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ORIGINAL PAPER

Seasonal dynamics in the numbers of parasitic bugs (Heteroptera, Cimicidae): a possible cause of roost switching in bats (Chiroptera, Vespertilionidae)

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Abstract The objective of the present paper is to extend the knowledge of roosting strategies of bats and the interaction of bats with their roost ectoparasites, the bat bugs *Cimex pipistrelli*. The project was focussed on the potential causality of bat movements and the variation in bug numbers. For 2 years, three model bat boxes with breeding female *Pipistrellus pygmaeus* were monitored inside floodplain forest. After the arrival of bats in May, adults and first instars of bugs were observed in the boxes. During the lactation period in June, when the bats did not occupy the roosts, the first instar bugs died out followed by the adults. The decrease in bug numbers began only several days after the bats had left the boxes. After a month of the bats' absence, the abundance of adult bugs decreased by half of their number. Only the eggs survived the period when the roosts were unoccupied in summer. In mid-July, after the arrival of lactating females, an increase in the number of bugs was observed. At the beginning of August, however, no new eggs were found. Although adult *C. pipistrelli* are able to survive the winter period in the boxes, the bats, by shifting the roosts within the vegetation season, prevent the massive reproduction of these parasites.

Introduction

Previous studies were mostly focussed on communities of ectoparasites of different bat species with no regard to their life strategies (e.g. Whitaker and Mumford 1978; Whitaker et al. 2000; Ritzi et al. 2001; Ritzi and Whitaker 2003). Few papers described the relationship between ectoparasite density and the reproductive cycle of its bat host (Dietz and Walter 1995; Christe et al. 2000). There are several studies in which the impact of ectoparasites living permanently on the host body (e.g. mites, Spinturnicidae) was analysed (Lewis 1996; Giorgi et al. 2001). Bugs of the family Cimicidae are the most important roost ectoparasites of bats. The family includes 91 species, 61 of which parasitize bats (Ryckman et al. 1981). Great mobility and ability to survive without their hosts for a long time makes the bugs important model ectoparasites, not only of bats (Usinger 1966). Several authors dealt with the taxonomy of bugs parasitizing bats, yet unsolved problems persist, including the status of *Cimex lectularius* and *Cimex pipistrelli* (Wendt 1941; Povolný 1957; Usinger 1966; Péricart 1972; Aukema and Rieger 1995–1996; Péricart 1996). In this paper, both taxa mentioned above are regarded as separate species.

Fast ontogeny enables the bugs to increase their numbers rapidly soon after a roost was occupied by bats. Due to the fact that it is also parasitizing man, the bed bug (*C. lectularius*) is the best-known cimicid species. Female bed bugs usually lay from two to four eggs per day. During its life, a single female can lay as much as 500 eggs (Davis 1964). Bed bugs suck blood in periods of few days and are able to starve for months (maximum 1.5 year). Due to their long starvation capacity, bed bugs survive the winter period or the absence of the host in its roosts (Johnson 1942; Povolný 1957). Usinger (1966) found that the temperature and humidity in the roost influences the survival of all ontogenetic stages and the promptness of adults to copulate. Bugs in general prefer lower roost temperature than other bat parasites do because they stay on bats for a short time to feed only (Usinger 1966). At present, scant information is available on the possible impact of microclimate fluctuation

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and the length of starvation on the survival of particular ontogenetic stages and adults of the two sexes (Rivnay 1932; Johnson 1940; Omori 1941).

