Acta Chiropterologica, 9(2): 517–526, 2007
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Influence of the microclimate of bat boxes on their occupation by the soprano pipistrelle *Pipistrellus pygmaeus*: possible cause of roost switching

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Between April and October 2003–2004, the changes in occupation of three bat boxes used by *Pipistrellus pygmaeus* were studied using a passive IR monitors and data loggers. Bat boxes were situated in a floodplain forest in south-eastern Moravia. Generalized additive models indicated that internal humidity described better the fluctuation in bat numbers during pregnancy and lactation than did changes in the internal temperature. Three variables (internal humidity, external temperature, and number of bats) described 87% of the variability in internal roost temperature, while the number of bats described only 29% of the variability. A negative correlation was found between the internal temperature and the number of bats roosting in a bat box the next day during pregnancy and lactation. The number of bats was also positively correlated with the internal humidity. The internal temperature of a roost with bats was biased by temperature strategies induced by the bats during particular reproductive periods. Mean temperature of occupied bat boxes was higher during pregnancy than during lactation. Females were able to go into torpor even during lactation period.

Key words: *Pipistrellus pygmaeus*, roost changing, microclimate, bat boxes

INTRODUCTION

Roost fidelity is low in many species, especially among tree-dwelling bats (Lewis, 1995). Field observations (Lausen and Barclay, 2002; Mazurek, 2004; Rancourt *et al.*, 2005) suggest that species of bats dwelling in holes and crevices switch their roosts several times during a season, even every few days. This behaviour was observed mainly in species roosting in tree hollows (Barclay and Brigham 2001; Kerth *et al.*, 2001; Willis and Brigham, 2004). However, several studies suggest that roost switching was registered even in *Pipistrellus pipistrellus* s.l., usually roosting in buildings (e.g., Thompson, 1992; Park *et al.*, 1996). Thompson (1990) or Feyerabend and Simon (2000) found large numbers of roosts exploited by one colony of pipistrelles. Small groups of female pipistrelles often leave their respective roosts and move into a main nursery roost a few days prior to parturition, probably to reduce costs associated with thermoregulation (Swift, 1980; Webb *et al.*, 1996; authors' personal observations).

Recent studies show that females of species using tree cavities are not restricted to individual trees and one colony may be spread among multiple trees on a given night, conforming with a fission-fusion model (Kerth and König, 1999; Willis and Brigham, 2004). The motivation underlying roost switching and reasons why groups disperse among several roosts is not well understood (Lewis, 1995; Vonhof and Barclay, 1996). This social structure may help maintain a number of potential benefits linked to living in a large colony. Roost switching might force social relationships among the small 'subgroups' that comprise a larger group. However, dispersion of colonies among tree cavities and bat boxes may result from a complex of different constraints. Roost switching and dispersion may reflect differences in group size between bats forming large colonies in caves and buildings and those roosting in smaller colonies in trees, perhaps due to thermal differences or to competition for space when the number of individuals is increasing and one cavity is too small (Whitaker, 1998; Lefebvre *et al.*, 2003). Roost switching could be a good mechanism by which bats select roost site with optimal microclimatic conditions (Kerth *et al.*, 2001; Lourenço and Palmeirim, 2004). Bats may know alternative roosts including their microclimate in advance, since the search for a new roost might be costly in terms of energy output (Lewis, 1995). Benefits associated with roost switching could also be positively correlated with decreasing the mortality of juveniles due to the impact of parasites (Wolz, 1986; Lewis, 1996).

We attempted to answer the following questions. (i) Are differences in microclimatic parameters among bat boxes dependent on particular parts of the reproductive season? (ii) Do reproductive requirements influence roost switching or roost sharing behaviour? (iii) Can internal temperature or other microclimatic parameters be used to predict the presence of bats in a roost?

