Bat bug *Cimex pipistrelli* transmission propensity in three bat species (Chiroptera: Vespertilionidae)

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Abstract. Bats, the only mammals capable of true flight, provide a unique opportunity to study the transmission of their ectoparasites. Transmission typically occurs intentionally and, if successful, can lead to new infestations. Bat bugs (*Cimex pipistrelli*) are seldom found on bats captured in mist nets, raising questions about their transmission by bats over long distances. Among the Palaearctic bat species, Nyctalus noctula was most frequently observed carrying bugs when mist-netted outside their roosts. Therefore, we aimed to investigate whether different bat species vary in the number of transmitted bugs. Previous research indicated that mated female cimicids, such as C. lectularius, tend to leave their colonies to initiate new infestations, which we hypothesized would also apply to bat bugs. To test our hypotheses, we used three bat species and examined both mated and virgin females to compare the number of bat bugs on bats emerging from bat boxes during aviary sessions. Our findings revealed that Myotis daubentonii had the fewest bat bugs, while Myotis myotis and Nyctalus noctula had significantly higher counts. Notably, N. noctula harboured more unfed bugs than M. myotis. In addition, the total number of mated females found on the body of N. noctula was higher than the number of virgin females, but the difference between the number of mated and virgin females per session was not significant. Our experiments indicate that bat bugs preferentially disperse on larger bats, and that they feed for longer durations on N. noctula compared to *M. myotis*, making *N. noctula* a more effective vector for bat bugs.

Key words. Ectoparasites, cimicids, vector, dispersal, bats, host specificity.

INTRODUCTION

The limited migratory dispersal behaviour of ectoparasites plays an important role in their movements. Dispersal of ectoparasites that stay in the host roost and feed occasionally when the hosts are in their shelter, i.e. bed bugs (*Cimex lectularius* Linnaeus, 1758) and bat bugs (*Cimex pipistrelli* Jenyns, 1839), is driven mainly by a transmission by humans or bats. However, bugs can move from place to place even actively, but only within one building, i.e. in large attics inhabited by a maternity colony (BARTONIČKA & RŮŽIČKOVÁ 2012) or among different floors in the building (USINGER 1966). Genetic research (based on both mitochondrial and nuclear markers) revealed that *C. pipistrelli* creates quite a homogenous and stable population across Central Europe, which indicates the species shows a high migratory level (BALVÍN et al. 2013). Different reasons for bugs to disperse were described, with the most important being sear-

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ching for a new host due to the lack of food, to avoid competition or to establish a new colony (PINTO et al. 2007). In cimicid bugs, the feeding efficiency, survival and development depends mainly on their hosts. However, bats as hosts vary in ecology, biology, physiology and roost choice, which may affect the transmission abilities of their parasites. Especially roost choice in bats plays an important role, some types of roosts seem to be even species specific (KUNZ & FENTON 2003). Roost choice differs also between seasons, between males and females, or is related to the reproduction status of the bats (BORKIN et al. 2011). BALVÍN et al. (2013) found considerable morphological differentiation among bat bugs collected from different bat species, although individuals representing particular mitochondrial haplogroups often live in sympatry and on the same host species. It seems that bat bugs are morphologically adapted to a particular bat host despite the low genetic structuring among individuals parasitizing different species of bats. Morphological adaptations depending on the host were found also in *C. lectularius:* bugs from the lineage feeding on bats have shorter and more hairy legs than those feeding on humans (BALVÍN et al. 2012a).

