

Population structure of Daubenton's bats is responding to microclimate of anthropogenic roosts

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Abstract: Roost microclimate plays an important role in the survival, growth and reproduction in microbats. Entering torpor is one of the main energy saving mechanisms commonly used by microbats. The use of torpor is affected by roost microclimate and seasonally differs between the two sexes in relation to their reproductive condition. Consequently, thermal properties of male and female roosts should differ. To test this hypothesis, we compared temperature parameters of two anthropogenic day roosts of Daubenton's bats with a different structure of the population inhabiting them. In accordance with our predictions, the roost occupied by a male-dominated colony was colder and more fluctuant than the maternity roost with a female-dominated population. However, using of the two roosts changed during the season in response to changing energetic demands of the two sexes. While males were almost absent in the warmer maternity roost during pregnancy and lactation, they appeared in this roost during the post-lactation when mating starts. In contrast, females did not use the colder (male) roost until the time of weaning of juveniles, i.e., the time when their thermoregulatory needs change and they may benefit from using colder roost. Our study provides the evidence that the same roost may be used by individuals of different sex and reproductive state in different periods of the year. Generalizations about roost selection without knowledge of temporal variation in roost use and microclimatic conditions should be taken with caution. Anthropogenic roosts may be advantageous to Daubenton's bats as these can provide a variety of suitable microclimates and/or more space for roosting than tree cavities.

Key words: population ecology; Chiroptera; *Myotis daubentonii*; roost microclimate; sexual segregation

Introduction

Roosts are vital to the survival and successful reproduction of bats (Kunz & Lumsden 2003). Although species-specific, roost selection particularly reflects energetic demands of individual bats that undergo dramatic changes based on their reproductive state. Roost microclimate acts as one of the primary cues that bats use to select their day roosts (Vonhof & Barclay 1996; Sedgeley 2001; Ruczyński 2006). For example, reproductive female bats select warmer roosts during gestation and lactation to provide ideal thermal conditions for juvenile growth and stable milk production (Hutchinson & Lacki 2001; Kerth et al. 2001; Lausen & Barclay 2003; Willis & Brigham 2005). By contrast, adult males and non-reproductive females profit from using cold roosts that allow them to minimize overall energy expenditures and to attain sufficient fat reserves prior to mating and/or hibernation (Hamilton & Barclay 1994).

Torpor is one of the main energy saving mechanisms commonly used by microbats (Willis 2006). Lowering body temperature can provide significant energy and water savings during cold ambient temperatures and food scarcity (Webb et al. 1993). However, it may reduce rates of fetal and juvenile development through

prolonged date of parturition or decreased milk production in pregnant and lactating females, respectively (Wilde et al. 1999). Therefore, reproductive females optimize development by minimizing torpor (Dietz & Kalko 2006).

Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) is a primarily tree dwelling species during the reproductive season (Rieger 1996; Boonman 2000; Encarnação et al. 2005; Lučan et al. 2009) but they frequently use anthropogenic roosts (Nyholm 1965; Gerell 1985; this study) and occasionally even caves (Zahn & Hager 2005). So far, it is the only single European species that has been subjected to a detailed study of sex-dependent seasonal changes in daily torpor patterns (Dietz & Kalko 2006). It was shown that while both sexes became torpid during the daytime, male bats used daily torpor significantly more often during the reproductive period (May–June) than females. Later on, a reverse pattern was observed and post-lactating females used torpor while adult males stayed in normothermy. End of lactation and onset of sperm production in late summer most probably caused this reversed trend in thermoregulatory behavior in females and males, respectively (Dietz & Kalko 2006).

The efficiency of entry into, and arousal from, torpor is affected by roost microclimate, primarily roost

temperature (Chruszcz & Barclay 2002; Willis 2006). Given the known differences in thermal needs between the two sexes in different periods of the reproductive cycle, we expected that male-dominated and female-dominated roosts should differ in their microclimatic parameters. We hypothesized that a roost used predominately by males should be colder than a maternity roost during the reproductive period. Further, we aimed to analyze the relationship between the population structure of bats in the studied roosts and microclimate in the light of changing energetic demands related to different periods of the reproductive cycle. Last but not least, we aimed to bring evidence that synanthropic roosts may provide a variety of suitable microclimates for both maternity and male colonies of originally tree-dwelling bat species.