MATERIALS AND METHODS

Study Area and Data Collection

The changes in microclimate and occupancy of bat boxes used by *P. pygmaeus* were studied in a floodplain forest in south-eastern Moravia (Czech Republic). The study was performed between April and October of 2003 and 2004. Three wooden bat boxes were studied, two of them were placed in trees situated within the forest and its edge, the third was placed on a hide at a forest edge. Altogether four boxes were installed in the study area, but only three of them were occupied periodically. The reproductive season under study was divided into three periods: pregnancy (until 7th June), lactation (8th June till 7th July, 30 days after first parturition observed) and post-lactation (after 8th July — cf. Bartonička and Zukal 2003). The time of first parturition was assessed in a nearby (14 km) nursery colony of *P. pygmaeus* in a building at Vranovice (T. Bartonička *et al.*, unpublished data). There, the bats were captured, examined and released. We also netted bats emerging from all boxes during the years 2001 and 2002, but never captured males. Therefore we suppose the absence of adult males during the study in 2003 and 2004. All captures were performed under the licence No. 922/93-OOP/2884/93 of the Ministry of Environment of the Czech Republic. The authors have also been authorized to handle free-living bats according to the certificate of competency No 104/2002-V4 (§ 17 of the law No. 246/ 1992).

Technical Equipment

The changes in bat activity with respect to the boxes were monitored continually by passive IR Trail Monitors, TM (TM550, TrailMaster, Goodson & Associates, INC., USA — used by Thomas *et al.*, 1995) and active IR gate (Berková and Zukal, 2004). The IR gate consisted of 2 infrared light emitters (diodes) and two receivers (phototransistors). This technique allows discrimination between those bats leaving and those entering the bat box. With the event delay set to 0.1 minutes the TM record 10 events in a single minute. Battery life of both types of recording systems was usually two weeks or more. One bat box was equipped by IR gate and two boxes by TM. The TMs were situated in front of the entrance (see Fig. 1) and the IR gate in the entrance of each bat box. Hobo Data Loggers (Onset Computer Corporation, USA), continuously recording the temperature (internal and external) and the internal humidity, were situated under the roof of each bat box. The sensors measuring external temperature were situated about 50 cm apart from each box. The relative humidity sensor had an accuracy of ± 4% and the temperature sensor ± 0.4°C. The bats flying out and in were also monitored using a digital video recorder HD-2166 and AVC-720 connected with IR diode cameras B/W AVC 307R.

FIG. 1. Wooden bat box. Monochrome (B/W) IR diode camera monitored the entrance of the box and was connected to a battery and digital recorder on the ground. Two grey shapes mark out a space monitored by passive IR Trail Master monitor (TM550) on a bracket in front of the bat box. Internal temperature was measured with help of Hobo Data Loggers (Onset Computer Corporation) (inside box). Sensor measuring external temperature was placed outside roughly half a meter from the bat box

Statistical Analysis

All variables showed a normal distribution after log transformation. Statistica for Windows 7.0 was used for data analyses (ANOVA, *t*-tests, correlations). The level of activity (from TM) in morning hours (1 to 5 a.m.) positively correlated with the number of bats which rested in the box during the same day from IR gate (Pearson's correlation coefficient, $r = 0.61$, $P < 0.05$). Therefore we chose medians of activity from TM only from this period and pooled them with data from IR gate to analyse impact of microclimatic parameters and changes in bat numbers among bat boxes. Generalised additive models (GAMs) were fitted using the R-Gui 2.0.1 software package. Functions for continuous variables were fitted using cubic smoothing splines, initially with four degrees of freedom. At the completion of the selection process the function for each selected continuous variable was reduced if this did not result in a significant ($P < 0.05$) reduction in goodness-of-fit. These models assume that the mean of the dependent variable depends on an additive predictor through a nonlinear link function. Generalized additive models permit the response probability distribution to be any member of the exponential family of distributions (Hastie and Tibshirani, 1990). Hourly values of microclimatic parameters correlated positively ($P < 0.05$) with their means during the light part of a day (sunrise to sunset) (internal temperature, $r = 0.53$; external temperature, $r = 0.69$; humidity, $r = 0.85$; in all cases the number of ligh parts of day $n_1 = 330$ and the number of hourly values $n_2 = 1771$). Therefore the model was fitted by means of microclimatic parameters from the light part of a day and the numbers of bats using a particular bat box as their day roost. This step removed the effect of shifts in temperature and other parameters during the respective day from sunrise until sunset.