Nursery colonies of several bat species dwelling in crevices of trees, hides or buildings switch roosts frequently during the reproduction season (e.g. Thompson 1990 in pipistrelles or Kerth and König 1999 in *Myotis bechsteinii*). In the territory of the present Czech Republic, the bugs (Cimicidae) were found in roosts occupied by *Pipistrellus pipistrellus* s.l. (Gaisler 1966; Hůrka 1988). New observations show that bat bugs *C. pipistrelli* occupy the roosts of two pipistrelle species, *P. pipistrellus* and *Pipistrellus pygmaeus* (Bartonička, unpublished). As in *P. pipistrellus*, females of *P. pygmaeus* switch roosts very often. Typically, groups of females leave their respective roosts in early June and move to the main nursery roost few days before parturition. They move back to their previous roosts with flightworthy juveniles in mid-July (Swift 1980; Webb et al. 1996). The so-called fission–fusion model common in primates, i.e. a temporary splitting of one nursery colony into sub-groups, was described in *M. bechsteinii* (Kerth and König 1999; Willis and Brigham 2004). Similar roost switching strategy was observed in *P. pipistrellus* and *P. pygmaeus* (Feyerabend and Simon 2000, own observation). Sub-groups of genetically close females occupied a complex of tree hollows and bat boxes within a small area and switched roosts every 2 days (Willis and Brigham 2004). Although the fact of roost switching was demonstrated, the cause or causes of this phenomenon were not understood completely till now (e.g. Lewis 1995; Vonhof and Barclay 1996; Brigham et al. 1997). There are several hypotheses explaining why bats switch their roosts. The movements may be caused by sudden changes in microclimatic conditions, restricting the circulation of air inside a crevice type shelter (Whitaker 1998; Lourenço and Palmeirim 2005) or changes in thermoregulatory requirements of bats regarding their reproduction cycle (pregnancy vs lactation) (e.g. Thompson 1990; Hamilton and Barclay 1994; Kerth et al. 2001). In addition, the impact of humans, animal predators or unknown factors can disturb bats (Lewis 1995).

In our study, we focussed on a hypothesis assuming that by switching roosts the bats avoid the increasing invasion by ectoparasites and keep their individual fitness (Wolz 1986; Lewis 1996). The large numbers of ectoparasites observed on adult females and young after parturition show synchronisation of the population cycles of ectoparasite and host. Seasonal changes in the numbers of *C. pipistrelli* in semi-natural roosts were evaluated regarding the presence of bats. We attempted to answer the following two questions: (1) Do temperature and humidity influence the numbers of bat bugs in the roosts? (2) Is there any correlation between the numbers of bats and bat bugs? We think that the data on roost infestation by parasites together with the knowledge of other parameters such as the microclimate of occupied roosts (Lourenço and Palmeirim 2005; Bartonièka and Øehák 2007) can be utilised for the purposes of conservation of bats and their shelters.

Materials and methods

Study area and technical equipment

Nursery and temporary colonies of *P. pygmaeus* with high densities of bat bugs *C. pipistrelli* were monitored in three wooden bat boxes inside the Křivé jezero floodplain forest (S Moravia, Czech Republic) for 2 years. In the first growing season (2004), all bat boxes were equipped with passive IR Trail Monitors, TM (TM550, TrailMaster, Goodson & Associates, USA) (after Thomas 1995) and thermometers (Hobo, Onset Computer Corporation) to record the presence of bats and the temperature in the boxes over the season. TM monitors were situated in front of the entrance to each box (Bartonička and Řehák 2007). Hobo Data Loggers continuously recording internal temperature and internal humidity were situated under the roof of each bat box. The accuracy of the relative humidity sensor was ±4% and that of the temperature sensor ±0.4°C. Monitoring of bat bugs was carried out by manually sampling from inside the box roof and recording the activity of insects by a video system (B/W AVC 307R+12 IR diode). In each of the three boxes, the IR diode camera monitored a particular inside area (3 × 10 cm) and recorded the relative activity of bugs in 30 min periods. All monitoring was carried out regularly in 10-day periods just before most bats left a particular bat box to limit the effect of human disturbance. Each sample of bat bugs was divided into four groups: (1) adults, males and females together, (2) first to third instars, (3) fourth and fifth instars and (4) eggs. Females prevailed among the adult insects. In each group, the number of bugs was recorded. Bug movements within the experimental inside area scanned by the camera were counted regardless of the groups.

