally, for each individual, we also counted the number of other individuals whose foraging range overlapped during a given period.

### Analysis of variability among individuals

Individual variation in foraging range and in maximal and average straight distances to foraging areas was analysed by means of a hierarchical analysis of variance (ANOVA)

(Quinn and Keough 2002). The ANOVA model included the period, with three levels (Pre-breeding, Lactation, and Weaning) treated as a random effect variable. Class was included as a nested variable within period, with six levels (females and males within pre-breeding, lactating females and other bats within lactation, and juveniles and adult females within weaning). In the analysis, class was treated as a fixed effect factor. This design allowed us to test the null hypothesis that classes had the same means during each period. In addition, because we expected the length of foraging sectors to be affected by tracking effort, a covariable measuring this effort (number of tracking days per bat) was included. In addition, we used the ANOVA model for the foraging sectors (a general linear model (GLM), adjusted with least squares) to estimate the average length of individual foraging sectors for a single night. Variables were squared or log transformed as necessary to adjust them to the assumption of normality. Statistics were computed using the GLM procedure of SAS 9.0 (SAS Inc., Cary, North Carolina, USA). $\alpha$ was set to 0.05 for the hypothesis test. Variables related to overlap of hunting sites among individuals were not analysed statistically, as their values were not independent among bats during the same period.

## Results

The tracked bats moved each night typically from the roost to the foraging areas, either following a water course or directly crossing terrestrial habitats. Once a bat had reached a foraging area, it could spend the whole night there or eventually move directly to a distant area. Typically, the tracked bats used one to three foraging sectors per night. On a few occasions, a bat spent part of the night following the network of rivers and channels, foraging for short periods in different locations. In general terms, the bats returned to the same river sectors on consecutive nights, but the use of specific patches in each sector varied from night to night.

The colony home range covered 344.6 km$^2$ over the entire course of the study (Fig. 1), although the range was smaller during each period: pre-breeding 72.9 km$^2$ (21%), lactation 250.8 km$^2$ (73%), and weaning 133.7 km$^2$ (29%). Overall, radio-tracked bats hunted along 49.2 km of aquatic habitat, which represented 39% of the total length available in the home range (126.2 km). Again, the lengths used during each period were lower: pre-breeding 7.7 km (6%), lactation 34.8 km (28%), and weaning 29.2 km (23%).

During pre-breeding, foraging clustered at two separated stretches of river, 3.3 and 4.4 km in length (Fig. 1a), and individuals' hunting sites largely overlapped (Fig. 2c). Conversely, during lactation, the foraging sectors spread (Fig. 1b), and overlap measurements reached their minimal

values (Fig. 2c, d). During weaning, 70% of the radio-locations concentrated at an 11.5-km stretch of the main river (Xúquer) (Fig. 1c); and, in accordance, the number of individuals with overlapping foraging ranges was highest (Fig. 2d), and overlap percentage between individual foraging sites approached 90% (Fig. 2c).

Averaged across all tracked bats, the distance travelled to hunting sites was less than 6 km, the maximum straight line distance was greater than 7 km, and the foraging range was somewhat higher than 2.5 km (Table 1). Although measured values of these three variables changed between classes during each period, these differences did not reach statistical significance (ANOVA, $F<2.8$, $df=3$, $p>0.05$ for the three variables). Instead, the foraging range and the straight distance between roosts and foraging sites were significantly different between periods (ANOVA, $F=5.19$, $df=2$, $p=0.01$ and $F=5.13$, $df=2$, $p=0.01$, respectively), and the difference of the maximum straight distance between periods approached significance (ANOVA, $F=3.02$, $df=2$, $p=0.06$). Foraging range pooled across classes was largest during weaning, and both average and maximum straight distances between roosts and foraging sites were largest during lactation (Fig. 2a, b). The absolute maximum straight distance flown from the roost (22.7 km) was recorded for an adult female during Weaning; reconstruction of that individual's presumed flight path gave a flown distance of around 35 km.

Because tracking effort differed among individuals and the number of tracking nights significantly increased the foraging range ($F_{1,\ 38}=5.4$; $p=0.026$), we estimated the individual foraging range for a single night by the ANOVA-adjusted equation (Table 1). Over the three study periods, the adjusted nightly foraging range for both classes combined per period was 1.0 km during pre-breeding (95% CI=0.5–1.9 km), 1.7 km during lactation (1.0–3.0 km), and 3.3 km during weaning (1.6–6.8 km), which follows a similar seasonal trend to that of the foraging range observed throughout the entire individual tracking time.