Materials

We monitored activity at the three bat boxes occupied by *P. pygmaeus* for 111, 105 and 115 days, respectively. Hourly values were available on internal and external temperatures, and internal humidity. For each day, the number of roosting bats was counted resting in the box via passive TM and/or active IR gate.

RESULTS

Insulating Properties of Bat Boxes

We found that the internal and external temperature neared equilibrium within five hours (median) after all bats left the particular bat box (max. 8 hrs, min. 3 hrs). Although each of the bat boxes under study differed in exposure, no significant difference among the boxes was found in the time needed to balance the level of internal and external temperatures (ANOVA, $F_{2,\ 19} = 0.69$, $P >> 0.05$). When the bats moved to another roost the next day, they left the respective box soon after sunset without returning to it during the night. Therefore, the five-hour period, after emerging, allowed us to exclude nightly observations i.e., data obtained between sunset and sunrise from further statistical analyses.

Impact of Internal Temperature and Humidity

Factors with possible impact on changes in internal temperature were only studied during the periods of pregnancy and lactation. The post-lactation period was omitted because of great fluctuations in numbers of roosting bats due to the weaning of young. The following independent variables were used in the GAM models: external temperature (tex), internal humidity (hum), reproductive stage [i.e., pregnancy versus lactation (sez)], exposure of bat box (box), and the number of bats roosting in the box during next the day [ind]. Normal distribution and link function identity was considered of the dependent variable, which was internal temperature (tin). The dependence of internal temperature was defined as the function of (tin) ≈ s(hum) + s(tex) + s(ind) + (sez) + (box), where s is a specific smoothing spline fit in a GAM. The interactions among variables were found to be insignificant and did not increase the proportion of variability within the sample. The impact of each of the first three independent variables on the dependent variable was significant (humidity, $\chi^2 = 16.08$, $P < 0.01$; external temperature, $\chi^2 = 26.11$, $P < 0.001$; individuals, $\chi^2 = 8.45$, $P < 0.05$; in all cases $n = 27$). Together they described 87.1% of variability of the internal temperature. The impact of reproductive stage and exposure of bat box was insignificant (*t*-test, $t = 4.21$ and $t = 5.23$, respectively; in both cases $P > 0.05$ and $n = 27$). There was an almost linear dependence between the values of internal and external temperature (Fig. 2). Internal temperature also increased with internal humidity (Fig. 2). The number of bats in the box explained only 29% of the residual variability of internal temperature (holding constant external temperature and internal humidity). Nevertheless, we found a negative correlation between the internal temperature and