The reproductive season under study was divided into three parts: pregnancy (till 6 June), lactation (7 June till 6 July) and post-lactation (since 7 July). The time of parturition was indicated by the presence of seven newborns in one of the three boxes.

Statistical analysis

No significant differences were found between the two seasons, 2004 and 2005, which allowed to pool the data. All variables showed a normal distribution (Kolmogorov–Smirnov test). Statistics for Windows 7.0 was used for data analyses (PCA, ANOVA, *t* tests, correlations). The level of morning bat activity (returning from foraging flights at 1–5 AM) (Trail Monitors) positively correlated with the number of bats found in a box later during that day when the boxes were checked manually (Pearson's correlation coefficient, $r=0.73$, $p<0.05$). The numbers of bugs, revealed from records of their activity by a video system, positively correlated with that obtained by manual sampling from inside the box roof ($r=0.84$, $p<0.05$). No significant differences were found in the numbers of bugs and presence of bats between particular bat boxes (ANOVA, number of bugs, $F=0.57$, ns; presence of bats, $F=2.10$, ns), therefore the data were pooled. Analysis of variance (ANOVA) was used to check the differences between the parts of season and *t* test as post hoc. Principal component analysis (PCA) was used to check the effect of partly correlated variables (internal temperature, internal humidity, numbers of bugs and bats). The model was fitted by means of microclimatic parameters from the light part of the day and the number of bats using a particular bat box as their day roost. Bonferroni correction was applied if multiple tests were used for the same data set.

Material

During the two growing seasons, the three bat boxes occupied by soprano pipistrelles (*P. pygmaeus*) were monitored for 151, 199 and 115 days, respectively. For each day, hourly values were available for internal temperature, internal humidity and the level of the bats' activity. The samples of bat bugs (*C. pipistrelli*) were taken on 19 occasions.

Results

Seasonal changes in the occupancy of bat boxes

The differences in the numbers of bugs and presence of bats among 19 checks were statistically significant (ANOVA, $F=1.89$, $p<0.01$). Two peaks in the occupancy of boxes by bats were recorded in May and August. Pregnant females used these roosts before parturition and some of them returned with flightworthy young (Fig. 1). During the pregnancy of bats until the parturitions in mid-June, a significant increase in the number of bat bug eggs was recorded (*t* test, $t=-6.69$, Bonferroni correction, $p=0.001$, $n_1=3$, $n_2=3$). A significant decrease was found from early June until the end of July. No bug eggs were found on subsequent checks (Fig. 1). The number of adult female bugs, surviving from previous winter, decreased until mid-June ($t=-83.59$, Bonferroni correction, $p=0.001$, $n_1=3$, $n_2=3$) when they died out. Only nymphal stages were present in the boxes during the first half of August. A rapid increase in the number of adult bugs was registered after the bats, mainly young ones, returned to the boxes in mid-August ($t=-3.34$, Bonferroni correction, $p=0.01$, $n_1=3$, $n_2=3$). After mid-September, when the metamorphosis of the last (fifth instar) nymphae was completed, the number of adults stagnated. Only adults survived the winter period. Two peaks in the presence of bats were distinct throughout the season. The first peak during pregnancy, however, was insignificant (*t* test, $t=2.03$, Bonferroni correction, ns, $n_1=3$, $n_2=3$). During the lactation period, the number of bats in the boxes was very low. A significant increase was found from the beginning of July until the second half of August ($t=-1.54$, Bonferroni correction, $p=0.001$, $n_1=3$, $n_2=3$) (Fig. 1). During the period in which the bats were absent (lactation, June), a rapid dying of the early stages of bugs (first to third instars) was recorded. After all the bats had left, the abundance of this bug group decreased to a half in 9 days. A similar decrease in the number of fourth and fifth instar bugs was observed in 16 days. Likewise, the number of adults decreased to less than a half during the absence of bats. In general, the population of bat bugs survived the summer absence of bats in the egg and nymphal stages.

