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Roost switching and activity patterns in the soprano pipistrelle, *Pipistrellus pygmaeus*, during lactation

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We studied roost switching and habitat selection of 16 *P. pygmaeus* females tagged in two nursery colonies. There were differences in overnight roosting and flying. The highest foraging activity was observed over water bodies, at forest edges and near street lamps. During each night, each female visited at least one night-roost, and five females regularly visited two roosts. On average, the females visited a roost 3.7 times per night. After parturition, the distances between night roosts and day roosts increased. The number of night roosts used declined as pups neared weaning. Five females changed day roosts after two nights. Based on the observation of flightless young in new roosts a conclusion was reached that some females transported their offspring to new roosts at night. After lactation began, some females visited roosts occupied by vocalizing males of *P. pygmaeus* and *P. nathusii*.

Introduction

Differences in peak frequency of echolocation calls (Ahlén 1990, Jones & van Parijs 1993), reproductive isolation and segment differences in the cytochrome *b* gene (Barratt *et al*. 1997) were the main reasons for distinguishing between the two species of common pipistrelle bats, *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. Although the discovery of the systematic status of the newly validated species *Pipistrellus pygmaeus* was interesting, little is known about its ecology, in particular its activity patterns and habitat use. *Pipistrellus pipistrellus* can forage in almost all habitat types (Oakeley & Jones 1998, Warren *et al*. 2000, Gaisler *et al*. 2002, Davidson-Watts 2003). By contrast, the composition of prey of *P. pygmaeus* suggests that it is more closely related to aquatic habitats (Barlow 1997). Davidson-Watts (2003) found that *P. pygmaeus* spends a considerable percentage of its foraging time over water. Furthermore, Russo and Jones (2003) showed that river habitats are very important for *P. pygmaeus* in the Mediterranean region. However, Glendell and Vaughan (2002) suggest that *Pipistrellus pygmaeus* selects semi-natural woodland and tree lines more often than water habitats.

Females of *P. pipistrellus sensu lato* often switch roosts during the season (Thompson 1990, 1992). Pregnant females usually inhabit more temporary and cooler roosts, moving to one main parturition roost a few days before parturition (Swift 1980, Webb *et al*. 1996). In England and Scotland, large nursery colonies of *P. pipistrellus sensu lato* rarely switch roosts (Haddow 1993), while individuals from less numerous nursery colonies in central Europe switch their roosts more often, as found in *P. pipistrellus sensu stricto* (Feyerabend & Simon 2000). Our preliminary results suggest that the nursery colonies of *P. pygmaeus* occurring in the floodplain area of southeastern Moravia change roosts during the summer.

Contrary to *P. pipistrellus*, which occupies buildings in almost 95% of cases (Simon *et al*. 2004), *P. pygmaeus* prefers forest and wetland habitats (Barlow & Jones 1999). However, nursery colonies of the latter were usually found in buildings (Park *et al*. 1996, Oakeley & Jones 1998, Sattler *et al*. 2003). In the Czech Republic, most records of *P. pygmaeus* come from low altitudes (Řehák & Bartonička unpubl. data). The main range of this species is in the lowlands of Moravia and central Bohemia and around fishponds in southern Bohemia, where the bat prefers floodplain forests and other wetlands in the alluvial plain of large rivers as well as pond landscapes (Bartonička & Řehák 2004). Regarding the relatively high foraging activity of *P. pygmaeus* in well preserved floodplain forest, we expected that pipistrelles would use natural roosts in hollows or similar types of roosts such as bat boxes, hiding in them more often than in buildings.

Our objectives were: (1) to test whether *P. pygmaeus* switches its day roost as often as *P. pipistrellus* throughout the lactation period; (2) to describe the movement patterns and habitat selection of females tagged in two nursery colonies of *P. pygmaeus*; (3) to consider whether the number of night/day roosts and frequency of roost switching are an important factor for the monitoring and conservation of pipistrelle bat populations; and (4) to describe other activities connected with possible energetic costs during lactation.