Material and methods

Study area and roosts

The study area was located in the central part of South Bohemia, Czech Republic. The region is dominated by two flat basins – the Budějovická basin and the Třeboňská basin. Both basins lie at an altitude of 380–420 m a. s. l. and are covered with a mosaic of semi-natural forests, agricultural landscapes and a very high number of water bodies (mostly fish ponds). The Budějovická basin is situated in the western part of the study area and represents a region significantly influenced by urban activities, comprising the large built up area of the regional capital city of České Budějovice, and vast areas of intensive agricultural landscapes (more than 50% of the area). The mean annual temperature is between 7–8°C and the mean annual precipitation is between 550–600 mm (Tolasz et al. 2007). The local bat fauna consists of 19 bat species with Daubenton's bat being the most common (Lučan et al. 2007). Contrastingly, the Třeboňská basin lies in the eastern part of the study area and represents a unique combination of well preserved natural habitats (wetlands, peat bogs) and semi-natural forests and agricultural landscapes (less than 30% of the area) with a low human population density. For this reason it has been established as a Biosphere Reserve under UNESCO and it is protected by the Ramsar convention. The mean annual temperature reaches 6–7°C and the mean annual precipitation is 600–650 mm (Tolasz et al. 2007). The local bat assemblage includes 16 bat species with Daubenton's bat being the most common (Hanák et al. 2006).

Roost A is located in the Českobudějovicko basin in the city centre of České Budějovice (approximately 48°58' N, 14°28' E). It is an underground water tunnel 180 m long, 2.5 m high and 5 m wide. Daubenton's bats roost in five nearby, vertically positioned crevices, up to 5 m long, 3–5 cm wide and up to 25 cm deep. The roost is located ca 30 m from one of the two entrances to the tunnel and is partly illuminated by the daylight. However, sunlight can not directly influence the roost temperature because the roost is located several meters under ground. Given the flowing water, the air humidity in the roost is high (85–100%). Although we did not measure the air circulation, it is much higher than in the roost B (cf. tunnel vs. closed room). Up to 80 Daubenton's bats occupy this roost on an annual basis.

Roost B is located in the northern part of the Třeboňsko basin (approximately 49°9' N, 14°41' E), 25 km east of roost A. It is a small abandoned cellar-like building made

of bricks, formerly used as a limekiln. The building is 5 m long, 4 m wide and 4 m high. The walls are about 1 meter thick. There are several crevices of variable size in the ceiling, the largest of them (entrance 20 × 20 cm, depth 60 cm) being the main roosting place of the colony of Daubenton's bats. Roosting bats are slightly illuminated by daylight. The temperature in the roost is directly influenced by sunlight because concrete walls of the building absorb the heat and keep warmth for a long time (Lučan, pers. obs.). There is no significant air circulation and air humidity is high (90–100%) throughout the season. This roost has been used by a maternity colony of Daubenton's bats numbering up to 200 individuals for more than 40 years (Lučan & Hanák 2002).

Periods of reproductive cycle and population structure of the colonies

Based on long-term observations of the reproduction and population dynamics of Daubenton's bats in the study area (Lučan & Hanák 2002; Lučan 2006), we divided the reproductive season into five periods: spring movements (March 15 – May 10), pregnancy (May 11 – June 10), lactation (June 11 – July 10), post-lactation (July 11 – August 15) and autumn movements (after August 15). To obtain data on the structure of the population, we caught up to 21 individuals (median = 10, range 4–21) from roost A between 2002 and 2009 ($N = 27$ samples, 270 individuals). Bats were caught during the day by hand directly from crevices where they roosted. In roost B, we sampled bats using a hand net or by mist-netting in front of the entrance to the roost building. We captured up to 140 individuals during one sampling event (median = 11, range 1–140) between 1969 and 2009 ($N = 90$ samples, 2441 individuals). All captured bats from both roosts were identified in terms of sex, age and the reproductive status, based on the routinely used criteria for this species (e.g., Encarnacao et al. 2005; Lučan 2006). To calculate the sex ratio for a particular sampling event, we used the ratio of adult males to all captured adult bats (Wilson & Hardy 2002). Adult bats were defined as those not born in a given sampling year. For calculations of the sex ratio, we used only samples with ≥ 4 and ≥ 10 bats captured during a single sampling event for roost A and B, respectively. Altogether, we obtained 27 and 53 such samples for roost A and B, respectively.