## Discussion

Most studies on bats' spatial foraging hitherto conducted have not split the effects of period and class on that behaviour (e.g., Racey and Swift 1985; Audet 1990; Shiel et al. 1999; Henry et al. 2002), and comparison of classes from different biological periods may have led to misleading conclusions about the singular foraging strategy of some classes, e.g., lactating females or juveniles. The design of the present study splits the two potential sources of variation (individual class and period) and thus allows a more accurate interpretation of behavioural differences between classes.

**Fig. 1** Distribution of radiolocations of 45 *Myotis capaccinii* in the study area during three periods (**a** pre-breeding, **b** lactation, and **c** weaning). The aquatic habitats used by the species are drawn in grey. *Black dots* represent the radiolocations of foraging bats. The *black asterisk* represents the main roost. *White asterisks* represent secondary roosts. The *black line* represents the colony home range for each period, a minimum convex polygon enclosing all the radiolocations (foraging, commuting, and resting). The *dashed black line* represents the colony range for the whole study. Scale=1 km
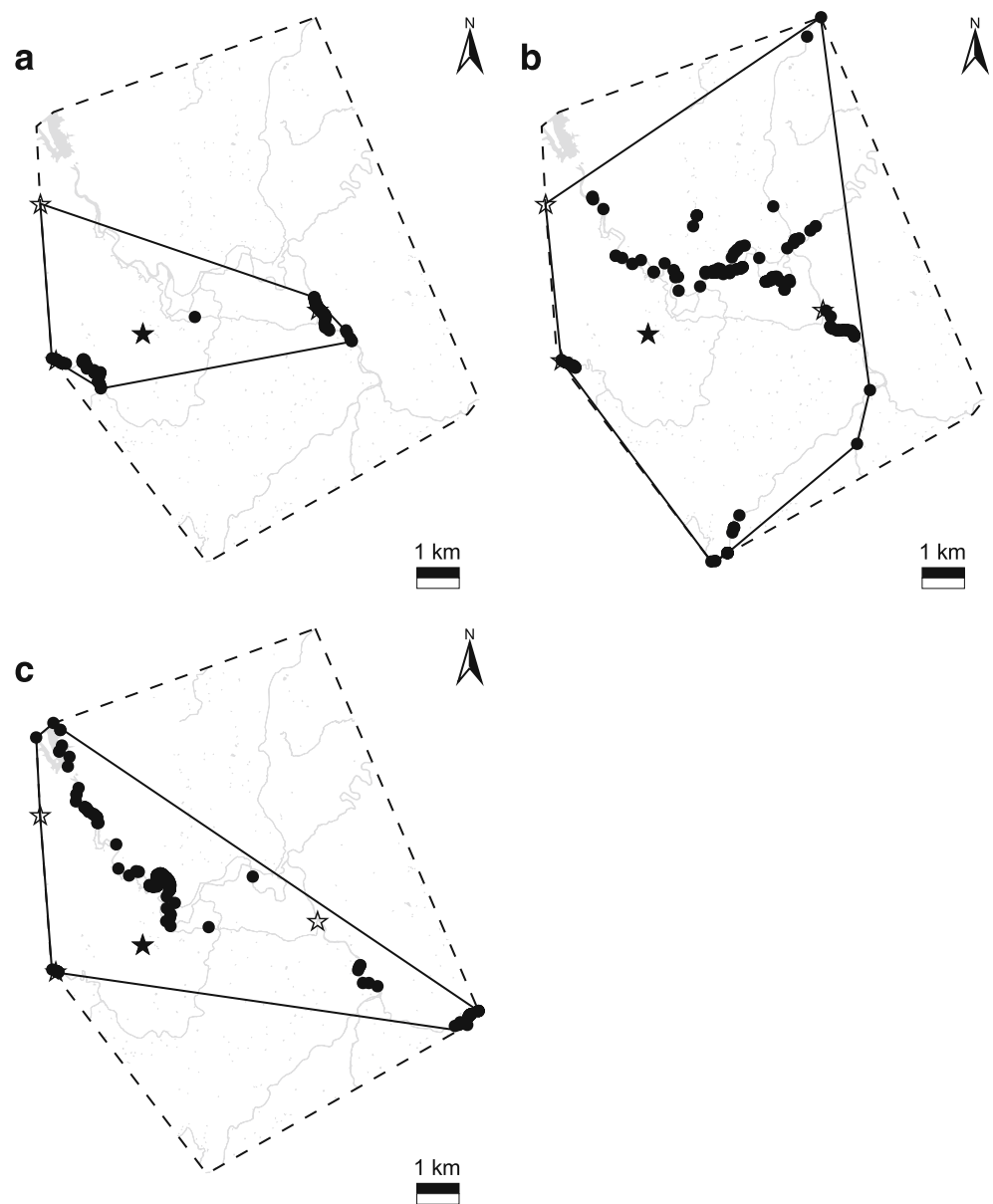