Material and methods

Study area

Fieldwork was carried out in southeastern Moravia (Czech Republic). One nursery colony (A) roosted under the roof of a pheasantry, a brick building in the vicinity of the village of Vranovice, in an oak wood forest along the Svratka River (48°57´45.4´´N, 16°37´48.2´´E). The surrounding landscape is characterized by patches of woodland, linear vegetation, and fields. The other colony (B) roosted in a guesthouse in the village of Nové Mlýny, situated in the neighbourhood of an old-growth floodplain forest along the Dyje River (48°51´22.2´´N, 16°43´50.8´´E). Each colony comprised ca. 150 adult females.

Equipment, tracking and spatial analyses

Between June and July 2004, lactating females were netted individually when emerging from a colony roost. After capture and tagging, the bats were held in cloth bags. Only visibly lactating females, identified by the presence of bare patches around their nipples and the expression of milk, had transmitters affixed. The lactation period was defined as 6 June–4 July based on the capture of the first lactating female and the first presence of flying young, respectively. Bats were captured and kept in captivity for a short time under licence No. 922/93-OOP/2884/93 granted by the Ministry of the Environment of the Czech Republic. The authors have been authorized to handle free-living bats according to the certificate of competency No. 104/2002-V4 (§17 of law no. 246/1992).

Studies have shown that low ambient temperatures reduce bat activity by reducing the availability of Diptera, the main prey of *P. pygmaeus* (Barlow 1997). Therefore, minimum night air temperatures were recorded on the nights of tracking outside buildings where colonies were roosting.

Fourteen females from colony A and two from colony B were equipped with 0.38 g radio-transmitters (LB-2N, Holohil Systems Inc. Carp, ON, Canada). Transmitter batteries lasted for a minimum of eight days. The transmitters were glued to the back of each bat between their scapulae, after trimming the fur, using liquid cement (Adhesin, Henkel Ltd., Germany). Neubaum *et al*. (2005) found that bats carrying transmitters representing 5% or less of their body mass were reproductively active and did not suffer from major long-term effects. Davidson-Watts and Jones (2006) successfully tracked bats of *P. pygmaeus* with tags representing 7% of body mass. Our transmitter mass amounted to less than 6% of body mass (range 4.8%–5.7%).

The bats were released and then tracked continuously from sunset to sunrise, using AR8000 hand held receivers (AOR UK LTD, Matlock, UK) and five-element Yagi antennas (Wildlife Materials Inc., Illinois, USA). The locations of the tagged bats were recorded throughout the night by (1) triangulation when two mobile workers co-ordinated their movements using hand-held FM radios (Motorola T5522) or cell phones, and (2) "homing-in" on a bat. Locations were assigned into three distance classes, which differed in open and forest habitats because of differences in the diffusion of sound waves. Therefore, we used different bufferings (circles around a location) in open spaces (< 50 m, 50–100 m, > 100 m) and in forests (< 20 m, 20–100 m, > 100 m). The highest accuracy class (< 50 m and < 20 m, respectively) could only be assigned when we were in close proximity, e.g. close to roosts or in small foraging areas when we could unlink the Yagi antenna, use patch wire only and still receive a signal. Classes of confidence in the accuracy of location were tested experimentally for each transmitter prior to attaching it to a bat in the two different habitats (forest and open space). One person positioned a transmitter while other researchers classified its position into the three distance classes mentioned above. Differences between the estimated locations (intersections) and exactly known locations were not significantly different (t-test: $Z = -4.8$, df = 8, $p > 0.1$) and an assignment of distance class between researchers differed by only 2.9% ($n = 61$, similarly to Zimmerman & Powell 1995). Behaviour of the bats, their location time, the position of the worker and the position's accuracy were immediately recorded on a handheld tape recorder. The location of bats was estimated using a handheld GPS (Garmin 12XL) and later entered into a geographic information system (GIS) ArcView 3.3 (ESRI, USA). Foraging activity was observed directly and vocalizations (foraging, commuting, territorial signals) were recorded with bat detectors (D 240x, Pettersson Elektronik AB, Uppsala, Sweden).