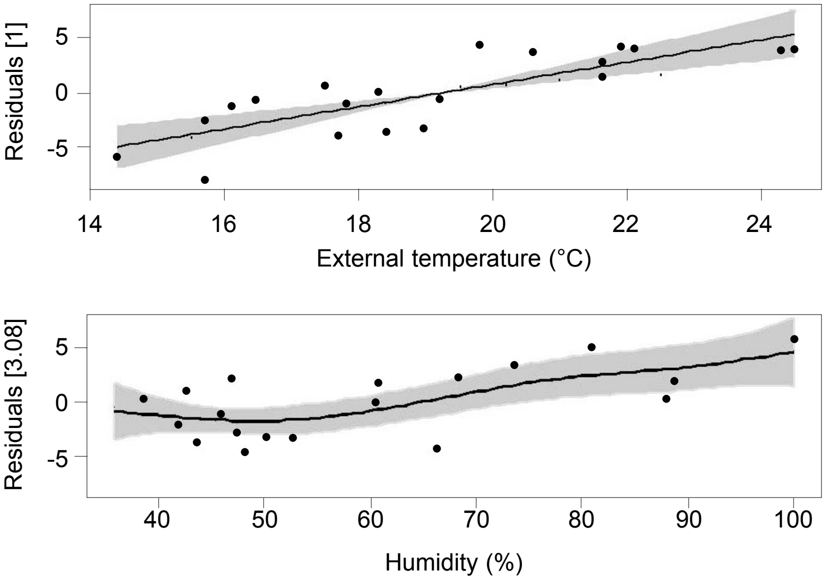

FIG. 2. Graphic output of a generalised additive model for the internal temperature. Both graphs depict the predicted probability of the external temperature (a) and internal humidity (b) holding other predictors constant. 95% confidence limits for the function are also shown as grey zone. Linear dependence between residuals of internal temperature from GAM and external temperature was found. Internal temperature as factor in GAM also increased with internal humidity. Degrees of freedom are in brackets in label of *y*-axes

the number of bats roosting in the box the next day (Fig. 3). The highest median of the number of roosting bats (75 individuals) was found during pregnancy, i.e. at the time when females form nursery colonies. The size of roosting groups was very low during the lactation and post-lactation periods. Cross-correlations were also tested, but the variability of internal temperature was better described by correlations with individual variables than with their combinations.

The dependence of internal humidity on the number of roosting bats was again tested by GAM [only pregnacy and lactation periods, hum ≈ s(ind) + s(tex) + s(tin) + (box)]. It was found that changes in internal humidity correlate with the number of bats much better than do the changes in internal temperature until 7th July (χ^2 = 76.82, *d.f.* = 607, $P < 0.001$, Poisson distribution, link function: log — Fig. 4). The impact of bat box exposure was insignificant again ($t = 6.16$, $P > 0.05$). The number of bats described 52.6% of the variability of internal humidity (holding constant external and internal temperature). The correlation found between the number of bats and humidity in bat boxes was positive (Pearson's correlation coefficient, $r = 0.40$, $n = 330$, $P < 0.05$). There was no correlation between rainy days and presence or absence of bats in bat boxes ($r = 0.03$, $n = 330$, $P >> 0.05$).

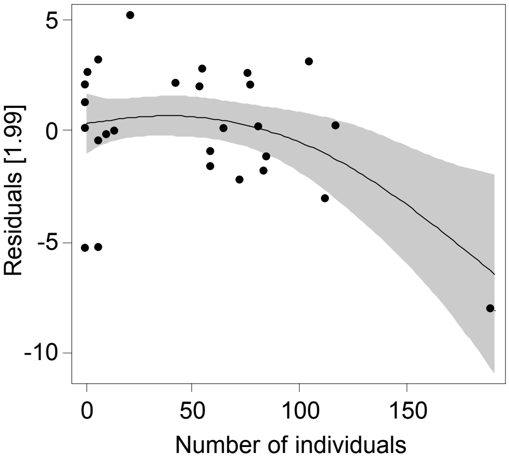

FIG. 3. Graphic output of a generalised additive model for the number of bats in bat boxes, holding all other predictors (external temperature, humidity, localization of bat boxes, seasonal aspect) constant at their mean value. 95% confidence limits for the function are also shown as grey zone. Degrees of freedom are in brackets in label of *y*-axis

