

Recolonization of bat roost by bat bugs (*Cimex pipistrelli*): could parasite load be a cause of bat roost switching?

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Received: 18 October 2012 / Accepted: 21 January 2013 / Published online: 6 February 2013
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Abstract Roost ectoparasites are believed to have a negative impact on fitness of their hosts as birds or mammals. Previous studies were mostly focussed on the synchronization between reproduction cycles of ectoparasites and hosts living in infested roosts. However, to date, it has not been examined how fast ectoparasites colonize new, non-infested roosts and thus increasing the impact on the local populations of hosts. The parasite–host model was studied, including bat bugs *Cimex pipistrelli* and soprano pipistrelles *Pipistrellus pygmaeus*, where bat behaviour was observed which tended to reduce the parasite load in bat roosts. We investigated (1) whether bats change their roosting behaviour when we discontinued synchronization of their reproduction and the life cycle of the bat bugs and (2) how fast and which stages of bat bugs reoccupy cleaned roosts. In a 3-year field experiment, we removed all bat bugs from six bat boxes in each spring. Pipistrelles bred young in all non-infested boxes during these 3 years. In addition, 8 years of regular observations before this experiment indicate that bats avoided breeding in the same bat boxes at all. Bat bugs were found again in clean boxes in mid-May. However, their densities did not maximise before the beginning of June, before parturition. A re-appearance of bugs was observed after 21–56 days after the first bat visit. Adult bugs, mainly females, colonised cleaned boxes first though at the same time there were a lot of younger and smaller instars in non-manipulated roosts in the vicinity.

Introduction

Roosts and their availability play a crucial role in bat ecology (e.g. Russo et al. 2004). Females have evolved to spend at least part of their lives roosting together in nursery colonies. Regarding the different requirements during reproduction, there is growing interest in identifying roosting strategies (Kunz and Lumsden 2003). A number of studies have provided critical insights into roost switching and have suggested several reasons for why bats change roosts, i.e. to minimize the costs of thermoregulation (e.g. Kerth et al. 2001, Willis and Brigham 2005), to reduce the risk of predation (Vonhof and Barclay 1996) and to allow for an optimal group size and increased survival (e.g. Barclay and Kurta 2007). Roost switching in bats is often phenomenon, is known as fission-fusion (Kummer 1971), where a social unit of roosting bats may split into several subunits when the bats select their diurnal roosts (e.g. O'Donnell 2000). Under this scenario, roost sharing and switching between roosts within a local area could serve to increase the knowledge of potential trees for roosting and/or maintain cohesiveness of the colony (e.g. Willis and Brigham 2004).

However, pipistrelles do not switch roosts as many times as typical forest species, e.g. *Myotis bechsteinii* or *Eptesicus fuscus*, where the causes of roost switching most probably relate to the fission-fusion social organization (Kerth and König 1999; Willis and Brigham 2004), although some roost selection to avoid ectoparasites was observed in tree-dwelling species like *M. bechsteinii* (Reckardt and Kerth 2007). Pipistrelles usually only switch roosts two to three times in one season, according to the reproduction phase. Typically, groups of females leave their respective roosts in early June and move to the main nursery roost a few days before parturition. They move back to their previous roosts with flightworthy juveniles in mid-July (Webb et al. 1996). Therefore, we think that there may be a cause other than

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social demands for this behaviour, which is probably related to a reduction in the parasite load. When leaving the shelter should lead to a reduction of parasite load, it is advisable to find out how long it will take for bugs to occupy new or abandoned roosts, and when they reach there the maximum population.

Avoiding infested habitats is known to be the most effective behavioural parasite defence strategy in order to reduce costs associated with infestation (e.g. Christie et al. 1994; Moore 2002). Most studies on bat ectoparasites have dealt with different species and their ontogenetic stages that permanently live on their hosts' bodies (e.g. Gannon and Willig 1995; Giorgi et al. 2001; Dick et al. 2009). These studies are not sufficient to elucidate the correlation between parasite load and roosting strategies related to movements within and outside the shelters. Probably only such strategies could be effective when avoiding pressure from ectoparasites that spend on the body of their host a short time only and have low ability to colonize new host roosts. Therefore, as an improved model, we chose bat bugs (*Cimex pipistrelli*) which, except for the time they spend engorging, mostly co-habit without physical contact with their hosts and are rarely found on bats netted out of roosts (Reinhart and Siva-Jothy 2007).