The foraging areas of the bats were determined by the minimum convex polygon method (95% confidence area, Harris *et al*. 1990, Kauhala & Tiilikainen 2002). The accuracy of foraging ranges was estimated using ArcView 3.3 with the Animal Movement extension (Hooge & Eichenlaub 1997). Tracking locations were buffered by circles with classes of accuracy and minimum polygons were separately calculated around these locations for each night and bat. Only bats with more than 30 telemetry locations were used in space and habitat analyses (Seaman *et al*. 1999). Habitats were divided into six categories, i.e. forests, tree-lines, vegetation edges, water bodies, pastures and fields, and street lamps. All habitats in the area were mapped into ArcView using 1:10 000 grids (Zabaged/2). Habitat use for each female was estimated via the kernel estimation method using 95% of point locations with least-square cross-validation (LSCV) as the smoothing parameter, to exclude the effects of random outliers for general home ranges (Worton 1989). Core foraging areas were defined by the 50% contour lines of the fixed kernel estimation in the program Biotas 1.03.1. This type of estimation more accurately encloses the foraging area in use (Schwartz *et al*. 2002). When area of a specific habitat class was negatively correlated with areas of other classes, we used the single animals instead of the locations as a sample unit in order to avoid the constraints of compositional analyses (Aebischer *et al*. 1993, Otis & White 1999). Autocorrelation, resulting from short sampling intervals, was not a problem with the data used in analyses (cf. Swihart & Slade 1985).

Statistical analyses and material

Females that were tracked for less than 60% of the night were excluded from evaluation. The night was divided into three parts, i.e., thirds (1: sunset–23:30; 2: 23:31–02:00; 3: 02:01–sunrise) (cf. McAney & Fairley 1988).

The bats carried active transmitters for an average of 3.1 ± 1.1 (SD) days (range 2–7 days). The two days with values below the 25th and above the 75th percentiles of mean daily air temperature, air temperature at 21 h, cloud cover, mean daily humidity, wind speed and rainy nights were excluded (cf. Roche & Elliott 2000).

We recorded and analysed data for a total of 35 nights for 16 different female bats. Generally, it is recommended to use data from individual animals as sampling units when testing habitat preference hypotheses (Bontadina *et al*. 2002). Habitat selection was investigated only in females from colony A ($n = 11$). All tagged females showed relatively similar patterns of behaviour and no significant differences among the days of study and the females themselves could be detected. Similar sample sizes were used in studies dealing with the same research questions (e.g. Nicholls & Racey 2006, Feyerabend & Simon 2000 in pipistrelles; Bontadina *et al*. 2002 in *R. hipposideros*) and make our data comparable with these studies. One location on a hunting ground or in a roost was considered a unit of the analysed set. The asymptote was attained at about 30 independent locations in each of the females studied. Home range size did not change significantly after adding further locations (> 30) (similarly in Smith & Racey 2005). However, for some of the females we were able to obtain more than 100 locations. In all, 15 roosts were used in the analysis to determine flight distances and types of roosts.

Roosting and foraging activity data were not normally distributed and were analysed using non-parametric tests (Kruskal-Wallis and Mann-Whitney tests). Data of roost visits were transformed successfully to approximate normality using arcsine transformation. ANOVA and logistic regression were used to check changes in roost switching and distances between night or day roosts and foraging sites. The Bonferroni correction was applied if multiple tests were used for the same data set. Differences in habitat use were tested using contingency tables (χ^2-test). We used Statistica for Windows 7.0 to conduct the analyses.

Results

Roosting and flight activity

No significant differences in roosting time (Kruskal-Wallis test: $H_{13} = 11.62$, $n = 61$, $p > 0.05$), commuting time ($H_{13} = 8.91$, $n = 61$, $p > 0.05$), and foraging time ($H_{13} = 17.76$, $n = 61$, $p > 0.05$) were found either among studied females or among successive nights of one female. Therefore, the data from different females and nights were pooled for subsequent analyses.