Relationship among particular variables

Internal temperature, relative humidity, number of bugs (adults, first to third instar, fourth and fifth instar), number of eggs and number of bats were included in the principal component analysis. The first two factors accounted for 78.8% of variability. Table 1 shows the relations of individual components and variables. The cluster of days during bat pregnancy differed due to the positive correlation of component 1 with the number of adults and first to third instar bugs and due to the negative correlation with the number of eggs, which increased rapidly in these days. A large number of eggs were also observed during lactation, but nymphal and adult bugs and bats were found in very low numbers. The cluster of days in the post-lactation period was characterized by positive correlation of numbers of adult bugs and bats at the absence of eggs (Fig. 2). Furthermore, significant differences using discrimination analysis were found related to the reproduction period (Wilks' $\lambda=0.34$, $F=2.91$, $p<0.002$).

A positive correlation was found between the number of adult and fourth and fifth instar bugs (Pearson's correlation coefficient, $r=0.52$, $p=0.005$) and between the number of eggs and number of individuals of first to third instar ($r=0.33$, $p=0.001$). The number of eggs and relative humidity correlated negatively ($r=-0.37$, $p=0.01$). The presence of bats positively correlated with the number of first to third instar bugs ($r=0.39$, $p=0.001$). The possible impact of temperature on the number of bugs was tested. A positive correlation was found only between the internal tempera-

Fig. 1 Changes in numbers of bat bug adults, all instars and eggs, and numbers of bats; mean—central tendency, SD—large box