Roost and ambient temperatures

We used four TK – 0063 (Gemini Dataloggers Ltd.) temperature dataloggers to record the temperature in both roosts and ambient temperature (T_{amb}) in their vicinity. Temperatures were recorded in 30 min intervals from 9th March until 2nd October 2008. The temperature probes were positioned ca. 30 cm from the roosting bats to avoid temperature bias via direct contact with roosting bats. To measure T_{amb} , one temperature probe was placed ca 4 meters above ground in the vicinity of each roost, out of direct sunlight. Technical failures of dataloggers resulted in gaps in measurements between August 15–28 in roost A and between August 3–25 in roost B. Minimum (T_{min}) and maximum (T_{max}) temperatures were measured as daily minimum and maximum values. Temperature amplitudes were calculated as daily differences between minimum and maximum temperatures.

Statistical analyses

We tested differences in daily mean T_{amb} using paired t -test. We used analysis of covariance (ANCOVA) with T_{amb} as a covariate and roost and period of reproductive cycle as dependent variables to test differences in temperature between the two roosts. Roost-days were the replication units in all

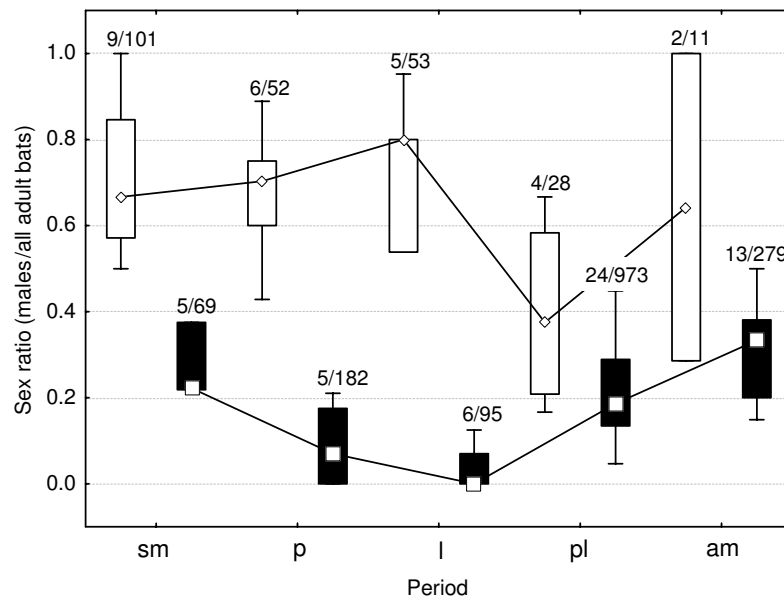


Fig. 1. Sex ratio during reproductive season in the two anthropogenic roosts of Daubenton's bats (*Myotis daubentonii*) studied in South Bohemia (1969–2009 and 2002–2009). Number of samples/total number of examined adult bats are given for each roost and period. White boxes – roost A, black boxes – roost B. Abbreviations: sm – spring movements, p – pregnancy, l – lactation, pl – post-lactation, am – autumn movements. Point: median; box: 25–75%; whiskers: min–max.

analyses. We used arcsine transformation of square-rooted values in the sex ratio data to achieve normal distribution prior to analyses (Wilson & Hardy 2002). We used factorial analysis of variance (ANOVA) where roost and period were dependent variables to test the differences in sex ratio between the roosts. Tukey HSD tests were applied to compare temperatures and/or sex ratios between roosts and periods. All statistical analyses were performed using STATISTICA 8.0 (Statsoft Inc.). All values are presented as mean $\pm$ S.E.

