Roosting ecology, phenology and foraging habitats of a nursery colony of *Pipistrellus nathusii* in the southwestern part of its reproduction range

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Abstract. The studied colony roost of *Pipistrellus nathusii* is located at the southwestern fringe of the species’ increasing reproduction range at lake Chiemsee (Upper Bavaria, Germany). In 2003 the bats arrived in April. During May and June the colony consisted of about 160 adult females. Parturitions began in late May, fledging in mid-June. When the maximum number was counted on 2 July (185 bats), the disintegration of the colony had already started. In late July the colony clusters included juveniles, adult females and also males. At that time advertising flights of males were observed in the vicinity of the studied roost. The bats roosted at temperatures ranging up to 39 °C. The temperatures over 40 °C were recorded regularly in the roost. In the evening, the bats left their roost 11–50 minutes after sunset. The mean emergence time varied during the season. The highest foraging activity of *Pipistrellus nathusii* in the study area was recorded over water habitats (stream, lake and pond; 85% of all records). At lake Chiemsee we recorded foraging bats at distances of up to 1.3 km from the shore. Woodland edges, gardens and orchards were less preferred habitats and the lowest foraging activity was found in spruce woodland, riparian woodlands and in open areas. The presence of the large lake, offering an outstanding food resource, might help to explain the existence of such a large colony far away from the traditional reproduction areas.

Roosting habits, reproduction, roost temperature, colony size, activity, habitats

Introduction

Nathusius’ pipistrelle (*Pipistrellus nathusii*) occurs from the Iberian Peninsula to the Urals, and as far north as Scotland, southeast Sweden, and southern Finland (Russ et al. 1998, 2001, Bogdanowicz 1999, Dietz et al. 2007, Baranauskas 2010). While breeding colonies are concentrated in lowlands of eastern, northeastern and central Europe, most mating and hibernation sites occur in western and southern Europe (Strelkov 2000, Petersons 2004). The species is a long-distance migrant (Strelkov, 1969) which typically leaves the northeastern regions of Europe in August and flies in a southwesterly direction.

Originally *P. nathusii* uses cavities in trees as nursery roosts (Vierhaus 2004). However, most colonies are found in bird- and bat-boxes (Heise 1982, Baranauskas 2010). During the mating season, territorial males use tree holes, crevices at buildings, spaces in hollow trees and behind the bark, as well as at the main breeding boxes (Vierhaus 2004). During winter, hibernating individuals can be found in crevices in cliffs, walls, hollow trees, woodpiles and caves (Meschede 2004).

In Central Europe nursery colonies of *P. nathusii* are known from north-eastern regions (Limpens & Schulte 2000, Schmidt 2000, Vierhaus 2004) and many studies about phenology and the behaviour of this bat species were conducted in these areas (e.g. Heise 1982, Schmidt 1984, 1985, 1994). In the western and southern parts of Central Europe the species appears during the
migration, mating and hibernation periods (Fiedler 1998, Vierhaus 2004). However, during the last years more and more nursery colonies were found at sites located southwest of the traditional reproduction range (including the southern parts of the Czech Republic) indicating a considerable extension of this area (Claussen 1999, Jahelková et al. 2000, Hochrein 1999, Martinoli et al. 2000, Lučan et al. 2007, Ohlendorf 1998, Řehák & Beneš 1996, Šefrová & Buřič 1998, Zöphel & Hochrein 2009). In Bavaria (southern Germany) the first regularly used nursery roost was found in

![Diagram of roost](image-url)

Fig. 1. Main roost of the colony behind the gable-boards (red rectangles). The drawing shows a profile of the roost. The animals hang between the black marked rafters. The crevice is 2–4 cm wide and 15 cm deep.

Obr. 1. Hlavní úkryt kolonie za prkny štítu (červené obdélníky). Kresba ukazuje průřez úkrytem; zvířata visela mezi černě vyznačenými trámy.
2000 at lake Chiemsee (Zahn et al. 2002). The colony consisted of about 200 adult bats – a high number compared to the sizes given in literature (Meschede 2004, Vierhaus 2004). In our study we analysed roosting behaviour, phenology and habitat use of this colony at the south-western fringe of the species’ increasing reproduction range. We compared our findings to data obtained in the traditional north-eastern nursery areas.