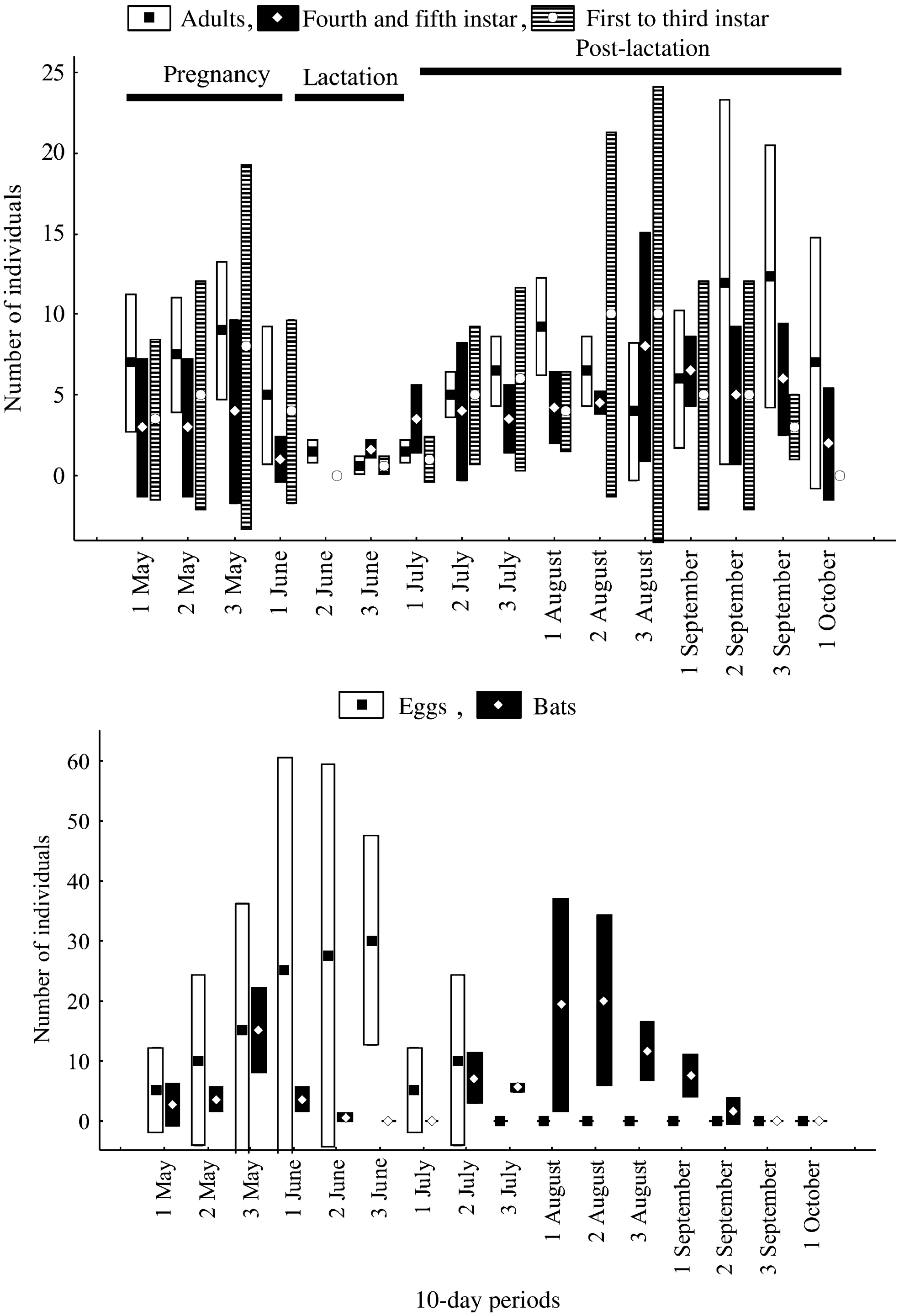

Table 1 Correlations (Pearson's correlation coefficient) between variables and components of PCA

	A	B	C	D	Bats	Tin	Hum
Component 1	0.68*	0.47*	0.39*	−0.69*	0.46*	0.04	0.34*
Component 2	0.23	−0.27	0.25	0.21	0.05	−0.62*	0.05

A: adult bed bugs, *B*: fourth and fifth instars, *C*: first to third instars, *D*: eggs, *Tin*: internal temperature, *Hum*: relative humidity. *$p<0.05$, all values are significant.