Changes in Microclimatic Parameters during The Season

Intraseasonal differences in microclimatic parameters (internal, external temperature, humidity) were evaluated with respect to the reproductive periods. We chose only days with the presence of bats. ANOVA showed significant differences in microclimatic parameters among the periods (pregnancy, lactation, post-lactation — $F_{2,\ 81} = 2.08$, $P < 0.05$). As shown by a *t*-test, the differences arose entirely from the fluctuation in internal temperature on days when bats were present during the periods of pregnancy and lactation ($t = 2.20$, $n_1 = 11$ and $n_2 = 13$, $P < 0.05$). Concerning the internal temperature, it was slightly higher during pregnancy than during lactation (Fig. 5). But the fact that external temperature was significantly higher in lactation than in pregnancy ($t = -3.81$, $n_1 = 11$ and $n_2 = 13$, $P < 0.001$) excludes its direct dependence on internal temperature. This indicates that different internal temperature could reflect differences in thermoregulatory strategies between pregnant and lactating females rather than different external temperature. To verify this result, we analysed the same microclimatic parameters on the days when bats were absent from the boxes. In such cases, insignificant differences were found among periods of the reproductive season (pregnancy, lactation, post-lactation) (ANOVA, $F_{2,\ 249} = 0.49$, $P >> 0.05$). Differences in internal temperatures between boxes occupied and not occupied by bats were insignificant during both pregnancy (*t*-test,

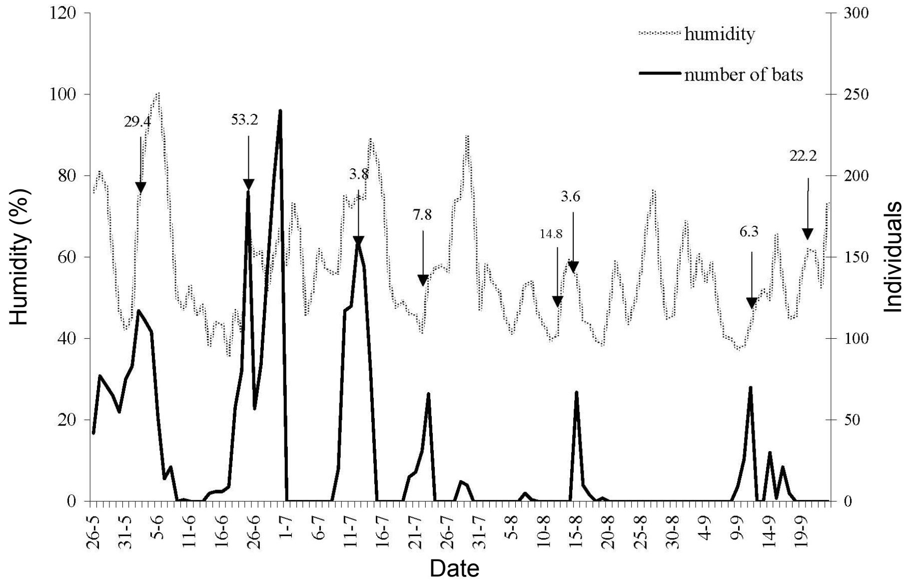

FIG. 4. Changes in internal humidity and number of bats. Pointers show days with daily sum of the precipitations higher than 2 mm. Numbers above pointers are precipitation values in mm. Progress in internal humidity along with bats occurence is noticeable during the pregnancy and lactation periods (until 7th July)

$t = 0.49$, $n_1 = 15$ and $n_2 = 13$, $P > 0.05$) and lactation ($t = 0.34$, $n_1 = 8$ and $n_2 = 19$, $P > 0.05$).

During the pregnancy period, the mean humidity (71.7 ± 19.4%) was higher than during lactation (55.1 ± 11.8%). During the lactation period, humidity was significantly higher in occupied than in not occupied boxes (t-test, $t = 3.49$, $n_1 = 8$ and $n_2 = 19$, $P < 0.05$), but insignificant differences were found during pregnancy ($t = 0.58$, $n_1 = 15$ and $n_2 = 13$, $P >> 0.05$).

Comparison of Microclimatic Parameters and Bat Numbers among Bat Boxes

Analysis of variance showed significant differences in microclimatic parameters and numbers of bats among particular bat boxes (ANOVA, $F_{2, 330} = 159.63$, $P < 0.001$). Students t-tests were used to investigate the impact of individual parameters. Significant differences (in all cases $n = 214$) were found concerning external temperature ($t = 2.10$, $P < 0.05$), humidity ($t = -6.25$, $P < 0.001$) and number of bats ($t = -8.60$, $P < 0.001$); no difference was revealed in internal temperature ($t = -0.45$, $P >> 0.05$).