Currently, it is unknown whether roost switching is an adaptation for reducing parasite load or whether the observed decrease in the number of parasites (e.g. Bartonička and Gaisler 2007) is only a side effect of switching. Prior to this field experiment, there were no bat boxes and no non-fledged young bats. Pipistrelles leave the roosts just before parturition because of a growing parasite load or different microclimatic demands during pregnancy and lactation (Bartonička and Řehák 2007). Bats can monitor the level of roost infestation during their repeated visits during pregnancy and choose a roost with a relatively low parasite load or even with none at all (Reckardt and Kerth 2007). The odour produced by bat bugs is very intense and is probably easily distinguishable by bats even outside the roost (Usinger 1966). Females become torpid more often during pregnancy than during lactation, and therefore are less available for bat bugs (Montes et al. 2002). Populations of bat bugs usually reach the first gradation at the end of May (Bartonička and Gaisler 2007). Laboratory experiments showed higher levels of infestation in young bats than in adults. The movement of females to non-infested roosts just before parturition could have an important role in the post-natal growth of the young and could be seen as a kind of maternal effect (Kunz and Stern 1995).

We present a field study in which a roost manipulation experiment was combined with a long-term study on the roosting strategies of pipistrelles (*Pipistrellus pygmaeus*). The aim of our study was to determine whether or not the removal of bat bugs from infested roosts would lead to a

change in the roost selection pattern and whether or not the females would bear and wean young in roosts with no bat bugs. The goal of this paper was to reveal, by a simple field experiment, what is the speed of (re)colonization of new roosts and whether or not the parasite load is a possible cause of roost switching in this particular bat species.

Methods

Study area and technical equipment

Nursery and temporary colonies of *P. pygmaeus* with high densities of *C. pipistrelli* bat bugs were monitored in eight wooden bat boxes inside the Křivé jezero floodplain forest and the Bulhary game-hunting ground. Both of these localities belong to one woodland complex near Milovice village (Milovice Wood), in southern Moravia, Czech Republic. Milovice Wood is one of the largest remaining oakwoods in this part of the north-western fringe of the Pannonian Basin. All of the bat boxes were regularly observed from the year 2000: at least once at month. At the beginning of the season in 2003, all of the bat boxes were equipped with active infrared gates (IRG, Litschmann and Suchý, AMET, Czech Republic) or passive IR Trail Monitors, TM (TM550, TrailMaster, Goodson and Associates, INC., Kansas, USA) and thermometers (Hobo, Onset Computer Corporation, Southern MA, USA) to record the presence and/or numbers of bats and the internal and external temperatures inside/outside the boxes throughout the seasons. Monitoring of the bat bugs was carried out by manually sampling from inside the box roof. In each spring of 2008, 2009 and 2010, we removed all bat bugs from six bat boxes (three boxes in the Křivé jezero and three in the Bulhary game-hunting ground). Only IRGs were used to monitor the bats during these three seasons. One box in each locality was left alone; therefore, the normal life cycle of the bugs could proceed. In January, the manipulated bat boxes were inserted into plastic bags, to which several drops of benzene were added. The next day, we returned the bat boxes to their original places in the field. Hobo Data Loggers, which continuously recorded the temperature (internal and external) and the internal relative humidity, were situated under the roof of each bat box. The sensors that measured the external temperature were situated about 50 cm apart on each box. The relative humidity sensor had an accuracy of $\pm 4\%$, and the temperature sensor had an accuracy of $\pm 0.4\text{ }^{\circ}\text{C}$. All bat boxes were regularly monitored over 10-day periods just before the end of July to limit the effect of human disturbance. Each sample of bat bugs was divided into four groups: (1) adults, males and females, (2) first to third instars, (3) fourth and fifth instars, and (4) eggs (cf. Bartonička and Gaisler 2007). The number of bugs in each group was recorded. The

number of young present was evaluated. The reproductive season studied was divided into three parts: pregnancy (up until June), lactation (7 June to 6 July) and post-lactation (from 7 July). In each season, the time of parturition (8 June 2008, 3 June 2009 and 15 June 2010) was indicated by the presence of the first newborns.