It was suspected that bats are one of the main reservoirs of global recuperation and massive expansion of bed bugs (SZALANSKI et al. 2008). Despite there is no evidence that bats could be responsible for bug expansion (BALVÍN et al. 2012a), synanthropic bats are forced to use alternative roosts in human settlements more intensively than ever. The common noctule, Nyctalus *noctula* (Schreber, 1774), is the most frequently reported species within Central European towns and cities since 1990 (HANÁK et al. 2009). At the same time, it is a species that logically most often gets into conflict with humans. Moreover, the refusal of close co-existence with this bat is strengthened as it is believed that this species is most responsible for carrying cimicids, which was explained by the fact that N. noctula carries cimicids most frequently of all mist-netted bat species (HEISE 1988, RUPP et al. 2004). BALVÍN et al. (2012b) found that 75% of caught bats with bugs were noctules, which was explained by many different aspects; N. noctula belongs to rather large-sized bats (up to 30 g); it is found mostly in small, closed tree cavities with stable microclimate but also in bat boxes or in crevice-like human shelters (GEBHARD & BOG-DANOWICZ 2004). The noctule's limited grooming capabilities in small roosts, combined with its larger body surface and frequent roost-switching behaviour, as well as its habit to migrate over large distances (exceeding 1,000 km, according to PETIT & MAYER 2000), may provide opportunities for bugs to spread and travel on it (BALVÍN et al. 2012b). Noctules were sometimes found in the same roost with other bats such as Myotis daubentonii (Kuhl, 1817) or Pipistrellus nathusii (von Keyserling et Blasius, 1839). This can be an important information concerning possible transmission of cimicids between different roosts – when shared with other bat species they can become infested by bugs or carry them further to another roost (BALVÍN et al. 2012b). However, it is not known whether there are any differences in the length of blood sucking or in the time spent on the body of different bat hosts. Differences in such behaviour could affect the likelihood of bug transmission to other shelters by different bat species.

In most bugs transmitted on mist-netted bats, adults by far outweigh the number of juveniles (BALVÍN et al. 2012b). While the early instars were found on bats only sporadically, adult females were the most frequent. However, to establish a new colony, the transported females must already be fertilized. Based on the points discussed, this study aims to test two main hypotheses: (i) *Nyctalus noctula* will carry more bugs on their bodies compared to the similarly sized *Myotis myotis*, as well as the smaller bat *Myotis daubentonii*, and (ii) mated female bat bugs (*Cimex pipistrelli*) will be more frequently found on bat bodies than virgin females, as mated females may enhance their chances of establishing new colonies elsewhere.

MATERIAL AND METHODS

Host specificity

We studied emergence behaviour of bats under experimental settings in an aviary. Twenty-five adult female bugs of *Cimex pipistrelli* were used in each session. Until the beginning of the session, the bat bugs were kept at 20 °C, relative humidity 70%, in the dark, for 10 days without feeding. Five mist-netted males of each of *Nyctalus noctula*, *Myotis daubentonii*, and *Myotis myotis* were used for the experiment. All bats were captured, handled, and temporarily kept in captivity under the licence by the South Moravian Regional Authority nos. JMK 24451/2013 and 63761/2017. In addition, the senior author (TB) is authorised to handle free-living bats under the Certificate of Competency No. CZ01297 (§17, act no. 246/1992), No. 922/93-OOP/2884/93 and 137/06/38/MK/E/07 of the Ministry of Environment of the Czech Republic.

The bats were fed every day after a session and had ad libitum access to water enriched by vitamins. All bats were returned to their original netting sites after the sessions. During captivity, the light regime was natural and air conditions stable.

All sessions were held in the outside aviary $(3 \times 3 \times 2.5 \text{ m})$ equipped with a wooden bat box. Bats usually used the box as a daytime roost. In the morning, bugs were placed in the bat box occupied by torpid bats, on a small shelf (Fig. 1). The bat box was equipped with a camera (Sony DCR SR 52E) to monitor bat behaviour before emerging. During the day, the bats moved freely inside the bat box, they became torpid at various places, but only in the upper part of the box, where a shelf for the discharge of bugs was placed in the centre. Therefore, the bugs had a similar chance to suck on each bat. In the evening after the bats came out from torpor and their body temperature raised, the bugs started to be attracted by them. The first movement in the bat box were recorded. After the bats left the box, they were caught and the numbers of bugs on bat body and inside the box, as well as the feeding status of the bugs (fed/unfed) were recorded. The experiment was repeated for 20 days during August and September 2015, i.e. 10 days for *Nyctalus noctula*, 10 days for *Myotis daubentonii*, and 10 days in August 2016 for *Myotis myotis*. All bats were juvenile males in a similar weight range (*Myotis daubentonii* – 8.3±1.4 g, *Myotis myotis* – 23.8±2.1 g, *Nyctalus noctula* – 22.7±2.6 g).