Overnight changes in activity

Significant differences in roosting (Kruskal-Wallis test: $H_2 = 10.62$, $n = 61$, $p = 0.005$) and foraging activity ($H_2 = 13.27$, $n = 61$, $p = 0.001$) were found among night thirds (early, middle and late). The highest foraging activity was recorded at the beginning of the night (1st third), and decreased during the following thirds. A significant increase in roosting activity was recorded during the 2nd third. Roosting activity was as high in the 3rd as in the 2nd night period. On the other hand, no differences in commuting activity were found (Fig. 1). Foraging activity was spread, on average, across 4.1 ± 1.6 (mean ± SD) foraging periods (range 1–10), i.e. periods when bats left the roost and foraged continuously.

Foraging areas and habitat use

Habitat selection was investigated only in females from colony A ($n = 11$). We found that range sizes depended on the number of telemetry locations. Maximum size of foraging areas was archived with approximately 30 locations. However, we located only five females at more than 30 locations. Therefore, using minimum convex polygons we calculated the absolute foraging area for those five bats and the minimum foraging area for the others (similar to Bontadina *et al*. 2002). The foraging areas of the bats ranged between 1.6 and 117 ha (median 57.5 ha).

Habitat use did not differ significantly among females, nights or thirds of a night (Kruskal-Wallis test: $H_{10} = 10.32$, $n = 111$, $p > 0.05$). The comparison of habitat use in the core foraging areas (50% contour line of the fixed kernel estimation) with colony range showed that bats preferred vegetation edges and water bodies more

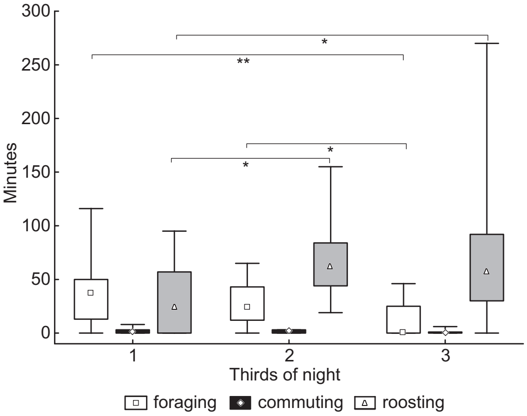

Fig. 1. Foraging, commuting and roosting of *Pipistrellus pygmaeus* (time in min) for the early, middle and late thirds of the night. Mean (square, diamond, tringle); box: 25% and 75% percentiles; whiskers: minimum–maximum. * $p < 0.01$; ** $p < 0.001$.

than forests and open fields ($\chi^2 = 118.89$, df = 5, $p < 0.001$). The colony range was predominantly fields and pastures (56.8%) and woodlands (30.7%, Fig. 2). The composition of habitats was not different between colony range and the availability of foraging habitats ($\chi^2 = 0.06$, df = 4, $p > 0.05$). To estimate the availability of foraging habitats we used the area of a circle of 1-km radius drawn around the colony site. Nonsignificant differences in foraging activity were found in open fields, pastures and forests. Often all females foraged at water bodies and vegetation edges, despite their low availability (Fig. 2). High foraging activity found in the vicinity of street lamps was not representative for all tagged females, as only six females foraged in this habitat type.

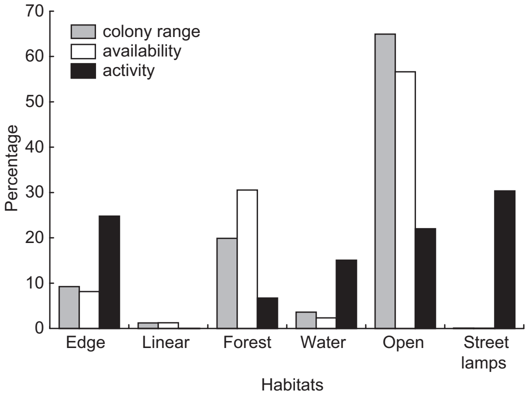

Fig. 2. Habitat use by *Pipistrellus pygmaeus*. Comparisons of habitat availability *vs.* habitat use are based on the minimum convex polygon of all females *vs.* the level of activity (mean percentage) per individual. Habitat selection was investigated only for females from colony A ($n = 11$).