We found that sex, reproductive stage, and age did not significantly affect the spatial dynamics of foraging long-fingered bats. Individuals of highly contrasting status did not show differences in their foraging behaviour when they shared resources: lactating females did not differ from other individuals during the same period, nor did adult females during weaning differ from juveniles. Nevertheless, flight distances of female bats increased from pre-breeding to lactation. It has previously been shown that the foraging range of female bats changes during lactation, although it may either decrease (Racey and Swift 1985; Shiel et al. 1999; O'Donnell 2001; Henry et al. 2002) or increase (Clark et al. 1993; Jones et al. 1995; Goiti et al. 2006) compared with previous seasons. Both the increased energy demands due to milk production and the need to return repeatedly to the roost to feed their pups during the night

are thought to affect the spatial behaviour of foraging females (Racey and Swift 1985; Shiel et al. 1999; O'Donnell 2001; Henry et al. 2002; Goiti et al. 2006). Surprisingly, in our research, the increased energy costs of lactation did not promote a distinct spatial behaviour in lactating females compared with other bats during the same period. Lactating *M. capaccinii* have not been observed returning to feed their pups during the night (Almenar 2008; see also Quekenborn et al. 2006; Peyrard and Nemoz 2007), which suggests that lactation in the studied bats might not limit their attainable range.

The range of juvenile bats increases as weaning progresses, and in some species can even be larger than that of adult bats (O'Donnell 2001). This is generally interpreted as a consequence of characteristic exploratory behaviour (Audet 1990; Jones et al. 1995; Shiel et al. 1999;

**Fig. 2** Variation among the three study periods (*1*, pre-breeding; *2*, lactation; *3*, weaning) in the individual variables of use of space: **a** individual foraging range; **b** straight distance from the last known roost to the foraging areas (*black circles*: maximum; *grey triangles*: average); **c** percent of overlap in the foraging sectors; **d** number of other bats overlapping. The average and standard error are shown for each period. Some variables were log-transformed to allow visualisation
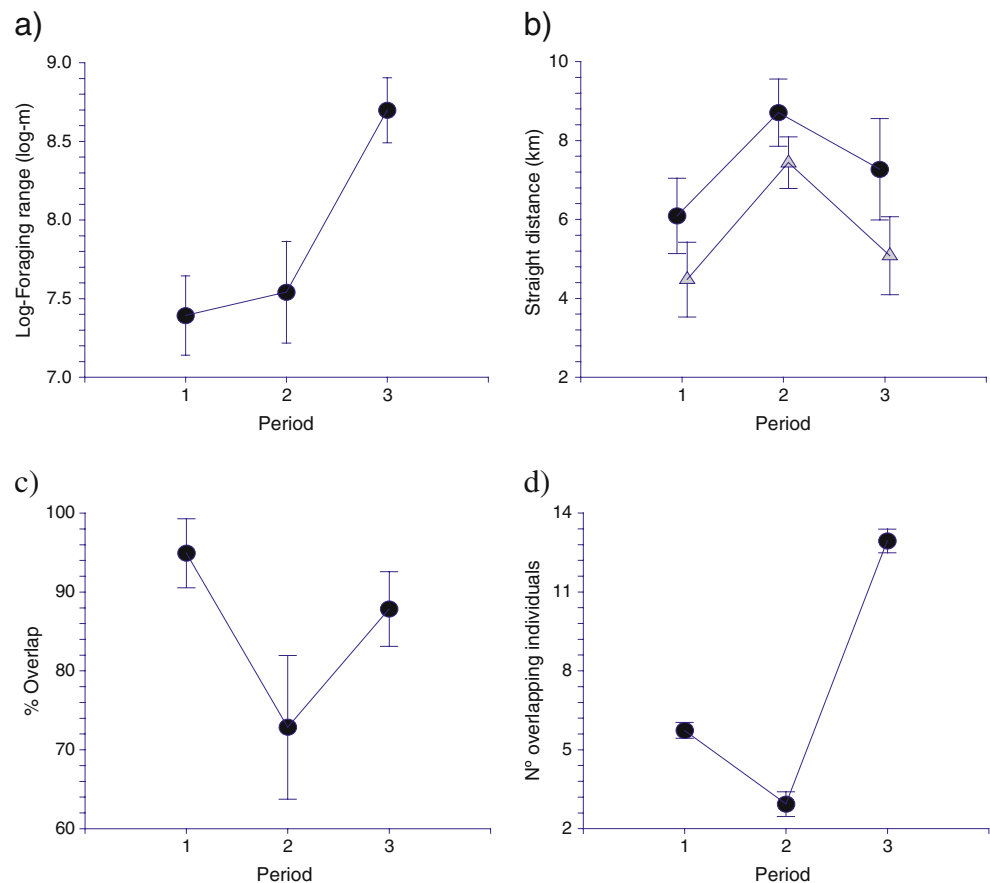