Transmission and fertility of bugs

Experimental setting was the same as in the host specificity experiment. We used mated females of bat bugs, i.e. those that were a day or two after mating with males, and virgin females, i.e. females that were freshly moulted from the 5th instar and kept separately from males. Virgin females were marked white



Fig. 1. Bat box interior designed for aviary experiments on bats, the landing wooden shelf that allows bugs to move freely in the box is visible (black).

on abdomen. Similarly to the previous experiment, 15 mated and 15 virgin bugs were added to the box in the morning, and after the bats left the box, the number of bugs present on bat body and staying in the box was noted, as well as the bug feeding status (fed/unfed). This experiment was conducted over a period of 10 days.

Statistical analysis

All variables showed a normal distribution. Statistica 12.0 for Windows and SPSS (IMB Statistic 21.0) were used for data analyses. We utilized one-way ANOVA to compare the three bat species as groups in order to assess the number and status of bat bugs, specifically unfed and fed bugs inside the box, unfed and fed bugs on the bats, and bat emergence behaviour. The significance of the numbers of bugs in each status (fed/unfed and mated/virgin) was further analysed using a two-sample t-test, applying the Bonferroni correction when conducting multiple independent tests simultaneously.

RESULTS

Transmission by different bat species

During 30 aviary sessions conducted with three bat species, we found significant differences in all variables, i.e. numbers of fed bugs (ANOVA, $F_{2,27}=10.28$, p<0.001) and unfed bugs ($F_{2,27}=58.56$, p<0.001) on bat body, numbers of fed bugs ($F_{2,27}=23.36$, p<0.001) and unfed bugs ($F_{2,27}=95.77$, p<0.001) inside the bat box (Fig. 2).



Fig. 2. Percentage of bat bugs found during the experiments in three bat species. OnBat indicates the number of fed and unfed bat bugs present on the bodies of bats that flew out of the box, while InBox represents the count of fed and unfed bat bugs that remained concealed in the bat box after the bats departed; a, b, c show significant differences among the numbers of bugs of different variables in one bat species (p<0.05).

Table 1. Emergence behaviour in the studied species; time – time after sunset, when the first bat emerged from the box (mean \pm SD), period – length of emergence period (mean \pm SD), first move – first movement of bats in the box before emerging (mean \pm SD)

species / variables	time (min)	period (min)	first move (min)	
Myotis daubentonii	44.6±8.51	21.0±5.89	146.8±39.09	
Myotis myotis	24.8±5.30	24.8±5.78	224.5±53.42	
Nyctalus noctula	0.6±14.57	20.5±7.79	62.4±25.61	

Higher numbers of bat bugs (pooled fed and unfed) were found inside the box ($F_{2,27}$ =11.98, p<0.001) than on the bat bodies (ANOVA, $F_{2,27}$ =44.43, p<0.001) in all bat species. Only few bat bugs were observed on *Myotis daubentonii* (1.6±0.69 bugs per one bat), while the numbers of bat bugs found on *Nyctalus noctula* body (7.5±1.87 bugs) were similar to those seen on *Myotis myotis* (4.9±2.06 bugs; t-test: t=-1.31, p=0.073).