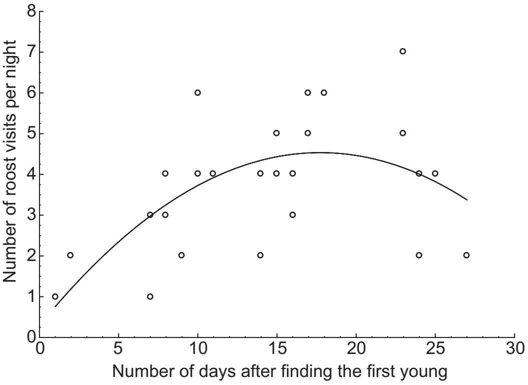

Fig. 3. Number of roost visits per night during the whole lactation period. A quadratic polynomial regression describes, significantly, the increase of roost visits at the beginning of lactation and the decrease at the end of lactation.

Night roosts and roost switching

Each female visited at least one roost per night, but five females visited two roosts during several nights, i.e. on 28% of the nights. Night roosts were visited on average 3.7 times (range 1–7) per night and female. A quadratic polynomial regression significantly described the increase in roost visits at the beginning of lactation as well as the decrease at the end of lactation ($R^2 = 0.45$, $F = 24.13$, $p = 0.008$, Fig. 3). In all, 13 roosts were found in tree cavities and only two in buildings (the main daily roosts of the two colonies). Five females (45%) changed day roosts after the night being tagged (32% of nights in total). For this reason, data from the first night after capture were not used in the roost switching analysis. Nursery colony A used six different day roosts, while nursery colony B only three during the study period. Tagged females from colony A used three roosts simultaneously consisting of ca. 60, 80 and 100 adult females, and three individual roosts.

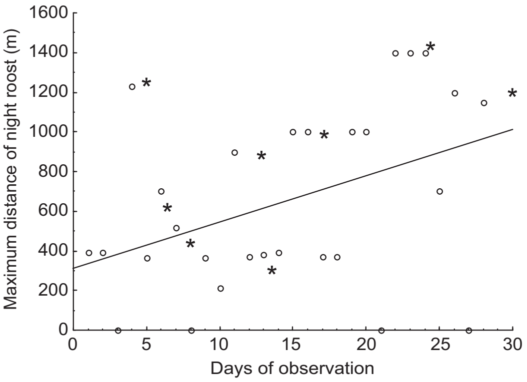

Fig. 4. Linear regression (R^2 = 0.18, F = 5.43, p = 0.027) describing changes in maximum distance between night and day roosts. * indicates nights when females visited a male roost.

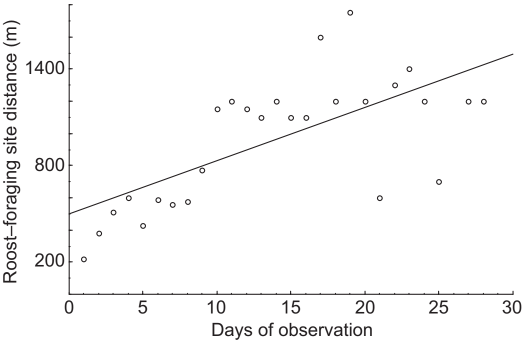

Fig. 5. Linear regression (R^2 = 0.47, F = 20.83, p = 0.001) describing changes of distance between roosts and foraging sites. An increase in distance between the roosts and the foraging sites was found towards the time of weaning.

Distances between roosts and foraging sites

The median distance between night and day roosts was significantly different (ANOVA: F_{26} = 7.79, $p < 0.001$) as were the medians of distances between foraging sites and roosts (F_{26} = 6.27, $p < 0.001$). Foraging sites were over 1 km away from the main roost for 8 of 15 females (maximum 1.75 km). The distances between night roosts were over 1 km in only 36% of all events (maximum 1.4 km). Three trends were obvious at the time of weaning: (1) a decrease in the number of roosts visited per night, (2) an increase in the distance between night and day roosts (Fig. 4), and (3) an increase in the distance between roosts and foraging sites (Fig. 5). Time spent by females in night roosts was constant (ANOVA: F_{78} = 1.17, $p > 0.05$). We tested the distances between day roosts and foraging sites which the females flew directly from their day roost. Five tagged females (during 11 nights) used foraging sites more distant from their original day roost in the building (mean ± SD = 446 ± 276 m). After day roost switching the distance between foraging areas and the new day roost in trees was lower (mean ± SD = 216 ± 84 m) (paired t-test: t = 2.50, n = 7, p = 0.04).