Statistical analysis

All variables showed a normal distribution after log transformation (Kolmogorov–Smirnov test). Statistics for Windows 9.0 was used for the data analyses (GLM, ANOVA, logistic regression). The level of returning and emerging bat activity (returning from foraging flights at 1:00–5:00 a.m.; Trail Monitors) positively correlated with the number of bats (IRG) found in the boxes (Pearson's correlation coefficient, $r=0.81$, $P<0.05$); therefore, the number of bats roosted in boxes during the day could be estimated. Analysis of variance (repeated measures ANOVA) was used to check for differences between the levels of bat activity, and logistic regression was used to test for changes in occupancy in the manipulated and non-manipulated bat boxes. Logistic regression was also used to check for differences between the internal temperature and bat numbers in different bat boxes.

Material

During the three seasons of 2008–2010, the six manipulated bat boxes occupied by soprano pipistrelles (*P. pygmaeus*) were monitored for 660 (2008, 110 days/box), 732 (2009, 122 days/box) and 780 (2010, 130 days/box) days, and two non-manipulated bat boxes for 216 (2008, 108 days/box), 194 (2009, 97 days/box) and 238 (2010, 119 days/box) days, respectively. On each day, hourly values of internal and external temperature, internal humidity and the level of the bat activity (presence/absence of bats, number of bats throughout the day, night exploring activity) were recorded. Samples of bat bugs (*C. pipistrelli*) were taken on 11 (2008), 9 (2009) and 13 (2010) occasions in each bat box. In addition, monthly observations of the numbers of bats and bat bugs were available for the 8 years preceding the present experimental study.

Results

Seasonal changes in occupancy of the bat boxes

No significant differences in number of bats were found between two localities (Křivé jezero and Bulhary), the seasons when the bat bugs were removed (GLM, $F=0.871$, NS, $df=2,154$; effect of bat box, Tukey test, $F=0.827$, NS; effect of season, $F=0.329$, NS) and among years when boxes were not manipulated (GLM, $F=0.331$, NS, $df=642$; effect of bat

box, Tukey test, $F=0.016$, NS; effect of season, $F=0.771$, NS), thus allowing us to pool the data to the two groups, i.e. manipulated and non-manipulated. Logistic regression showed significant differences in the patterns of bat box occupancy between the manipulated and non-manipulated boxes ($F_{(1, 2,171)}=30.48$, $p<0.001$; Fig. 1).

Exploration activity of the bats and bug transport

The use of infrared gates allowed us to evaluate the numbers of bats that roosted in the bat boxes during the daytime, when the bugs could suck onto the bats, but also the level of bat exploration activity overnight, when the bat bugs could be transported to clean boxes. Although the bats were not observed in manipulated bat boxes during the lactation period, a high exploration activity was noted during most of the nights. When we tested the exploration activity between the manipulated and non-manipulated bat boxes, significant differences were found (logistic regression; $F_{(1, 2,171)}=4.62$, $p=0.032$; Fig. 2).

In the non-manipulated boxes, from which bat bugs were not removed, two peaks in bat numbers were observed—at the end of May and at the end of July (Fig. 1). Although there were many overnight visits by the bats (Fig. 2b), no young were found in these boxes in any of the three experimental years. The manipulated bat boxes were re-occupied by adult bugs, mainly females, whereas many first to third instars were observed in the non-manipulated boxes. The first bat bugs were usually found in manipulated boxes from mid-May to mid-June (21 May in 2008, 13 May in 2009 and 16 June in 2010) 21–56 days after the first bats had flown. Other than adult bugs, we found several first instar individuals, but always later on in each year. Although bat bugs were observed early in the growing season in 2008, and even in mid-May, no first stages of gradation were found, and only the second gradation stage appeared at the end of July (only in 2008) (Fig. 3).

