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Roost selection and roost switching of female Bechstein's bats (*Myotis bechsteinii*) as a strategy of parasite avoidance

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Abstract Ectoparasites of vertebrates often spend part of their life cycle in their hosts' home. Consequently, hosts should take into account the parasite infestation of a site when selecting where to live. In a field study, we investigated whether colonial female Bechstein's bats (*Myotis bechsteinii*) adapt their roosting behaviour to the life cycle of the bat fly *Basilia nana* in order to decrease their contact with infective stages of this parasite. *B. nana* imagoes live permanently on the bat's body but deposit puparia in the bat's roosts. The flies metamorphose independently in the roosts, but after metamorphosis emerge only in the presence of a potential host. In a field experiment, the bats preferred non-contagious to contagious day-roosts and hence were able to detect either the parasite load of roosts or some correlate with infestation, such as bat droppings. In addition, 9 years of observational data on the natural roosting behaviour of female Bechstein's bats indicate that the bats largely avoid re-occupying roosts when highly contagious puparia are likely to be present as a result of previous occupations of the roosts by the bat colony. Our results indicate that the females adapted their roosting behaviour to the age-dependent contagiousness (emergence probability) of the puparia. However, some infested roosts were re-occupied, which we assume was because these roosts provided advantages to the bats (e.g. a beneficial microclimate) that outweighed the negative effects associated with bat fly infestation. We suggest that roost selection in Bechstein's bats is the outcome of a trade-off between the costs of parasite infestation and beneficial roost qualities.

Keywords Behavioural parasite defence · Co-evolution · Habitat selection · Host–parasite interaction · Roost fidelity

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Introduction

In vertebrates, parasite defence can involve both the physiological immune response (Pastoret et al. 1998) and the behaviour of the host (Hart 1994; Moore 2002). Compared to physiological immunity, behavioural parasite defence has long been neglected by both parasitologists and behavioural biologists (Hart 1994) and has only recently been recognised as an important part of the immune system of many hosts (Møller 1993; Hart 1997; Moore 2002). One of the most effective behavioural parasite defence strategies is to reduce the number of encounters with infective parasite stages by avoiding infested habitats (Hart 1994; Moore 2002). Studies on the effect of parasite infestation on habitat choice, however, are still rare and predominantly concentrate on the relationship between breeding birds and nest living ectoparasites (Christe et al. 1994; Oppliger et al. 1994; Richner 1998; Stanback and Dervan 2001).

Many ectoparasites live in their host's home and/or deposit inactive instars (eggs or larvae) there (Marshall 1981). Songbirds seem to recognise the parasite load of potential nest sites and choose the location of their nests on the basis of a trade-off between the expected reproductive success and the costs associated with infestation (Christe

et al. 1994). This behaviour significantly reduces parasite loads in birds and hence increases the birds' fitness (Oppliger et al. 1994; Richner 1998; Stanback and Dervan 2001). However, after having chosen a nest site, the egg-laying behaviour and the immobility of nestlings bind birds to their nest while rearing unfledged offspring. This gives ectoparasites time to reproduce in the nests (Tripet and Richner 1999).

The situation is different if the host can easily switch its living place. Mammals with the ability to transport their young are able to control parasite load by leaving an infested site before the parasite's instars finish development. Roost or nest site switching is commonly observed in mammals (e.g. Hausfater and Meade 1982; Lewis 1995, 1996; Roper et al. 2001, 2002; Kunz and Lumsden 2003; Peinke and Brown 2005), and such moves could break the life cycle of ectoparasites, providing an effective defence against parasite infestation. It has been shown that the frequency of site switching is negatively correlated with parasite loads in European badgers (*Meles meles*; Butler and Roper 1996) and Brants' whistling rats (*Parotomys brantsii*; Roper et al. 2002; see Lewis 1996 for indications of a positive correlation in pallid bats, *Antrozous pallidus*). Yellow baboons (*Papio cynocephalus*) switch their sleeping groves in accordance to the life cycle of their intestinal parasites (Hausfater and Meade 1982), and in bats roost switching can significantly reduce the reproductive success of ectoparasites (Reckardt and Kerth 2006; Bartonička and Gaisler 2007). It is, however, unknown whether the site-switching behaviour of these species is an adaptation to reduce infestation with parasites or if the observed decrease of parasite loads is a side effect of the switching behaviour, which may be performed for other reasons. Alternative reasons for site switching include improving microclimatic conditions (Kerth et al. 2001), avoiding predators (Lausen and Barclay 2002) and reducing commuting distances to food patches (Hausfater and Meade 1982; Lewis 1995).

We present a field study where we combined a roost selection experiment with long-term observations on roosting behaviour in female Bechstein's bats. Our aim was to investigate whether roost switching and roost selection can be understood as a strategy of Bechstein's bats to reduce infestation by parasitic bat flies. Two different mechanisms may help female Bechstein's bats avoid contact with contagious bat fly puparia. First, the females of a colony may be able to detect the infestation (or some correlate of infestation, such as bat droppings) when they explore possible new roosts (Kerth and Reckardt 2003). A mechanism of this kind could help colonies to avoid occupying unfamiliar roosts that are infested with puparia from bats that are not members of their colony (for example, solitary males). Second, females may avoid re-occupation of their previous day-roosts if those roosts are likely to be heavily infested.

This second scenario may be particularly important, since colonies of Bechstein's bat are demographically isolated (Kerth et al. 2000), so that roost infestation depends largely on the colony's own previous roosting behaviour (Reckardt and Kerth 2006). Therefore, females could use information about their previous roosting behaviour to assess the possible infestation of roosts before they decide to re-occupy them. This mechanism would allow the bats to adapt their roost use behaviour closely to the life cycle of the bat flies and thus make the most efficient use of their available roosts.