Material and Methods

The colony roosts in crevices (2–4 cm × 15 cm) behind the gable-boards on the east and west sides of a wooden shed (Fig 1.) in Übersee at lake Chiemsee (Upper Bavaria, 47° 48’ N, 12° 29’ E). In the same roost, behind the eastern gable-boards, but at a distance to the clusters of *P. nathusii*, a colony of about ten *Myotis mystacinus* can be found every year. At the end of the nursery season *P. nathusii* additionally used crevices in two neighbouring sheds. To determine the colony sizes, the emerging bats were counted simultaneously at all used roosting sites every 1–2 weeks. For each day we calculated the mean emergence time (mean of all emerged individuals). The onset of the birth period was established by direct observations of juveniles in the roost. The activity at the roost during the night was recorded by counting the leaving and arriving bats (whereby numbers were grouped in 15-minute intervals) during three full nights before the birth period, after the birth period and during fledging of the juveniles. Once a month a sample of the emerging bats was caught by mist netting for age and sex determination. To study the influence of temperature on the use of the roosts, we measured the temperature in the roosting crevices behind the gable-boards on the eastern and western sides of the building using digital thermographs and i-buttons (type DS1921G), which recorded the temperature every 2 hours.

*P. nathusii* forages at distances of over 6.5 km from its roost (Arnold 1999, Flaquer et al. 2009). Therefore we regarded all habitats in a radius of 5 km around the nursery colony as within easy reach for the bats. In this area we distinguished nine main habitat types and determined their area (in %) based on aerial photographs: “spruce dominated woodland” (24.8% of the area), “riparian woodland” (dominated by *Alnus, Salix, Fraxinus* and *Acer*; 9.3%), “riparian woodland edge” (2.6%, assuming an average width of the edges of 30 m), “village, garden & orchard” (7.9%), “pond” (0.6%), “lake Chiemsee” (11.6%), “stream” (1.2%), and open areas (“meadows & fields” and “moor”; together 42.0%). In order to study the habitat use, we randomly selected 4 sample sites in each habitat type (altogether 36 sites) within the 5 km radius. In case of “lake Chiemsee” the records were made at the shore. All “ponds” were located in woodland or surrounded by shrubs and trees. In the habitats “spruce woodland”, “riparian woodland”, “woodland edge”, “garden & orchard”, “pond”, “lake Chiemsee” and “stream” we determined the foraging activity in 4 periods: during preparturition (May – early June), during lactation (mid June – early July), after fledging (mid July – early August), and after the majority of the bats had abandoned the roost site (late August – mid September). Within each period we recorded bat calls with the help of a Peterson 240x bat detector (Pettersson Elektronik Ltd., Upsala, Sweden) and a minidisk recorder (Sony MZ-R37), three times at each of the sample sites (except “open areas”) for 10 minutes: in the first, second and third hour after sunset. Since open areas without water bodies are known not to be normally used for foraging (Arnold 1999), each of the sample sites in “meadows & fields” and “moor” was only investigated once in every period. During one night (14 July) we additionally studied the activity on the lake at a distance of 0.3–1.3 km from the shore by boat. We conducted the recordings only on evenings without rain, strong wind or temperatures below 8 °C.

The recorded bat calls (including social calls of males for mate attraction) were determined according to the criteria given by Skiba (2003) and Pfalzer & Kusch (2003). *Pipistrellus kuhlii*, a related species with very similar calls does not occur in the study area (Zahn et al. 2002).

We regarded as “foraging activity” during a 10 minute recording at a sample site, if a) at least two final buzzes were heard or b) *P. nathusii* had passed several times from different directions, to exclude sites where the bats only flew on commuting flights without hunting. To compare the foraging activity in different habitats, we calculated the percentage of visits with foraging activity for each sample site.

Results

Phenology and seasonal dynamics of the colony

The bats arrived in April 2003 and in early May the colony was complete (Fig. 2). During May and June between 150 and 165 adults were recorded during the regular counts. The first young were observed at the beginning of June, whereby their size indicated that the birth period had started at the end of May. The maximum number of bats counted during the evening emergence was 185 on 2 July. Already in mid July the colony size declined considerably and in August and
early September, less than 10% of the maximum number of individuals still used the studied roosts. In mid September, the sheds were abandoned. While in April the eastern gable-board was preferred as a roosting place, in May and June about 80% of the bats roosted on the western side. In early July, some bats began to use a crevice in a neighbouring shed and from late July onwards they only settled in the latter roost and in another shed nearby. During preparturition and lactation, only adult females (n=12) were found in the conducted catches. On 18 June the first fledged juveniles were observed during emergence and on 25 June the majority of the caught bats (8 of 11) were juveniles, indicating that fledging occurred about 3–4 weeks after birth. In late July (28 July) the sampled bats included 1 adult female, 10 juveniles and 3 adult males. All adult and 4 of 7 young males showed filled testes and epididymis (the young males to a lower extent). From 20 July onwards, social calls of males during advertising flights (small circles around the roost, interrupted by short landings at the gable-boards) were observed and recorded. At the most, two males displaying such behaviour at the same time were observed. However, we did not observe mating behaviour at the studied roost.