O'Donnell 2001; Goiti et al. 2006). We found that juvenile bats had large individual ranges that increased over the tracking time (personal observation), which are two features consistent with exploratory behaviour. However, adult females during the same period also showed increased individual foraging range. This means that factors other than the exploratory behaviour by youngsters may regulate the observed foraging pattern. Energy requirements of adult females recovering from lactation and of growing juveniles are surely high during weaning. Hence, we cannot discard the possibility that high energy demands led these two bat classes to a foraging behaviour similar to that observed in lactating females.

Foraging individuals from different periods of the year showed contrasting spatial strategies regardless of class, which we suggest represent gross seasonal effects. For example, dispersion of individual foraging sites over the colony home range and their distance to neighbouring foraging sites likely increased during the period of gestation, reached a maximum during lactation, and showed a lower value again at the end of the breeding season. Consequently, the total length of foraging ranges was highest during lactation. The size of foraging sites was noticeably higher during weaning than any previous period; however, the high number of individuals with overlapping

foraging ranges and the reduction in average straight distance from roosts to hunting sites resulted in a smaller colony foraging range during weaning than lactation. Temporal changes in environmental conditions, as well as their interaction with the number of animals in the colony, might explain that seasonal pattern.

Foraging bats should respond to seasonal changes in the distribution of prey resources along the river system by shifting their hunting grounds accordingly. Individual decisions based on prey availability are generally thought to be involved in the processes that directly influence patch selection in animals (e.g., Stephens and Krebs 1987), and they must obviously shape the spatial distribution of foraging individuals. In a simultaneous study, we found that arthropod abundance in the river and tributaries of the study area changed through time, and, to some extent, the foraging activity of long-fingered bats matched these changes (Almenar 2008). For instance, most of the foraging activity during weaning was concentrated at the main river (Xúquer), which reflected the increase in prey available there compared with prey available in the tributaries (Almenar 2008). Interestingly, during that period, the tracked bats shifted between the two permanent roosts, allowing them to reach their foraging sites by shorter flights.

**Table 1** Means and standard deviations (in brackets) for the variables of use of foraging space by 45 *Myotis capaccinii*