Results

Population structure

We found significant differences in the sex ratio of bat aggregations between the two roosts ($F_{(1,64)} = 57.74$, $P < 0.0001$). On average, adult males greatly outnumbered females in roost A, while the reverse situation was observed in colony roost B (Fig. 1). However, the sex ratio varied significantly with respect to the period of reproductive cycle ($F_{(4,64)} = 3.24$, $P < 0.05$). While the two colonies differed significantly in the sex ratio during pregnancy and lactation ($P \ll 0.001$), there were no differences during spring-movements ($P = 0.08$), post-lactation ($P = 0.89$) and autumn movements ($P = 0.3$) due to the high variability in the samples. Although not statistically significant, females tended to prevail in roost A during the post-lactation period when compared with the pregnancy and lactation period.

With exception of two newborn pups observed on 4 June 2009, we never found non-volant juveniles in roost A ($N = 8$ years). By contrast, roost B served as a maternity roost during lactation over the entire monitoring period ($N > 30$ years) and several tens of non-volant juveniles were observed here each year on a regular basis (Lučan & Hanák, in press). In roost A, volant juvenile bats appeared as early as during late

Table 1. Results of analyses of covariance describing microclimates in two roosts of Daubenton's bats (*Myotis daubentonii*) with different occupancy.

Source	<i>F</i>	<i>P</i>
Mean Temperature		
Period	54.18	< 0.001
Roost	156.61	< 0.001
Roost $\times$ Period	6.21	< 0.001
T_{amb}	852.86	< 0.001
Minimum temperature		
Period	40.13	< 0.001
Roost	115.09	< 0.001
Roost $\times$ Period	1.67	0.157
T_{amb}	772.67	< 0.001
Maximum temperature		
Period	81.27	< 0.001
Roost	121.67	< 0.001
Roost $\times$ Period	18.05	< 0.001
T_{amb}	412.16	< 0.001
Amplitude in temperature		
Period	6.07	< 0.001
Roost	9.28	0.002
Roost $\times$ Period	21.72	< 0.001
T_{amb}	170.35	< 0.001

Explanations: Models describe mean roost temperature, minimum roost temperature, maximum roost temperature and daily amplitude in roost temperature. Roost and period of reproductive cycle was included as main effect for all temperature comparisons and T_{amb} was a covariate. D. f. = 4, 368 for Period and Roost $\times$ Period interaction; d.f. = 1, 368 for Roost and T_{amb} .

lactation (second half of June) and were present in the roost until late autumn. In roost A, juvenile bats made up 39.1% ($n = 46$) of total bats during post-lactation and 45% ($n = 20$) during autumn movements. In roost B, juvenile bats were present from their parturitions un-