Other general observations

Three females probably transported their young to night roosts, as evidenced by records of the presence of flightless young inside roosts only used at night. Four lactating females visited sites where we recorded song-flight calls of *P. pygmaeus*. The song flights were performed by males near their roost along fixed flight paths. However, we located only one male roost. A tagged female, accompanied by a male, zigzagged for on average 70 minutes (n = 6, mean ± SD = 70 ± 13) among the trees in the vicinity of a male roost. In general, sites where males vocalized were more distant from the day roost than night roosts used only by females (mean ± SD = 989 ± 176 m *vs*. mean ± SD = 646 ± 231 m). A lactating female was even found in a company of one male *P. pygmaeus* and one *P. nathusii* in the same roost during a day. Other females switched their day roosts in the vicinity of male territories. All new female day-roosts within male territories were over 1 km away from their main day roost (range 1.0–1.4 km).

Discussion

Changes in activity

We found differences in some aspects of flying behaviour and roost switching between pipistrelle populations in central Europe and in England (e.g. Bartonička & Řehák 2004, Davidson-Watts *et al*. 2006). Maier (1992) found a bimodal nocturnal activity pattern in *P. pipistrellus* *sensu lato* during the lactation period. During the same period, Davidson-Watts and Jones (2006) observed 1.1 foraging bouts on average in *P. pygmaeus*. However, in our study the number of foraging periods was higher, 4.1 per night. On the other hand, several bouts were shorter, less than 15 minutes. In our study, the average flying time was 76 minutes per night. This value is considerably lower than those found by Davidson-Watts and Jones (2006) for the two pipistrelle species. Longer flying times were also found by Jenkins *et al*. (1998) and Maier (1992) for *P. pipistrellus sensu lato*. The relatively short time spent foraging could be due to the availability of rich food sources in the Czech floodplain forests as compared with those occurring in different habitats in England or Scotland.

Foraging areas and habitat use

Davidson-Watts and Jones (2006) found that *P. pipistrellus* used more habitat types than *P. pygmaeus*. Their results show that *P. pygmaeus* seems to prefer a limited spectrum of habitat types, while *P. pipistrellus* is more opportunist and uses a wider range of habitats. The association of *P. pygmaeus* with water is well known (Vaughan *et al*. 1997, Oakeley & Jones 1998). Rydell *et al*. (1994) found higher activity in pipistrelles above cluttered rather than open water surfaces. Our results support the unambiguous preference of water habitats in core foraging areas as compared with a cluttered forest or open field and meadow, respectively. We confirm that *P. pygmaeus* also prefers vegetation edges characterized by a high density of potential prey, which can also be used more frequently due to their proportionately greater presence in the landscape under study compared to infrequent water surfaces. Our results also agree with those of de Jong and Ahlén (1991) who found that pipistrelles prefer vegetation edges.

Roost switching and distances

Roost switching is often identified in pipistrelles, *Pipistrellus pipistrellus*/*pygmaeus* (e.g. Thompson 1992, Park *et al*. 1996). We chose the lactation period to study roost switching because of high roost fidelity during this period (Racey & Swift 1985). Colony size is important for thermoregulation which affects the frequency of roost switching (Haddow 1993, Barlow & Jones 1999). In England, the mean size of *P. pygmaeus* nursery colonies is about 200 females (Barlow & Jones 1999). We found considerably fewer females in colonies in buildings (median = 65, *n* = 39, author's unpubl. data). The lower number of bats in pipistrelle colonies in central Europe may be due to more frequent roost switching — induced by changes in preferred temperatures during the reproductive season — as compared with large pipistrelle colonies occupying stone houses in Scotland (Haddow 1993). Feyerabend and Simon (2000) observed bats moving even between eight different shelters in a colony consisting of nearly 200 adult females. We found three parallel shelters visited by females coming from the main colony (with 80 bats on average). The whole colony did not move between shelters all at once, as Feyerabend and Simon (2000) found in *P. pipistrellus*. Nevertheless, almost half the females moved between six shelters discovered every other day.