Throughout the season, the numbers of bats roosting in the boxes differed significantly (ANOVA, $F_{2, 330} = 20.45$, $P < 0.001$). However, insignificant differences were revealed by the paired test used to compare

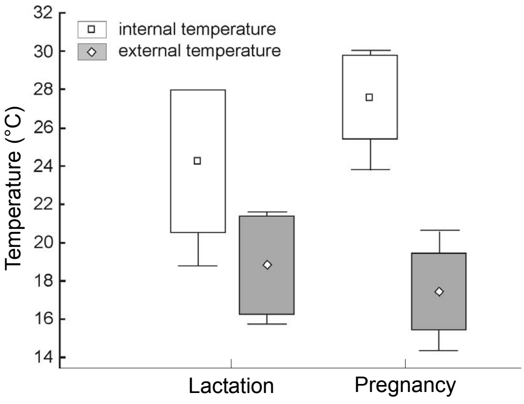

FIG. 5. Differences in external and internal temperatures found between pregnancy and lactation period. Internal temperature, when bats are present, was significantly higher during pregnancy than during lactation. Mean — central tendency, SD — large box, and min–max range as 'whiskers'

the number of bats in a box the day before the bats had left it, with the numbers of bats in the remaining two boxes the following day (Friedman ANOVA, $\chi^2 = 5.57$, $n = 14$, $P > 0.05$). During the lactation period, the largest number of bats was observed in the box showing highest internal temperature (20.5 versus 18.3 and 18.4°C; ANOVA, $F_{2,27} = 8.76$, $P < 0.001$).

Discussion

Changes in Microclimatic Parameters over The Season

Bats of temperate zones, when reproducing, may have strict thermoregulatory requirements on their shelters because low roost temperatures induce torpor, which can delay the development of embryos and offspring (Racey and Swift, 1981; Kunz, 1982; Wilde *et al.*, 1995). For heterothermic bats living under conditions of cool climate, warm roosts are very important and allow them to extend their natural range (Kunz, 1982). Lactating females may sometimes choose warmer roosts to avoid torpor, whereas pregnant females sometimes choose cooler roosts to decrease their thermoregulatory costs (Lewis, 1996; Kerth *et al.*, 2001). In contrast to the actual opinion, we found that the internal temperature of bat boxes with animals inside was higher during pregnancy than during the lactation period. In our study area, females were able to become torpid also during lactation, not only during pregnancy. Our observations come from similar (even lower) altitude (170 m a.s.l.) in central Europe as the study areas of authors who offered similar results (e.g., Kerth *et al.*, 2001; Heise 2005), therefore they are fully comparable. Heise (2005) found lactating females of *P. pygmaeus* to be able to go into torpor, frequently in periods with low temperatures. The negative correlation between low internal temperature and presence of a large number of bats could also be the consequence of their flying off when the bat box was overheated. It seems that high internal temperature is the factor restricting occupation of roosts during pregnancy and lactation periods (Weigold, 1973). We cannot assume that box overheating is a possible risk, because the test of internal temperature between occupied and non-occupied boxes was insignificant. We found empty boxes when internal temperature reached above 40°C at all times (cf. Kerth *et al.*, 2001; Lourenço and Palmeirim, 2004). Box overheating may not be so dangerous if a sufficient supply of alternative roosts, mainly tree cavities, are available in the vicinity. Awareness of natural and/or artificial roosts facilitates the maintenance of thermal comfort due to roost switching which, at the same time, strengthens the social relationships.

Keeping other predictors constant, presence of bats in bat boxes significantly influenced internal temperature and humidity even despite of high variability of microclimatic conditions throughout pregnancy and lactation periods. The comparison of internal temperatures in the days when boxes were and were not occupied shows differences in bat thermopreferences during the season. This fact complicates the use of internal temperature as an indicator of bat presence in the roost. Despite our expectation, internal humidity indicated much better the presence of bats, especially when large numbers of bats were present in a box. Internal humidity positively correlated with the number of bats due to their respiration.