Microclimatic conditions

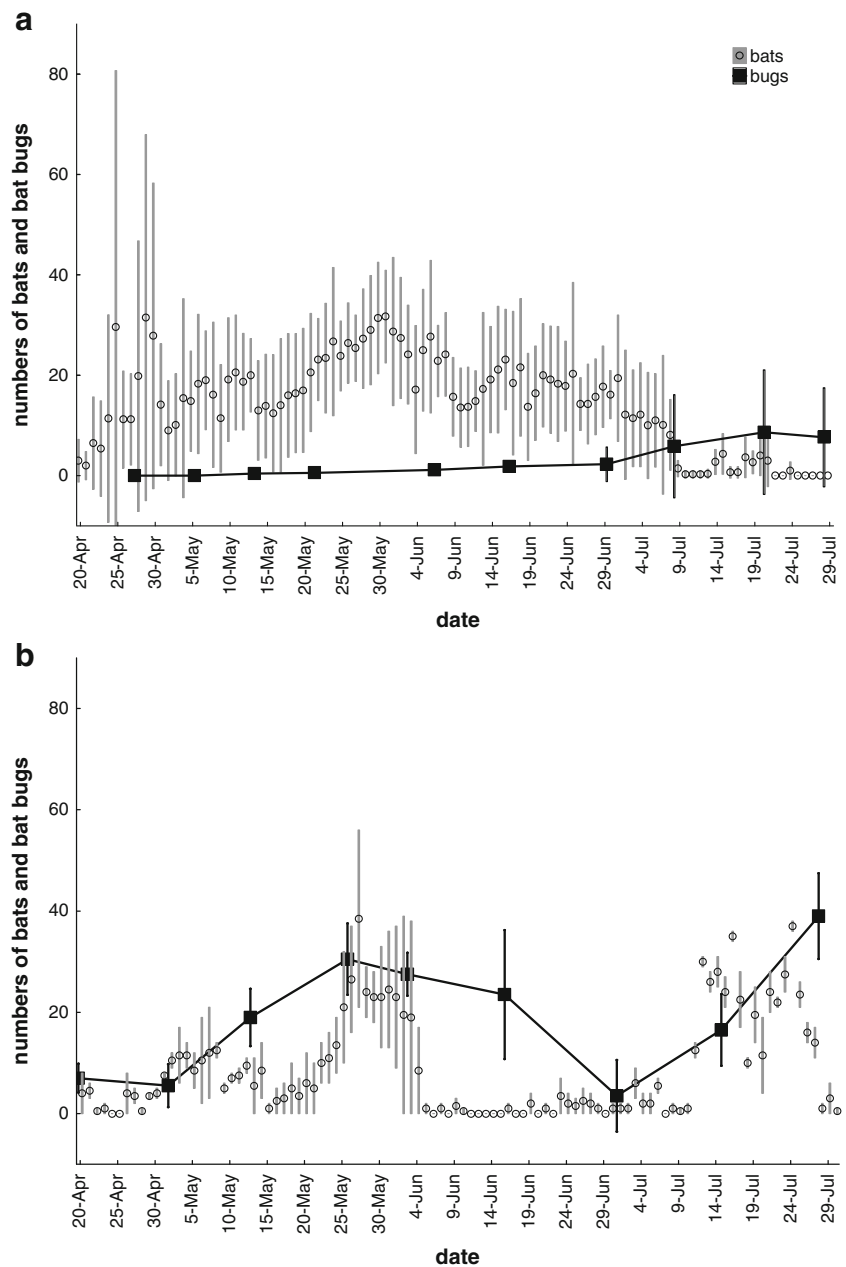
Regarding the positions of the non-manipulated bat boxes and the manipulated boxes in the two forest locations, we determined how they differed in internal temperature throughout the daylight hours. Although each of the bat boxes studied differed in the degree of exposure, no significant difference was found among the boxes in the daily mean internal, external temperatures and humidity (ANOVA, $F_{(7, 2,819)}=0.69$, NS).