There are no genetic data available to determine kinship among bats within colonies of *P. pygmaeus*, but the simultaneous use of more shelters by females coming from one colony indicates an analogy with the fission–fusion model used in *Myotis bechsteinii* (Kerth & König, 1999) and *Eptesicus fuscus* (Willis & Brigham 2004). Most authors (Racey & Swift 1985, Jenkins *et al*. 1998, Davidson-Watts & Jones 2006) assume that the foraging areas are close to the roosts. Feyerabend and Simon (2000) found the distance between day roosts to be several times longer than the distance between the roost and the foraging site. Although the sample was small (only seven movements between day roosts), our results support the hypothesis that females may change their roosts because they are closer to attractive foraging sites (e.g. Feyerabend & Simon 2000). The distance between the first night foraging site and the previous day roost was always longer than the distance between the new day roost and the foraging site in the subsequent night. However, females can also use different roost types due to different microclimatic conditions inside them (buildings versus natural hollows) as conditions change during the reproductive season (Thompson 1990).

Our data show that it is extremely difficult to determine the actual size of a *P. pygmaeus* colony in central Europe because females use simultaneously more than one roost. By contrast, numerous pipistrelle colonies in England do not switch roosts for most of the reproductive season (e.g. Davidson-Watts & Jones 2006). This observation is very important especially in view of long-term monitoring programmes in which the size of maternal colonies is considered a basic index of population dynamics.

Transport of young

Suckling female *P. pygmaeus,* similarly to *P. pipistrellus*, were found to use several day roosts during the reproductive season (Bartonička & Řehák 2007). In the area exploited by colony B, bat boxes equipped with IR diode cameras were installed for our earlier research. Owing to all-night recordings, we found that one female carried its naked suckling infant into the empty box and returned for it some hours later. A similar behavioural pattern was also observed (by means of radio-tracking) during this study in case of two tagged females from nursery colony A. Juveniles were observed during the night in all roosts. For lactating females, transporting young and depositing them in a temporary roost within the hunting ground can be less costly than flying back and suckling the young in a distant nursery.

Paying visits to males

Four lactating females visited sites where we recorded song-flight calls of *P. pygmaeus*. We concluded that they might have been uttered by a male flying along the same flight route (Barlow & Jones 1997) although male advertisement calls were registered later, after weaning the young. However, Gerell-Lundberg and Gerell (1994) already found the first territorial vocalization during the lactation period at the end of June. Social calls undistinguished from song-flight calls were also emitted during group foraging but no feeding buzz was found during our recordings. Calls were produced at regular intervals indicating their attractive character (Lundberg & Gerell 1986). All four females mentioned above showed signs of nursing but we cannot exclude the possibility that their young died soon before, or during our study. The day after males were visited, three females chose their night roost in a tree hole in the vicinity of the male territory they had visited the previous night. Most observations were carried out for 15 days following the first find of an infant in the main roost. Hughes *et al.* (1989) never found pipistrelle females suckling offspring other than their own, therefore we suppose that the females had to carry their own young. The possibility of the young remaining inside a roost in the absence of its mother during daylight needs to be tested in more controlled experiments. Our results suggest that lactating females must be able to invest some of their stored energy in visits to male territories even during lactation, a period of highest energetic cost.

In summary, our results suggest that females of *P. pygmaeus* from a maternal colony use more than one roost and the movements among these roosts are often. This observation makes colony-counting as a method commonly used to evaluate changes in population dynamics unreliable and should be consulted within the framework of international conservation and management measures. Roost switching and the transport of young by females reduce energy costs related to movements in foraging sites. New findings that lactating females visit territorial males and share their roost suggest that the lactation period is less costly than is generally accepted.

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