| | Pre-breeding | | Lactation | | Weaning | | All classes |
|---|---|---|---|---|---|---|---|
| | Female (*n*=7) | Male (*n*=8) | Lactating (*n*=10) | Other adult (*n*=5) | Juvenile (*n*=10) | Adult (*n*=5) | Combined |
| Individual foraging range (km) | 1.2 (0.4–3.6) | 2.1 (1.1–3.9) | 1.7 (0.6–4.8) | 2.2 (0.7–7.1) | 6.9 (4.1–11.5) | 4.5 (1.4–15.1) | 2.6 (1.9–3.7) |
| Individual foraging range per night (km) | 0.6 (0.2–1.6) | 0.9 (0.3–2.5) | 1.0 (0.5–2.3) | 1.5 (0.6–3.9) | 2.3 (1.07–6.4) | 2.1 (0.7–7.8) | 1.3 (0.7–2.6) |
| Maximum straight distance (km) | 3.7 (2.99) | 8.2 (2.56) | 8.4 (3.74) | 9.3 (1.34) | 6.9 (2.59) | 8.0 (7.42) | 7.3 (4.10) |
| Average straight distance (km) | 3.1 (3.23) | 5.7 (3.34) | 7.0 (2.59) | 8.4 (1.79) | 4.5 (1.61) | 6.3 (5.8) | 5.7 (3.55) |
| Overlap (%) | 89.3 (22.61) | 99.8 (0.37) | 66.9 (36.24) | 84.8 (25.22) | 94.1 (8.53) | 75.4 (23.64) | 85.2 (26.05) |
| Number of overlapping bats | 5.3 (1.39) | 6.1 (0.6) | 2.8 (1.89) | 3.2 (1.47) | 13.0 (2.05) | 12.8 (0.4) | 7.2 (4.54) |

Individual foraging range and individual foraging range per night are given as geometrical mean and 95% confidence interval (in brackets)

Prey availability cannot only be thought of in terms of abundance and production, but also in terms of the combination of these factors with intraspecific competition. Larger colonies may suffer stronger intraspecific competition, mainly near roosts, and some individuals may find it profitable to forage in more distant areas to avoid conspecifics (Hamilton and Gilbert 1969; Hamilton and Watt 1970). Thus, the increase in dispersion of foraging sites matched the increase in colony size by 138 individuals from pre-breeding to lactation (Almenar 2008). We suggest that this reflects the narrow and specialised foraging niche used by long-fingered bats (freshwaters with calm smooth surfaces, Almenar et al. 2006) and their restricted availability in the study area. A similar pattern has been seen in other species with similarly narrow foraging niches, such as *Myotis dasycneme* (Limpens et al. 1999) and *M. moluccarum* (Barclay et al. 2000). By contrast, bats in the genus *Myotis* that forage in a broad array of habitats usually fly shorter distances (less than 10 km) to hunting areas (*M. emarginatus*, Krull et al. 1991; *M. evotis*, Waldien and Hayes 2001; *Myotis septentrionalis*, Owen et al. 2003; *Myotis sodalis*, Murray and Kurta 2004; *Myotis volans*, Johnson et al. 2007).

However, we did not observe a complete dispersion of individuals along the available aquatic habitats in spite of the wide hunting range observed during lactation, with bat foraging apparently being spatially aggregated. Some degree of foraging aggregation has been found in other bat species (Audet 1990; Robinson and Stebbings 1997; O'Donnell 2001; Goiti et al. 2006), but this behaviour seems to be more pronounced in *M. capaccinii* (Ahlén 1990; Spitzenberger and von Helversen 2001; Quekenborn

et al. 2006; Némoz and Brisorgueil 2008; personal observation). In this respect, the observed overlap of foraging areas is remarkable. We calculate that the 140 bats counted in the main colony would need a freshwater resource of 180 km, which is 3.7 times more than the total length used during the study (49.2 km), assuming no overlap between individuals and the observed average foraging length (Table 1). The high insect richness usually associated with freshwater (Racey 1998) may mitigate the adverse effect of competitive exclusion and allow coexistence of several individuals at the same stretch. Clustering does not necessarily mean "group foraging"; in fact, Ahlén (1990) described spatial segregation of individuals within collective foraging areas. Accordingly, active defence of individual foraging grounds within collective stretches of aquatic habitats has been described in *M. daubentonii* (Dietz and Kalko 2007).

During the breeding season, females and juveniles are constrained to use the main maternity roosts, and their location is the primary determinant of flight distances to hunting sites. However, outside the breeding season, roost requirements may be relaxed, allowing individuals to optimise the energetics of their foraging strategies by shifting roosts to place themselves closer to hunting sites. Similarly, bat species with flexible roosting behaviour are able to reduce their foraging range, placing the roost close to hunting areas. For instance, the average straight distance to hunting areas of nursery colonies of *M. daubentonii* is rather small (2.3 km, Dietz et al. 2006), even though its foraging niche is also narrow.