Discussion

Different factors lead to roost switching

Day roosts in trees or artificial bat boxes are essential for tree-dwelling microbats, providing shelter, protection from

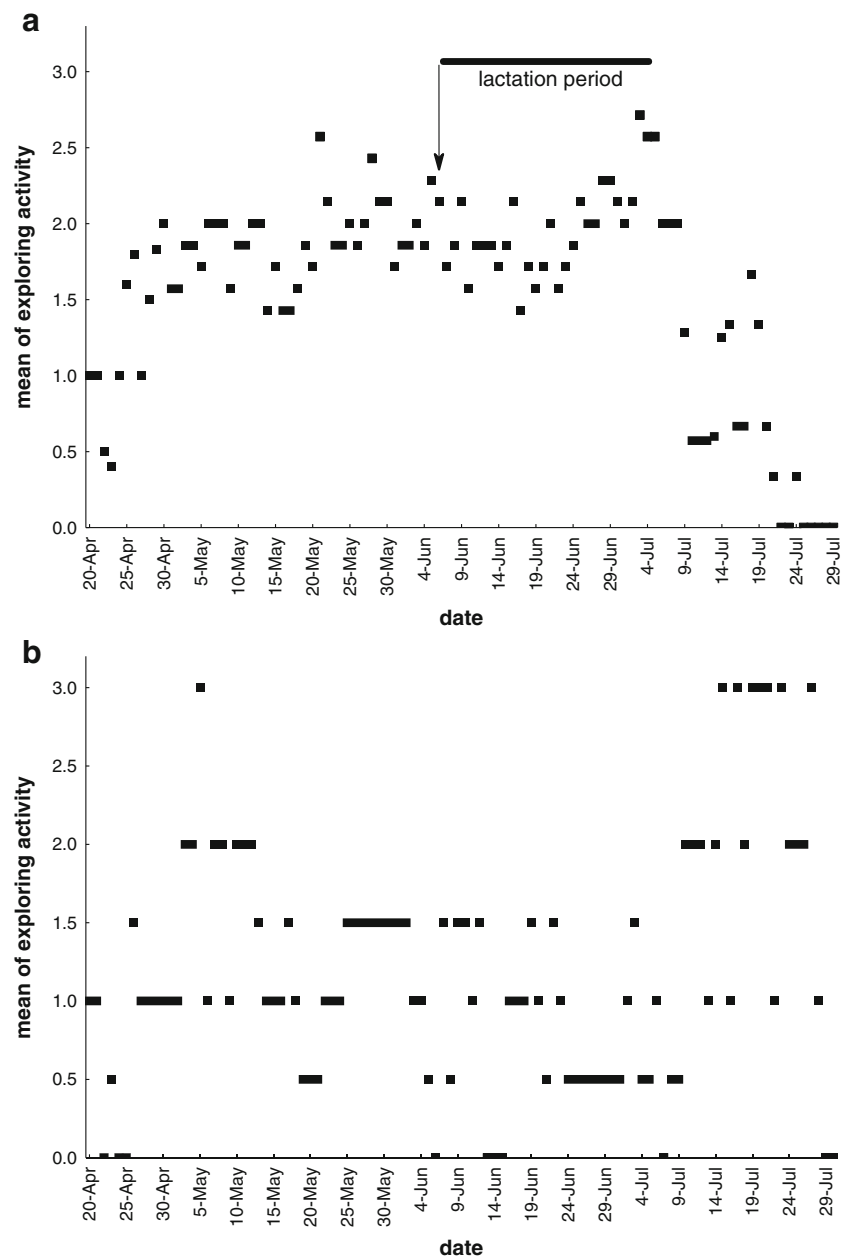
Fig. 1 Changes in the numbers of bats and patterns in the numbers of all bat bug stages **a** in boxes from which the bat bugs were removed and **b** in control boxes from which the bugs were not removed during the same seasons; mean—central tendency, standard deviation—large box