Nyctalus noctula had a significantly higher number of unfed bugs on its body (5.7±0.67) compared to *Myotis myotis* (2.2±1.47; t=-6.82, p<0.001). However, the number of fed bugs on the bodies of *M. myotis* (2.1±0.99) and *N. noctula* (1.8±0.79) was not significantly different (t=0.74, p=0.464; Fig. 2). Bat bugs appeared to feed more quickly and/or effectively on *M. myotis* than on *N. noctula*, as evidenced by the higher number of fed bat bugs discovered in the box after the session (Fig. 2). Although the period during which the bats were emerging from the box was similar among species (ANOVA, $F_{2,27}$ =0.4725, p=0.634), *N. noctula* left bat box earlier than the other species ($F_{2,27}$ =26.25, p<0.001; Table 1). Moreover, *N. noctula* started being active as the latest of all three bat species ($F_{2,27}$ =12.05, p=0.011).



Fig. 3. Numbers of mated and virgin females of bat bugs found on *Nyctalus noctula* per session (A) and number of all fed mated and virgin females during all sessions found on bat bodies (B).

Transmission of mated and virgin females

A larger number of mated than unmated females of bat bugs (28% of mated females and 17% of virgins) were found on *Nyctalus noctula* bats that emerged from the roosts (Fig. 3B). Although the total number of mated females observed on the bodies of emerged bats was significantly higher than the number of virgin females (t-test, t=3.35, p<0.046), there was no difference in the number of mated and virgin bugs in one treatment (t=1.19, p>0.05) (Fig. 3A).

DISCUSSION

Our results indicate that Nyctalus noctula transported more bugs from the roost than Myotis *mvotis* and *M. daubentonii*, despite the fact that *M. mvotis* was confirmed as one of the most frequent hosts along with Myotis emarginatus (Geoffroy, 1806) and Pipistrellus spp. (BALVÍN et al. 2013). RUPP et al. (2004) found cimicids on 15% of 221 individuals of mist-netted N. noctula, while no single bug was found on 793 individuals of the other 17 bat species. The highest number of bugs found on mist-netted N. noctula was reviewed also by BALVÍN et al. (2012b), though they confirmed three other bat species as occasional vectors of bugs, i.e., Myotis daubentonii, Nyctalus leisleri (Kuhl, 1817), and Vespertilio murinus Linnaeus, 1758. However, most reviewed papers do not indicate whether the bats were captured immediately after leaving their roosts or only at foraging/drinking sites and thus at a distance from their day shelters. The lack of presence of bat bugs on other larger-sized netted bats, which are highly infested by those ectoparasites in their roosts, was explained by roosting conditions, i.e. *Myotis myotis* or *M*. *emarginatus* roost in spacious attics or caves where the bats can more easily groom and get rid of bugs than N. noctula roosting in tight crevices (BALVÍN et al. 2012b). During the reproductive period, females of *N. noctula* change their roost quite frequently (RUCZYŃSKI & BARTOŃ 2020). and new shelters can sometimes be tens of kilometres away (POPA-LISSEANU et al. 2007). Therefore, these bats may represent a less stable food source for roost parasites, which thus may be more likely to attempt to transfer to a new roost. By contrast, maternity colonies of M. myotis and *M. emarginatus* are a stable blood source due to their high roost fidelity, with females and juveniles found to be faithful to some roosting and foraging sites (ZAHN 1999, KAPFER et al. 2008), which makes more suitable conditions for bugs to stay in the bat roost rather than to be transmitted to another place. In addition, our aviary experiments show differences also in the emergence behaviour among the three bat species. Despite the length of the period during which the bats were emerging from the bat box was quite similar among the bat species. Nvctalus *noctula* left the bat box much earlier but aroused from daily torpor as the latest of all examined species. Thus, the bat bugs had the shortest time to feed on noctules, which correlates with the high number of unsucked bugs found on emerged bats. Juvenile bats normally stay in the roosts where they were born until autumn and are commonly infested by roosting ectoparasites such as bat bugs. However, males may exhibit a different thermal behaviour during the day compared to reproducing females. In particular, solitarily roosting adult males will spend more time in torpor than lactating females (KURTA 1990, HOSKEN 1997, WILLIS et al. 2006, JOHNSON & LACKI 2014). Lactating females of all studied bat species rarely use torpor and stay active for most of the time so they attract bugs most of the day, therefore the possibility of the coincidental bug transport is less probable compared to males which often use torpor and after being awake they attract ectoparasites that come to feed and can be carried by coincidence on their body (DIETZ & KALKO 2005, BALVÍN et al. 2012b).