Finally, we do not believe that local conditions of the study area are responsible for the observed values of the

spatial parameters, as large commuting ranges of *M. capaccinii* have also been reported elsewhere (e.g., 21 km, Biscardi et al. 2007; 31 km, Némoz and Brisorgueil 2008). Some stretches of the tributary rivers became dry only at the end of the weaning period, and thus changes in habitat availability are unlikely to have affected our study.

# References

Ahlén I (1990) Identification of bats in flight. Swedish Society for Conservation of Nature, Stockholm

Almenar D (2008) Uso y selección de recursos por el murciélago patudo (*Myotis capaccinii*): presas, hábitats y áreas de caza. Ph. D. thesis, University of the Basque Country, Leioa.

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

Almenar D, Aihartza J, Goiti U, Salsamendi E, Garin I (2009) Foraging behaviour of the long-fingered bat *Myotis capaccinii*: implications for conservation and management. End Spec Res 8:69–78

Aldridge HDJN, Brigham RM (1988) Load carrying and maneuverability in an insectivorous bat: a test of the 5% 'rule' of radio-telemetry. J Mammal 69:379–382

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

Barclay RMR, Chruszcz BJ, Rhodes M (2000) Foraging behaviour of the large-footed myotis, *Myotis moluccarum* (Chiroptera: Vespertilionidae) in south-eastern Queensland. Aust J Zool 48:385–392

Biscardi S, Russo D, Casciani V, Cesarini D, Mei M, Boitani L (2007) Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. J Zool (Lond) 273:372–381

Bowyer RT, Testa JW, Faro JB (1995) Habitat selection and home ranges of river otters in a marine environment: effects of the Exxon Valdez oil spill. J Mammal 76:1–11

Clark BS, Leslie DMJ, Carter TS (1993) Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. J Mammal 74:422–427

Chytil J, Vlašín M (1994) Contribution to the knowledge of bats (Mammalia: Chiroptera) in Albania. Folia Zool 43:465–467

Dietz M, Kalko EKV (2007) Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentonii*. Can J Zool 85:653–664

Dietz M, Encarnação J, Kalko EKV (2006) Small scale distribution patterns of female and male Daubenton's bats (*Myotis daubentonii*). Acta Chiropt 8:403–415

Encarnação J, Dietz M (2006) Estimation of food intake and ingested energy in Daubenton's bats (*Myotis daubentonii*) during pregnancy and spermatogenesis. Eur J Wildl Res 52:221–227

Fellers GM, Pierson ED (2002) Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. J Mammal 83:167–177

Fenton MB (1997) Science and the conservation of bats. J Mammal 78:1–14

Garin I, Zuberogoitia I, Zabala J, Aihartza J, Clevenger AP, Rallo A (2002) Home ranges of European mink *Mustela lutreola* in southwestern Europe. Acta Theriol 47:55–62

Goiti U, Aihartza JR, Garin I, Zabala J (2003) Influence of habitat on the foraging behaviour of the Mediterranean horseshoe bat, *Rhinolophus euryale*. Acta Chiropt 5:75–84

Goiti U, Aihartza JR, Almenar D, Salsamendi E, Garin I (2006) Seasonal foraging by *Rhinolophus euryale* (Rhinolophidae) in an Atlantic rural landscape in northern Iberian Peninsula. Acta Chiropt 8:141–156

Hamilton WJ III, Gilbert WM (1969) Starling dispersal from a winter roost. Ecology 50:886–898

Hamilton WJ III, Watt KEF (1970) Refuging. Ann Rev Ecolog Syst 1:263–287

Henry M, Thomas DW, Vaudry R, Carrier M (2002) Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). J Mammal 83:767–774

Johnson JS, Lacki MJ, Baker MD (2007) Foraging ecology of long-legged myotis (*Myotis volans*) in north-central Idaho. J Mammal 88:1261–1270

Jones G, Duvergé L, Ransome RD (1995) Conservation biology of an endangered species: field studies of greater horseshoe bats. Symp Zool Soc Lond 67:309–324

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and animal populations. Academic, San Diego, pp 125–166

Krull D, Schumm A, Metzner W, Neuweiler G (1991) Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behav Ecol Sociobiol 28:247–254