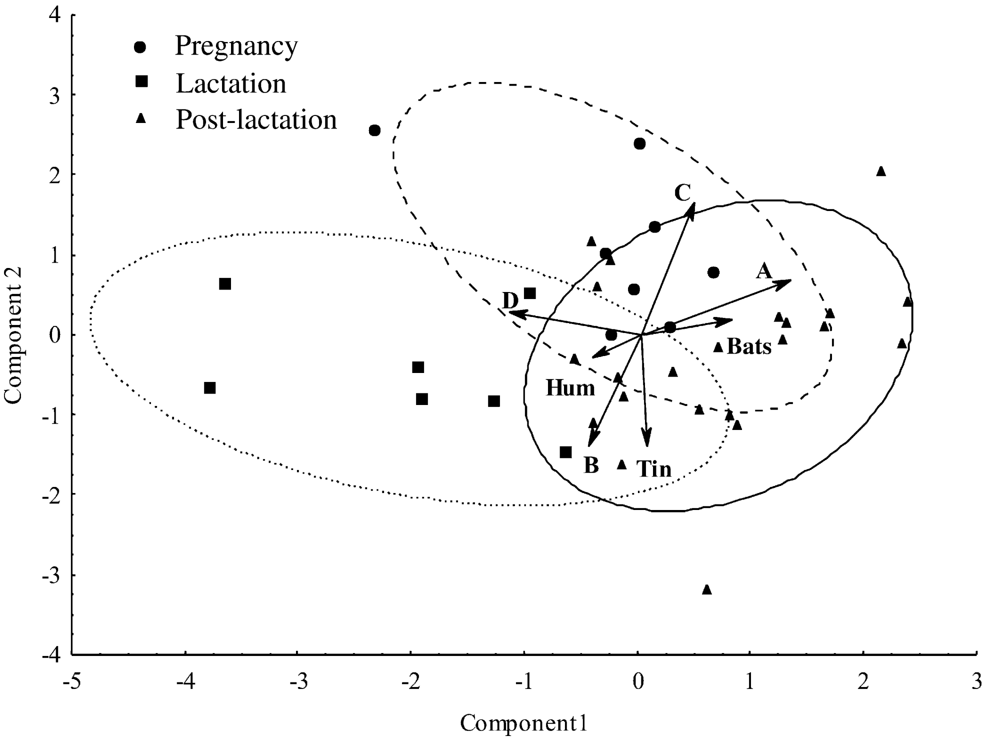

Fig. 2 Principal component analysis (PCA): on the axes are values of the two first factors (describing 78.8% of inner variability). *Ellipses* represent the 75% confidence interval for the days of the reproduction periods—pregnancy (*dashed line*), lactation (*dotted line*) and post-lactation (*solid line*). *A*: Adult bat bugs, *B*: fourth and fifth instars, *C*: first to third instars, *D*: eggs, *Tin*: internal temperature, *Hum*: relative humidity

ture 10 days before the checks and the number of first to third instar bugs (Pearson's correlation coefficient, $r=0.41$, $n=38$, $p<0.005$).

Discussion

Microclimatic conditions

From among various environmental factors, temperature seems to be the most important because it influences the development and activity of bugs. In most roosts, temperature varies significantly during both the season and the day, being rather constant only in large caves and similar shelters (Usinger 1966). In this paper, however, nearly no correlation between the temperature and the number of bat bugs was revealed. The only exception was a positive correlation between the temperature in the boxes and the number of early developmental stages of bugs found 10 days later. This may have been due to the accelerated embryonic and nymphal development at optimum temperature. In contrast to *C. lectularius*, no information is available concerning the response of *C. pipistrelli* to various microclimatic conditions (e.g. Rivnay 1932; Johnson 1940; Omori 1941) but the main aspects may be similar in the two species. In *C. lectularius*, the embryonic development is accelerated by temperature increasing up to 30°C, when it is the shortest (3.7 days, Omori 1941). The upper temperature limit, blocking the hatching, nymphal development and adult activity, is 37°C in *C. lectularius* (Omori 1941). Mortality sets in at 44–45°C (Hase 1917) but for a short time, in the order of hours, bed bugs are able to survive even such high temperatures. During our study, the temperature in the boxes reached values of this kind on 13 days yet the daily mean temperature never exceeded 30°C. Laboratory testing is required to reveal the impact of temperature on the timing of development in bat bugs.

Relative humidity of air is another factor that possibly influences the seasonal dynamics of bat bugs. The experiments with *C. lectularius* suggested that in some instars their development was shortened at 32°C when the humidity was low; in contrast, at 22°C the development was shortened when the humidity was high (Rivnay 1932). According to Kemper (1936), extremely low relative humidity (0–20%) often causes the death of nymphae in the course of ecdysis. The negative impact of low humidity on the first instar may even be greater. At relative humidity <60%, its survival is reduced to a fifth (Jones 1930). Mortality is caused by dehydration (Mellanby 1932). In the bed bug, both high and low temperatures when combined with high humidity cause up to 90% mortality of eggs (Johnson 1940). Correspondingly, the results of our study on the bat bug show negative correlation of the number of eggs with relative humidity. The combination of low temperature and high humidity was typical for the post-lactation period when no new eggs were recorded. As indicated by the results of laboratory experiments with *C. lectularius*, the survival of eggs of *C. pipistrelli* during the humid autumn season is reduced if not impossible. The hibernation of adults and not of eggs, therefore, could be an adaptation to the cold and humid climate of the temperate zone.