predators and an appropriate microclimate for energy balancing and reproduction. Bats often make use of multiple roosting sites, frequently shifting between roosts. Previous experimental studies of bat behavioural responses to ectoparasites indicated that the costs to bats differed, with the costs caused by ectoparasites found in the roost eliciting a stronger response than those remaining permanently attached to the hosts (Côte and Poulin 1995). Therefore, long-term monitoring data, along with field-based experiments, were used to examine the influence of roost ectoparasites on roost selection patterns and roost fidelity. There are at least three commonly cited causes of roost switching in vespertilionid bats, i.e. (1) different microclimatic demands during reproduction, (2) high ectoparasite loads and (3)

social organization, for example the fission-fusion model (Lewis 1996). However, the pipistrelles left their respective roosts in early June, a few days before parturition, and moved back to their previous roosts with flightworthy juveniles (e.g. Swift 1980; Webb et al. 1996). This behaviour is different from that found in *E. fuscus* bats, which were found to switch roosts every 1.7 ± 0.7 days (Willis and Brigham 2004). Therefore, the behaviour of the pipistrelles could not be explained by the fission-fusion model based on social interactions alone. More probable are movements related to different microclimatic demands between pregnancy and the lactation period or parasite load. Willis and Brigham (2007) calculated that individuals would save 53 % of their daily energy budget by roosting in a group (45 bats).

Fig. 2 Changes in exploration activity (1–4, where 1 is the lowest activity) in **a** boxes from which the bugs were removed and **b** control boxes where the bat bugs were present; the *arrow* shows when the first bat young was observed. The *arrow* shows when the first instance of bat suckling was observed, and the line *shows* the duration of the lactation period



Bartonička and Řehák (2007) tested the microclimatic theory of pipistrelle movement because the demands between the pregnancy and lactation periods are completely different. They assumed that the role of the bat boxes studied was as “satellite” roosts, separate from a larger communal roost,



Fig. 3 Bat bugs (*C. pipistrelli*), adults and early instars have successfully colonized the new roost (photo by O. Balvín)

that were only occupied during pregnancy and the post-lactation period. They also assumed that the bat boxes were microclimatically suboptimal roosts because for a few days in each season the internal temperature exceeded 40 °C, and the bats left the overheated boxes. Unfortunately, they did not consider ectoparasite load. We cannot confirm that the bats could survive in overheated boxes because internal temperature in the present study (at least during three manipulated years) did not exceed 40 °C. Humidity and evaporative water loss may also be important and could influence the bats to select roosts close to sources of water (Jenkins et al. 1998). However, all of the bat boxes studied were equidistant from the nearest calm water source. In this study, we did not evaluate prey availability, but Bartonička et al.

(2008) showed similar distances of foraging sites of bats coming from non-manipulated or in future manipulated bat boxes.

Switching the roost may be related to the decrease of food supply in foraging area and moving to other foraging sites (e.g. Feyerabend and Simon 2000). Bat boxes in the Křivé jezero have been monitored since 2000 and within the 8 years, pipistrelles occupied boxes only during pregnancy and then in the postlactating period. Between June and July 2004 during radiotracking research on pipistrelles, lactating females roosted in a guest house in the village of Nové Mlýny, situated 1.5 km far from Křivé jezero (Bartonička et al. 2008). However, all tagged females foraged in the old-growth floodplain forest Křivé jezero. Therefore, it is unlikely that change in the roost occupation after reducing parasite load could be explained by change of the foraging sites due to e.g. decreased prey availability there.

Pre-natal maternal effect

Unfortunately, we could not determine the primary mechanisms that enabled the bats to distinguish between infested and non-infested roosts. Bartonička (2008) assumed that the bats left their roosts after bug bites. It is improbable that all bats visiting the bat boxes during the night were attacked by bat bugs; however, if only one bat was bitten, the other bats would have realized that bat bugs were present from the behaviour of the bitten bat (Bartonička 2008). In addition, bats might be able to recognize an infested roost by other signs, i.e. the smell of fresh bug faeces, which is very intense (Usinger 1966). The fact that females leave an infested roost just before parturition could be an interesting example of pre-natal maternal behaviour similar to the maternal effect of androgens or milk composition, which might also influence offspring competitiveness (Pontier et al. 1993; East et al. 2009). However, there are also bat species that roost in one infested shelter throughout the entire reproduction season, but no switching strategies are currently known in such nursery colonies (e.g. *Myotis myotis*). Only a few life history analyses of bats have included representatives of such behaviour (e.g. Read and Harvey 1989), and further examinations of the main factors that influence post-natal growth are desired.