Kurta A, Bell GP, Nagy KA, Kunz TH (1989) Energetics of pregnancy and lactation in free-ranging little brown bats *Myotis lucifugus*. Physiol Zool 62:804–818

Kurta A, Kunz TH, Nagy KA (1990) Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. J Mammal 71:59–65

Limpens HJGA, Lina PHC, Hutson AM (1999) Action plan for the conservation of the pond bat (*Myotis dasycneme*) in Europe. Council of Europe, Strasbourg

Meyer CFJ, Weinbeer M, Kalko EKV (2005) Home-range size and spacing patterns of *Macrophyllum macrophyllum* (Phyllostomidae) foraging over water. J Mammal 86:587–597

Murray SW, Kurta A (2004) Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). J Zool (Lond) 262:197–206

Némoz M, Brisorgueil A (2008) Connaissance et conservation des gîtes et habitats de chasse de 3 Chiroptères cavernicoles. Société Française pour l'Etude et la Protection des Mammifères, Toulouse

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Phil Trans R Soc B 316:335–427

O'Donnell CFJ (2001) Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. J Zool (Lond) 253:253–264

Owen SF, Menzel MA, Ford WM, Chapman BR, Miller KV, Edwards JW, Wood PB (2003) Home-range size and habitat used by the northern myotis (*Myotis septentrionalis*). Am Midl Nat 150:352–359

Papadatou E (2006) Ecology and conservation of the long-fingered bat *Myotis capaccinii* in the National Park of Dadia-Lefkimi-Soufli, Greece. Ph.D. thesis, University of Leeds, Institute of Integrative and Comparative Biology.

Papadatou E, Butlin RK, Altringham JD (2008) Seasonal roosting habits and population structure of the long-fingered bat *Myotis capaccinii* in Greece. J Mammal 89:503–512

Peyrard Y, Nemoz M (2007) Etude de l'activité et des habitats de chasse des murins de Capaccinii (*Myotis capaccinii*) de la colonie des gorges du Gardon (Gard, France) en vue de sa conservation. SFEPM-SMGG/GCLR. Available at: http://www.sfepm.org/LifeChiropteres/Resultats.htm. Accessed Jan 2009.

Quekenborn D, Deblois S, Bouquier L (2006) Rapport d'etude des territoires de chasse du murin de Capaccini (*Myotis capaccinii*) en période de gestation dans le Verdon. SFPM-GCP. Available at: http://www.sfepm.org/LifeChiropteres/Resultats.htm. Accessed Jan 2009.

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Racey PA (1998) The importance of the riparian environment as a habitat for British bats. In: Dunstone N, Gorman ML (eds) Behaviour and ecology of riparian mammals. Cambridge University Press, London, pp 69–91

Racey PA, Entwistle AE (2003) Conservation ecology. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 680–743

Racey PA, Swift SM (1985) Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J Anim Ecol 54:205–215

Robinson MF, Stebbings RE (1997) Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. J Zool (Lond) 243:117–136

Russo D, Almenar D, Aihartza J, Goiti U, Salsamendi E, Garin I (2005) Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). J Zool (Lond) 266:327–332

Rydell J (1993) Variation in foraging activity of an aerial insectivorous bat during reproduction. J Mammal 74:503–509

Shiel CB, Shiel RE, Fairley JS (1999) Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. J Zool (Lond) 249:347–358

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 430–492

Spitzenberger F, von Helversen O (2001) *M. capaccinii* (Bonaparte, 1837)-Langfußfledermaus. In: Krapp F (ed) Handbuch der Säugetiere Europas. AULA-Verlag, Wiebelsheim, pp 281–302

Stephens DW, Krebs JW (1987) Foraging theory. Princeton University Press, Princeton

Swartz SM, Bishop K, Aguirre M-FI (2006) Dynamic complexity of wing form in bats: implications for flight performance. In: Zubaid A, McCraken GF, Kunz TH (eds) Functional and evolutionary ecology of bats. Oxford University Press, New York, pp 110–130

Tuttle MD (1974) An improved trap for bats. J Mammal 55:475–477

Waldien DL, Hayes JP (2001) Activity areas of female long-eared myotis in coniferous forests in western Oregon. Northwest Sci 75:307–314

White GC, Garrot RA (1990) Analysis of wildlife radio-tracking data. Academic, London