Availability of food

In the bed bug, the availability of food affects oviposition, duration of individual instars and total length of life (Usinger 1966). The frequency of bloodsucking is positively correlated with temperature, e.g. every third day at 27°C in adults (Kemper 1936). The nymphae are able to feed 24 h after ecdysis but they suck in shorter intervals than the adults do. Concerning various developmental stages, early instars are the most vulnerable if they do not have enough food. Food deficiency has a negative impact mainly when ambient temperatures are high. Such temperatures, though not yet lethal, force the bugs to suck more often because they prevent bug torpidity and increase the danger of dehydration. The availability of food affects the weight of a particular adult female, which is positively correlated with the number of eggs laid. When feeding regularly twice a week, the females produce 2.76–8.26 (average 5) eggs per week for about 18 weeks (Johnson 1942). The adult life span may encompass 12–18 months and after harvesting, they usually die (Usinger 1966). The results of this study correspond to these data in that the early instar bugs will die soon after their hosts have left the boxes and no eggs were found at the end of July. The presence of pregnant female bats after the end of April is essential to start the process of gradation of the bug numbers and assure the production of sufficient number of eggs that will survive the absence of bats during lactation.

Impact of bugs on bats

Abundant bat bugs may induce heavy stress to their hosts. The trouble they cause may lead to disquiet of bats resulting in their abnormally frequent scratching, cleaning of fur and wing membranes and efforts to catch the parasites on their body. Several authors argue that the increased number of roost parasites forces the bats to leave the roost and find another one (e.g. Wolz 1986; Lewis 1996; Walter 1996). Roost switching seems to be a good anti-parasitizing strategy of bats with respect to *C. pipistrelli*. This bug species was by far not recorded in all maternity colonies of bat species known as its potential hosts. According to Reinhardt and Siva-Jothy (2007), only 12% of *Myotis myotis* colonies were parasitized by *C. pipistrelli*. In shelters of bat species preferring tree hollows and various fissures in summer, such as *P. pipistrellus* and *Nyctalus noctula*, the presence of bat bugs was recorded more often (K. Hůrka, unpublished). However, it is more difficult to check fissure-like roosts than spacious shelters such as lofts of buildings for the presence of bugs. At present it seems that in the territory of the Czech Republic, *C. pipistrelli* is common in “fissure” bat species that often change their roosts, while *C. lectularius* occurs rarely and only in “space” bat species with a high degree of philopatry to their summer shelters (O. Balvín, unpublished). Further research is needed to specify the differences in seasonal dynamics between the two species of bugs.

In Europe and North America, the highest abundance of bat ectoparasites has usually been recorded in the second half of May when maternity colonies of bats are well-established (e.g. mites, Estrada-Peña et al. 1991; Lučan 2006). The simultaneous use of more shelters by females coming from one colony was observed in certain bat species during pregnancy (e.g. Kerth and König 1999; Willis and Brigham 2004). Shortly before parturition, heavily pregnant females return to their original large maternity shelter. They give births there and suckle their young. Among other initially tree bats, this is also the case of pipistrelles (Swift 1980). During the lactation period, most satellite roosts are empty (bat-free). The present study shows that the absence of hosts, coupled with high temperatures and natural mortality of parasites reduces the number of bat bugs in bat boxes to less than a half of the number recorded before the bats left. Immature bugs die almost totally. However, why do female bats return to the satellite roosts after lactation and perhaps show them to their young in spite of the previous bad experience with bat bugs? The answer may be that the roost selection of female bats is governed by their thermopreferendum: they seek thermally optimum shelters that differ within their reproduction cycle (Thompson 1990).

The bugs are not the only ectoparasites of temperate bat species. Very likely, bat anti-parasitizing strategies against mites, fleas, nycteribids and bugs are mutually different. In bat species parasitized mainly by spinturnicid mites, e.g. *Miniopterus schreibersii* and *M. daubentonii*, the course of clustering and shift of shelters of reproducing females during the season is different from that in bats parasitized mainly by bugs (Estrada-Peña and Serra-Cobo 1991; Dietz and Walter 1995). To conclude, the study shows that pipistrelle bats are able to prevent the massive reproduction of bat bugs by temporarily abandoning particular roosts. Nevertheless, they are unable to rid their roosts of the ectoparasites completely, which is the obvious consequence of the co-evolution of *Pipistrellus* bats and *Cimex* bugs under the conditions of the temperate climate.

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