Colonization of new roosts by bat bugs

Reckardt and Kerth (2007) found that *M. bechsteinii* re-occupied bat boxes just 1 month after their first occupation, when they were infested by the bat fly (*Basilina nana*). During this period, the bats were safe in terms of bat fly infestation because fly puparia only become contagious later on. Such an adaptation in bats occupying bug-infested roosts is inconvenient because adult bugs are always

prepared to suck. Whenever infested bats roosted in a bat box in spring during the daytime, a bug outbreak was always observed at the end of May. We found that non-manipulated bat boxes were repeatedly visited during the lactation period even though bats did not roost here during the daytime. However, commuting bats transported bat bugs to different roosts. The probability of bug transport is very low, as shown by the low number of bat bugs found on commuting or foraging bats (e.g. Heise 1988). Since only a few early instars, better transported because of their size, were found in the manipulated bat boxes, we believe that they are not able to stay in the fur of a flying bat or they cannot survive the microclimate changes in the new roost. A re-appearance of bugs in the manipulated boxes was observed during the period when a high number of early stages were observed in non-manipulated boxes (May and June), when adult females were rapidly dying off (Bartonička and Gaisler 2007). It seems that the transport of bat bugs by their hosts to new roosts is not entirely random (cf. Balvín et al. 2012). Heise (1988) supposed that the bugs may travel on the body of their hosts on the purpose of dispersal, not only because they did not manage to escape when the bats emerged from roost to forage. Pfister et al. (2009) found that the females actively disperse earlier than males when bedbug abundance is increasing. Unfortunately, it was not shown if the dispersing females were mated or virgin. However, in almost all manipulated boxes we found a few new eggs and early instars after the appearance of first adult bug. This fact showed that at least some females were mated before the transport.

The period of high fluctuation in the numbers of roosted bats during pregnancy is very convenient for the colonization of new roosts. But the time for transport to the other roosts is limited. At about 27 °C, recently emerged adult bed bugs (*Cimex lectularius*), when fed and mated, will start ovipositing about 3 days later. When bugs are fed weekly but not mated again, which is most probable when they are moved to different roosts separately, three eggs per day are produced over a period of 5 weeks. Oviposition ceases after 11 days if the bugs are not fed again (Davis 1966). The limited time available for the successful transport and settling of a new population could be optimized by asynchronization in the timing of oviposition between different bug females. However, this theory needs to be tested further.

A second gradation stage in the bug populations was only observed in 2008, probably because of the early transport of bat bugs to the manipulated bat boxes, when bugs were found in boxes 21 days after the first appearance of bats. No other gradation stages were observed in 2009 or 2010, when the re-appearance of bugs occurred later in the vegetation season. In 2008, fed and mated females were transported. Therefore, the bug population grew and reached the original numbers at the end of July. Bat bugs transported in

2009 and 2010 were probably not fed or mated (cf. Davis 1966). The fact that bat bugs are able to move to a different roost and reach a high population density all in one season correlates well with the very fast ontogenesis that is reportedly even faster than in the bed bug (*C. lectularius*; Bartonička 2010). A fast ontogenesis could be a consequence of the coevolution between bugs and roost-switching bats.

Acknowledgments We are very grateful to J. Gaisler for his valuable comments on the manuscript and Josef Chytil for help with fieldwork. This study was supported by grant no. 206/07/P098 of the Science Foundation of the Czech Republic and the Czech Bat Conservation Trust, and by grants from the Ministry of the Environment and the Ministry of Education, Youth and Sports of the Czech Republic no. MSM0021622416. The boxes were checked under the licence no. 922/93-OOP/2884/93 and 137/06/38/MK/E/07 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, law no. 246/1992).

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