**Roost temperature**

In the crevices where the bats roosted, the temperatures varied between 10 °C and 48 °C from June until the end of August. The highest mean and maximum values were recorded behind the gable-boards on the western side, the most intensively used roost. Normally, variations of 20–30 °C occurred in the roost during one day, and temperatures of over 40 °C were reached on most sunny days. However, cooler places, e.g. sites closer to the roost entrance were always available and therefore the bats may have moved to cooler parts of the roosts during hot days.

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Fig. 2. Mean emergence time of the colony members after sunset and the number of emerging bats.

Obr. 2. Průměrná doba výletu členů kolonie po setmění počet vyletujících netopýrů.
During our visual inspections, temperatures of up to 40 °C were measured close to roosting bats. On 11 June, we inspected in detail the distribution of bats within the roost in relation to different temperature conditions. The temperatures in the roost varied between 31 and 39 °C. 72% of the bats roosted at sites of 36–39 °C, the rest at 34–35 °C.

**Emergence behaviour and overnight activity**

The bats left their roost 11–50 minutes after sunset (the earliest and latest bat observed during all counts). The mean emergence time varied during the season (Fig. 2). The bats left comparatively late during preparturition (May) and after the fledging period (July) but early during lactation (June) and during the late mating season (August–September). On two days it was raining during the observation but the bats left their roost as usual.

The first all-night-observation was conducted on 22 May. The whole colony started to emerge 30 minutes after sunset. All bats left within 10 minutes (21:27–21:37). Between 23:00 and 2:00, few foraging individuals were heard around the sheds. At 3:00 two bats entered the roost and between 4:00 and 5:00 the whole colony arrived. At the same time, swarming behaviour of 5 to 10 individuals was observed at the roost entrance between 4:30 and 4:45.

During lactation (6 June), the emergence lasted 20 minutes (21:15–21:35). About one third of the females did not leave and could be observed in the roost. However, between 21:35 and 22:07 some individuals returned, others left the roost and additionally foraging bats could be recorded around the shed. After a period without bat activity, we observed regularly arriving, leaving or

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**Fig. 3.** Foraging activity of *Pipistrellus nathusii* in different habitats (percentage of sample visits with records of foraging activity and area of the habitats within the 5 km radius, in %).

Obr. 3. Lovecká aktivita netopýra parkového (*Pipistrellus nathusii*) v různých biotopech (procentuální vyjádření počtu kontrol s pozitivními nálezy lovecké aktivity a plochy biotopů v průměru 5 km, v %).
foraging individuals between 23:00 and 4:00. From 4:00 to 4:45 all bats returned, whereby up to 50 were swarming around the roost entrance.

During postlactation, on 10 July, the activity pattern was similar to that in May. After emergence (lasting from 21:36 to 21:57) only few foraging bats were recorded until the colony members arrived again and entered the roost between 3:57 and 4:54, whereby up to 30 individuals showed swarming behaviour.

**Foraging habitats and foraging activity**

The comparison between the landuse patterns in a radius of 5 km around the roost and the intensity of foraging activity showed a significant difference between availability and usage of different habitats (Chi-square test, $\chi^2 = 54.5$, $p<0.001$). *P. nathusii* hunted its food preferably over water: most records of foraging bats (85%) were taken in the habitats “stream”, lake Chiemsee” and “pond”, whereby the maximum number was observed at “lake Chiemsee” (Fig. 3). While at “woodland edges” and in “gardens & orchards” the presence of foraging *P. nathusii* could be proven several times, observations were very rare in the “spruce woodland”. In the “riparian woodland” only passing individuals but no foraging activity could be recorded.

Within the regularly used habitat types the activity was not evenly distributed between sample sites. Foraging bats were found only at two “woodland edges”, in two “gardens & orchards” and at three sites at “streams”. Only in case of “ponds” and “lake Chiemsee” we detected hunting bats at all sample sites.

When we surveyed bat activity on lake Chiemsee by boat (14 July), we recorded several foraging individuals at the distances between 0.6 and 1.3 km from the shore.

In the habitat “moor”, foraging activity of *P. nathusii* was recorded only once. In “fields & meadows” no foraging *P. nathusii* were observed.

Most records (45%) of foraging *P. nathusii* were made during the first hour after sunset. However, the activity level was the same in the second and third hour (27 and 28% of the records). The activity of *P. nathusii* differed considerably between study periods: during preparturition (May – early June) only 3% of all foraging records were made. During lactation (mid June – early July) and after fledging (mid July – early August) the activity of *P. nathusii* was higher (31% and 40%). After departure of the adult females, from late August onwards, it decreased again (26%). At sites where foraging *P. nathusii* were found, we simultaneously recorded foraging individuals of *Myotis daubentonii*, *M. mystacinus / M. brandtii*, *Plecotus auritus*, *Eptesicus nilssonii*, *Pipistrellus pipistrellus, P. pygmaeus, Nyctalus noctula*, and *N. leisleri*.