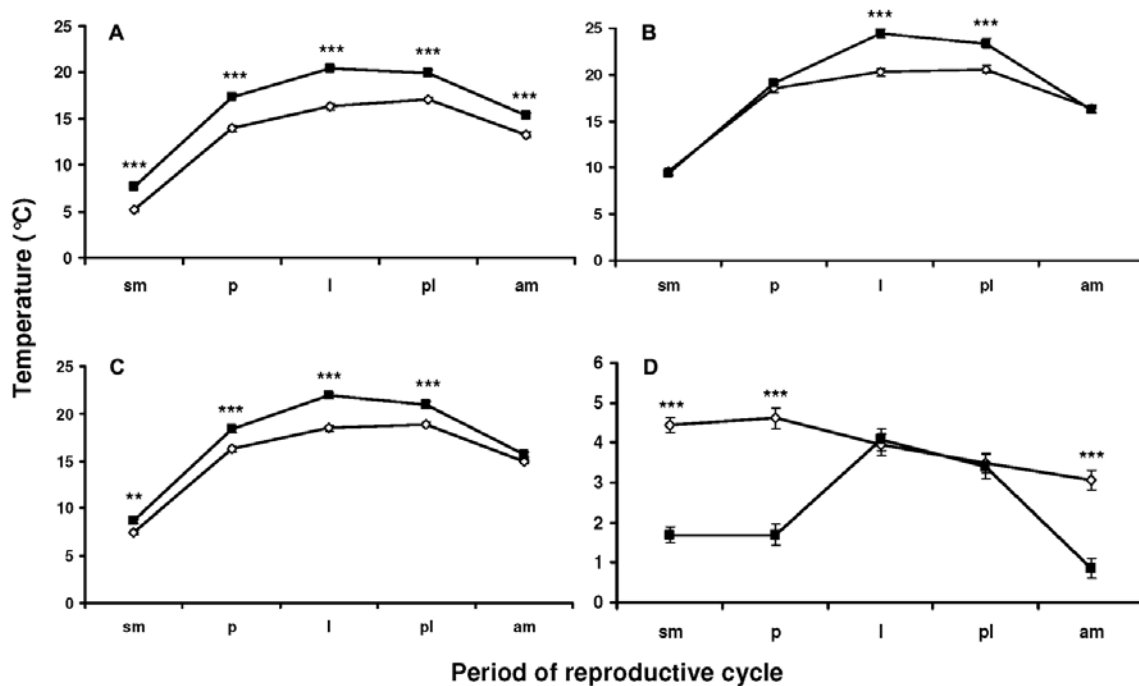


Fig. 2. Seasonal changes in microclimate characteristics of two anthropogenic roosts of Daubenton's bats (*Myotis daubentonii*) studied in 2008, South Bohemia. Minimum roost temperatures (A), maximum roost temperatures (B), mean roost temperatures (C) and daily amplitudes in roost temperatures (D) are shown. Values are given as mean $\pm$ S.E. Statistically significant differences of Tukey HSD post-hoc tests are marked with asterisks (** $P < 0.01$; *** $P < 0.001$). Abbreviations: sm – spring movements, p – pregnancy, l – lactation, pl – post-lactation, am – autumn movements. Empty symbols – roost A, full symbols – roost B.

til late autumn. The proportion of juveniles in roost B was 38.4% ($n = 1598$) during post-lactation and 42.4% ($n = 545$) during autumn movements.

Roost temperatures

The mean, minimum, and maximum daily temperatures and temperature amplitudes in the two investigated roosts are shown in Figure 2. Results of statistical analyses provided significant differences between the two roosts in majority of tested microclimatic parameters (Table 1). Mean ambient temperatures were higher at roost A than at roost B ($t_{(1,206)} = 10.54$, $P < 0.0001$). By contrast, roost A had lower mean temperatures than roost B. The most pronounced differences in the mean temperature occurred during the lactation when roost A was on average colder by 3.4°C than roost B (roost A = $18.5 \pm 0.3^\circ\text{C}$, roost B = $21.9 \pm 0.3^\circ\text{C}$). Roost A also had lower maximum temperatures than roost B. However, the maximum temperatures significantly differed only during the lactation and the post-lactation periods (Fig. 2B). Roost A cooled more than roost B throughout the season. The greatest differences occurred during the lactation period, when the minimum temperatures of roost A were lower by 4.1°C than those of roost B. The minimum roost temperature was higher than the minimum ambient temperature by $3.9 \pm 0.13^\circ\text{C}$ and $5.6 \pm 0.13^\circ\text{C}$ in roost A and B, respectively. The mean daily temperature amplitudes were higher in roost A than in roost B, but there were significant seasonal differences. Roost B had more stable temperatures (i.e., smaller daily fluctuations) than roost A during the spring, the pregnancy period and the autumn movements period

and was subjected to similar temperature fluctuations as roost A during the lactation and the post-lactation periods (Fig. 2D). While mean daily temperatures in roost A did not differ from mean T_{amb} throughout the season ($F_{(1,390)} = 0.36$, $P = 0.550$), roost B had higher mean temperature than T_{amb} ($F_{(1,383)} = 34.5$, $P < 0.0001$).