species	M [g]	B [cm]	S [cm ²]	ar	N/m ²	TI
Myotis myotis	26	38	233	6.3	11.2	1.22
Myotis daubentonii	7	25	98	6.3	7	1.22
Nyctalus noctula	26	34	161	7.4	16.1	1.43

Table 2. Comparison of wing measurements; M (g) – body mass, B (cm) – wingspan, S (cm²) – wing area, ar – aspect ratio (B^2 S), N/m2 – wing loading, TI – tip length ratio (from NORBERG & RAYNER 1987)

Nyctalus noctula and Myotis daubentonii are both tree-dwelling bats, nevertheless their roosts in trees may vary considerably regarding for example microclimate (HUMPHREY et al. 1977). BOONMAN (2000) observed that *N. noctula* was using woodpecker cavities more often than *M. daubentonii*, preferring them to natural cavities, while *M. daubentonii* used more spacious roosts (NATUSCHKE 1960, SWIFT & RACEY 1983).

On the body of *N. noctula* we found a higher number of unfed bugs compared to *M. daubentonii* and *M. myotis*. It was observed by many chiropterologists that the skin of the wing membrane of *N. noctula* is tougher than in bats of the genus *Myotis*, even the similar sized *M. myotis* (e.g. KUNZ & FENTON 2003). The wing membrane is where the bugs are mostly found, not only to feed but also to be transported (HEISE 1988). It is therefore possible that the thicker membrane is not so irritated by the bat bugs, and at the same time the bugs need more time to become adequately engorged. This may increase the likelihood of them emerging from their roost on the body of *N. noctula*, despite the fact that *M. myotis* has a larger surface of the wing membrane (Table 2).

In the total dataset, we observed mated females of bat bugs more often than virgins on the bat body. Although it is not clear why mated females stay on the bat longer than virgins, such behaviour has already been documented as not coincidental (HEISE 1988). Most of the mated females were found attached by proboscis to the emerging bats. Whereas virgins and nymphs always suck at more sites and for shorter periods (SASÍNKOVÁ et al. 2024), mated females are probably able to suck longer at one site and hence strengthen the bat body and reduce the likelihood of dropping out.

Adult bug females were often found solitary, separated from other bug groups, meaning they do not produce the aggregation pheromone at all or just in a smaller amount, which allows them to leave the group without being followed by other bugs (SILJANDER et al. 2007). PFIESTER et al. (2008) suggested that this fact helps females to move to other niches and establish new bug colonies and that females are responsible for bug movements and dispersal. That would confirm earlier observations of female bed bugs found far from aggregations (SILJANDER et al. 2008). Moreover, all bugs found on mist-netted bats were adults and mostly females. No instars were found, despite they are very abundant in bat roosts (BALVÍN et al. 2012b). All the above suggests that female bat bugs stay on the host longer and, if mated, increase the likelihood of (re)colonizing new host roosts. Our experiment shows that bugs prefer to move on larger bat species, such as the common noctules or greater mouse-eared bats, than on smaller hosts. It is not fully clear whether the body size is the only reason, as both larger species used in our experiment had a similar weight.

To clarify the reason why higher numbers of bugs are found on noctules, it would be useful to compare the daily profiles of several bat hosts. Some bat species awake from diurnal lethargy

earlier than others (GEISER & STAWSKI 2011). Their activity leads to an increase in roost temperature and a change in the carbon dioxide concentration, which are the main factors stimulating the foraging behaviour of bed bugs (RIVNAY 1930). Bat bugs also learn during their lifetime, and there may be differences between adult, experienced females and newly developed virgins in host body exploration, sucking time, body parts used, and willingness to disperse.

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