**Discussion**

The bats gathered in mid April, the same time when the nursery colonies aggregate in the traditional reproduction areas in northeastern parts of Germany (Schmidt 2000), indicating that the shorter migration (Bavaria is a typical hibernation area – Meschede 2004) has no strong influence on the arrival time at the roost. Parturition began in late May (a warm month in 2003), which coincided with the timing of births during warm years in the northeastern areas (Schmidt 1984). There, the adult females leave the roosts shortly after fledging of their offspring, normally in early or mid July (Heise 1982, Schmidt 1994). In our colony the first bats left even earlier: considering that in this species most females have twins (Vierhaus 2004), the only very slight increase of the colony size in early July after fledging of juveniles indicated that the disintegration of the colony had already started at this time.
In the northern reproduction areas, groups of fledged juveniles stay longer in the studied roosts (bat boxes) but usually in early August most of them leave (Niethammer & Krapp 2004, Schmidt 1994). However, few individuals are still observed in September or October (Schmidt 2000). Adult males appear at the colony in July and the peak of mating behaviour occurs in late July and August (Heise 1982). These patterns are very similar to the observed phenology at lake Chiemsee.

However, in areas without known colonies in western Germany, where males wait for females during the migration season, mating seems to occur somewhat later, from August until October (Arnold 1999, Fiedler 1998).

The timing of evening emergence in European bats can be regarded as a trade-off between the advantage of emerging early, when small insects are most abundant, and the risk of being caught before dark by diurnal predators relying on vision (Fenton et al. 1994, Jones & Rydell 1994, Rydell & Speakman 1995, Russo et al. 2009). Therefore it can be expected that bats emerge earlier if food is scarce or if energy needs are very high. In fact, *P. nathusii* left its roost particularly early after parturition, when the energy demand of the lactating females peaks. Similarly, the colony emerged early in autumn, when the lower temperatures soon reduce the insect activity after dusk.

Differences from other studies were found in colony composition. After fledging of the young bats, males were found between the juveniles that still stayed in the roost. In northeastern Germany juveniles and adults are normally separated during the mating season (Heise 1982, 1984). Maybe these behavioural patterns are influenced by the roost type (in northeastern German bats were studied in bat boxes and not in buildings), because in *Nyctalus noctula*, a species with similar roost preference and migration habits, mixed groups of adult males and juveniles occur in buildings too, whereas nursery colonies and mating roosts are found in hollow trees and bat boxes (Zahn et al. 2004).

When available, the majority of the bats roosted at sites of over 35 °C – a range that is avoided by many other bat species in central Europe (Zahn & Henatsch 1998, Zahn 1999, Kayikcioglu & Zahn 2004, Scheunert et al. 2009). However, crevice dwelling species may prefer higher temperatures than attic dwelling bats. E.g. *Pipistrellus pygmaeus* and *Nyctalus noctula* occupy roosts where temperatures close to 40 °C can be recorded (Bartonička & Řehák 2007, Lourenco & Palmeirim 2004, Zahn et al. 2000).

Wetlands such as ponds and lakes were the preferred foraging areas of *P. nathusii*. Intensively foraging bats were found at lake Chiemsee even at a distance of over 1 km from the shore. Obviously *P. nathusii* does not need foraging sites sheltered by trees and shrubs, a factor which generally favours the bat activity at water bodies (Zahn & Maier 1997).

The colony at lake Chiemsee restricted its foraging activity even stronger to streams, lakes and ponds than other studied populations (Schorcht et al. 2002, Arnold 1999). Similarly Ciechanowski (2001) and Ciechanowski et al. (2009) reported high activity of *P. nathusii* over water bodies. According to the results of Arnold (1999) and Flaquer et al. (2009) based on radio tracking, colonies of *P. nathusii* use a range of more than 130 km² around the roost. Due to the large size of lake Chiemsee, the expanse of available wetland and lake habitats within the potential foraging area of the colony is similar to other habitats such as forests and settlements. Therefore, the high percentage of foraging activity recorded over water indicated a real habitat preference and was not only the effect of concentration, which might be the case if a high activity is found in a small habitat (Cefuch & Zahn 2008).

Lake Chiemsee can be regarded as an essential foraging region for the studied bats. The presence of the large lake, offering an outstanding food resource, might help to explain the existence of such a large colony far away from the traditional reproduction areas.
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Souhrn


References


Nyctalus mausarten am Beispiel von Rauhhautfledermäusen (Chiroptera): relevance for the design of bat boxes.

From Southern Bohemia (Czech Republic), breeding in Ireland.

With an abstract in English.)


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