Changes in The Occurrence of Bats

Previous studies have shown that a colony of bats can occupy a complex of tree cavities in one area (e.g., O’Donnell and Sedgeley, 1999; Cryan *et al.*, 2001). Many of the arguments about roost switching in tree dwelling bats are based on predator avoidance, impact of parasites (Wolz, 1986) or finding large numbers of short-lived roosts (Barclay and Brigham, 2001), but also on microclimatic conditions (Kerth *et al.*, 2001).

The data obtained from infrared activity readers show the highest median numbers of bats in boxes during pregnancy, while they were usually lower during the lactation and post-lactation periods. After weaning the numbers of bats fluctuated considerably. The boxes can be used by weaned young either as temporary night roosts or as shelters for several days, due to the increased competition for warmer roosts (Entwistle *et al.*, 1997). At that time, bat boxes were occupied by only few non-reproducing adults during most of the days.

Concerning *P. pygmaeus*, this could be confirmed by records of its high flight activity in close vicinity of a big shelter throughout the season, although the bats did not use the shelter at every recording (Bartonička and Řehák, 2004). Among European bats, the fission-fusion model was shown by *M. bechsteinii* groups (Kerth and König, 1999), but this may not apply to other tree dwelling species (Willis *et al.*, 2003). We found small fluctuations in the numbers of bats in particular bat boxes during pregnancy. In the same period, Willis and Brigham (2004) found a higher roost-sharing index for female *Eptesicus fuscus*. High metabolic activity dependent on high internal temperature positively influences embryo development speed (Racey and Swift, 1981). On the other hand, reproductive stage and information exchange can enhance the sharing of a low number of cooler roosts by females facilitating their torpor during early pregnancy (Kerth and König, 1999).

Numbers of females in colonies determine an effectivity of thermoregulation and affect the level of roost switching (Haddow, 1993; Barlow and Jones, 1999). In the Czech Republic, lower mean numbers of female *P. pygmaeus* in buildings were found (65 individuals, authors' personal observations) than in Britain (200 individuals — Barlow and Jones, 1999). The size of colonies roosting in natural roosts is even lower than in buildings. Therefore smaller colonies roosting partly in hollows may switch roosts more often due to difficult thermoregulation than larger colonies roosting in stone buildings e.g. in Scotland (Haddow, 1993).

Positive impacts of thermally different roosts can have important implications for the management of bat populations via their shelters in forests. Not only must large numbers of natural hollows be maintained, but enough bat boxes also have to be recruited. On the other hand, bat boxes alone can be insufficient for successful reproduction of bats in monoculture forests with little or no natural cavities of adequate space. Our data are consistent with the theory of Willis and Brigham (2004). Bats roosting in caves or big spaces in buildings are in a situation different from tree-roosting bats because the shelters fulfill their microclimatic requirements. Tree-roosting bats are dependent on shelters with different microclimate and must often switch among several cavities or boxes. Pipistrelles (both *P. pipistrellus* and *P. pygmaeus*) are classified as hemi-synanthropic species, the nursery colonies of which usually roost in buildings. But concerning *P. pygmaeus*, it seems that the roosts in buildings do not provide them with microclimatic conditions suitable for the whole reproduction season. They therefore choose the strategy of roost-switching, typical of forest-roosting bats.

ACKNOWLEDGEMENTS

We are very grateful to J. Gaisler, R. Obrtel and anonymous reviewers for valuable comments on the manuscript. V. Hanák and H. Jahelková are heartily acknowledged for their unpublished data of colonies and D. Motl for his effort in the development of the IR gate. M. Konečná provided excellent assistance in the field. The study was supported by the grants of Grant Agency of the Czech Republic No. 206/02/0961, 206/06/0954 and the grant of Ministry of Education, Young and Sports of the Czech Republic No. MSM0021622416.

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Received 25 September 2006, accepted 23 June 2007