Discussion

In accordance with our predictions, we brought the evidence that the population structure of bats in the studied roosts was responding to microclimatic differences between them. The colder roost with unstable temperatures was occupied mostly by males, and the warmer and more stable roost served as a maternity roost to a female-dominated colony. It is well known that the two sexes of Daubenton's bat display different distribution patterns and relative abundance in relation to quality of foraging habitats and altitude. The female-dominated populations occur mostly in the vicinity of large water bodies in lowlands whereas males are more commonly found in habitats at higher altitudes (Russo 2002; Senior et al. 2005; Dietz et al. 2006). However, both roosts in our study were located at the same altitude in areas that provide habitats commonly occupied by reproductive colonies (cf. numerous and large water bodies in flat landscapes) and our previous research suggests the populations in both areas are female dominated (Hanák et al. 2006; Lučan et al. 2007; Lučan, unpublished data). Consequently, if the structure of population in the two roosts reflected regional

population structure, there would be no differences in the composition of bats between the two roosts. At both studied anthropogenic roosts, numerous natural roosts (tree cavities) are present in their proximity and movements between these roosts and the studied roosts were proven by ringing and radiotracking (Lučan & Radil 2010; Lučan & Hanák in press; Lučan, unpublished data). Since the colder roost A was in a climatically warmer area than roost B and *vice versa* (Tolasz et al. 2007; this study), we suppose that bats may actively select these roosts based directly on suitable microclimate. Therefore, we assume that the observed differences in the population structure reflected primarily the energetic demands of both sexes during the reproductive season (Hamilton & Barclay 1994; Grinevitch et al. 1995; Dietz & Kalko 2006).

Furthermore, we observed a tendency of the populations in the two roosts towards a reversed change in the sex ratio as the season progressed from the lactation to the post-lactation period (see Fig. 1). The proportion of adult males decreased in the colder roost A and increased in the warmer roost B. By contrast, females increased their numbers in the colder roost A from the end of lactation period. This observation fully corresponds with observed seasonal differences in the use of torpor between the two sexes of Daubenton's bat. While females kept high body temperature during pregnancy and lactation, they used deep torpor during post-lactation. Males, on the other hand, used deep torpor in the pregnancy and lactation period but stayed in the normothermy in the post-lactation period (Dietz & Kalko 2006). The post-lactation period corresponds with increased spermatogenetic activity in adult males of Daubenton's bats (Encarnação et al. 2004). Since the use of deep torpor is significantly reduced during spermatogenesis (Dietz & Kalko 2006), we expect that adult males may benefit from moving to warmer roosts. Moreover, apart from thermoregulatory reasons, reproductively active males may benefit from moving to the roost occupied by adult females through easy access to potential mates. In accord with this hypothesis, the findings by Encarnação et al. (2004) suggest that a large proportion of mating in Daubenton's bat occurs in day roosts within the summer habitat.

Our observation fully supports the objection by Boyles (2007) against generalizing differences in roosts selection of forest bats without taking into account a temporal variation in roost use and microclimatic conditions. Indeed, most studies comparing, for instance, roost selection between male and female bats were based on observations within short time period (e.g., Broders & Forbes 2004; Encarnação et al. 2005; Perry & Thill 2007). However, our study clearly demonstrated that the same roost may be more or less preferred by particular sex in one period and avoided in others. Consequently, given roost could be, for instance, erroneously interpreted as a typical male roost based solely on observation from the lactation period despite it is used by both sexes in the post-lactation. Such situa-

tion could be common in many forest bats, particularly those species that reuse their roosts for many consecutive seasons (Lučan et al. 2009).

The majority of originally tree dwellers, such as *Myotis nattereri* (Kuhl, 1817), *Nyctalus noctula* Schreber, 1774 and *Plecotus auritus* (L., 1758) commonly roost in buildings, but it is rare in Daubenton's bat in the Czech Republic (Hanák & Anděra 2006). When roosting outside tree cavities, Daubenton's bats likely prefer roosts located in underground water tunnels, bridges or cellar-like structures (Barva 2000; Dietz et al. 2006; Hanák & Anděra 2006; Čeluch & Ševčík 2008) in Central Europe. Zahn & Hager (2005) found a maternity colony with up to 302 Daubenton's bats in a cave in Bavaria (Germany) with a temperature as low as 13.8°C. This observation provides evidence that Daubenton's bats are able to exploit a variety of roosts and may use anthropogenic roosts much more frequently than previously reported. We assume that population increase of this species during the last decades may be, apart from trophic reasons (cf. Kokurewicz 1995), the result of its increasing use of anthropogenic roosts that may be beneficial through providing enough space for large colonies and a variety of suitable microclimates.

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