In a roost selection experiment, we investigated whether female Bechstein's bats recognise potential roosts infested with bat fly puparia and avoid their occupation without prior knowledge of these roosts. We provided pairs of bat boxes, each consisting of an uninfested (new) and an infested (old) box, hanging side by side at the same tree. If parasite avoidance is a major cause for roost switching and roost selection of female Bechstein's bats, new boxes should be preferred over old boxes within box pairs, irrespective of the location of the box pairs.

In addition to this roost experiment, we analysed data on the natural roosting behaviour of female Bechstein's bats collected over 9 consecutive years. Our aim was to assess whether bats use information about their previous roosting behaviour to reduce contact to contagious bat fly puparia when they decide which roosts to re-occupy. If this were to be the case, we predict a negative correlation between the age-dependent contagiousness (emergence probability; Reckardt and Kerth 2006) of the bat fly puparia and the probability that the roosts were re-occupied by the colony females during the same breeding season. We further predict that roosts that were used intensively by the females, and thus are more likely to be heavily infested, should be re-occupied with a lower than average probability once the puparia in these roosts become contagious.

Methods

Study species

Female Bechstein's bats (*Myotis bechsteinii*) are strictly philopatric and communally breed in colonies of about 10–45 adult females, which stay in the breeding habitat (forest) from the end of April until September (Kerth et al. 2000). Different colonies do not share roosts (Kerth et al. 2002). Female colonies, however, occasionally occupy roosts previously used by the solitarily living males (Kerth and Morf 2004). The females switch their day-roosts (tree cavities and bat boxes) on average every 2–3 days (range 1–17 days), and colonies use up to 50 different roosts (some of them repeatedly) during a breeding season (Kerth and

König 1999; Kerth and Morf 2004). Mothers switch roosts together with the other females, carrying their non-volant young with them (Kerth 1998).

Basilia nana (Diptera, Nycteribiidae), the hematophagous and wingless bat fly species that infests Bechstein's bats, lives in the host's fur but deposits its larvae in the bat's roosts, where they pupate and metamorphose irrespective of the host's presence. Almost all (96%) of the roosts occupied by female Bechstein's bats become infested with bat fly puparia (Reckardt and Kerth 2006). After metamorphosis, the bat flies only emerge when a potential host has occupied the roost (uses the roost as a day-roost). *B. nana* puparia need at least 29 days to metamorphose; thereafter, the probability of emergence (the contagiousness of the puparia) depends on the number of days since deposition (Schulz 1938; Ryberg 1947; Löhrl 1953; Reckardt and Kerth 2006). The puparia do not survive the winter in central Europe (Reckardt and Kerth 2006). Thus, bat roosts are free of contagious bat fly puparia in the spring. Bats returning from hibernation re-infest their day roosts with bat flies that have survived the winter as imago on their host's body. As a result, bat roosts are not contagious during the first 29 days after their first occupation in any one year but thereafter are very likely to contain contagious puparia until the end of the bats' breeding season.

Roost selection experiment

In 2002 and 2003, we carried out the roost selection experiment in the home ranges of four Bechstein's bat colonies (Blutsee, Höchberg, Guttenberg2, Unteraltertheim) living in deciduous forests near the city of Würzburg (Germany). All four colonies regularly roost in bat boxes during the breeding season (Kerth et al. 2002). During our study, the colonies comprised between 13 and 35 adult females, all marked with passive integrated transponders (PIT-tags; Kerth and König 1996). During the breeding seasons 2002 and 2003, we provided the four colonies with 42 pairs of bat boxes (2FN, Schwegler, Germany) in addition to the

boxes already existing in their home ranges (Table 1). Each box pair contained a *new* box (not infested) and an *old* box (infested) placed side by side on the same tree. We randomised the order of the boxes within pairs by flipping a coin.

The old boxes were further classified as (1) *old* boxes that had been used by members of the respective colony *in previous years*, but not in the year of the experiment, and thus contained dead puparia, which were not contagious (15 of the 42 box pairs), and (2) *recently used old* boxes that had been occupied by female colony members in the year of the experiment (remaining 27 of the box pairs). Recently used boxes thus contained living puparia, which were likely to be contagious. Twenty-one box pairs were placed on trees where single boxes had hung previously and had been used by the females as day-roosts in the year of the experiment or in the year before (*old locations*). The remaining 21 pairs were placed on trees where no boxes had hung previously (*new locations*). This experimental design allowed us to test whether familiarity with a site had an influence on the roost selection of the bats.

After placing the boxes, we checked for the presence of bats at least 3 days per week throughout the breeding season in which the boxes had been placed. Mobile and automatic PIT-tag readers allowed us to identify the individuals without opening boxes and disturbing the bats (Kerth and Reckardt 2003). The data from the four colonies were pooled, and differences in the occupation between both new versus old boxes and new versus old locations were analysed with binomial tests (SPSS ver. 11.5; SPSS, Chicago, IL) that provide a direct measurement of probability and, given our sample sizes, seemed to be the most appropriate. Both boxes of some box pairs were occupied during the experiment. We therefore performed two statistical tests, one including only the *first occupied* box per pair and another including all *occupied* boxes among the experimental pairs. We used logistic regression analysis to test if differences in the occupation probability of the old boxes during the experiment depended on differences in the intensity of their previous usage by the bats (SAS ver. 9.0,

Table 1 Design of the roost selection experiment

Box types	Colony name	Old locations	New locations	Number of adult females	Number of boxes in the colony (incl. experimental boxes)
New versus old recently used	Blutsee	8	9	16–18	116–123
	Guttenberg2	2	5	27–35	51–52
	Höchberg	1	1	14–16	36–38
	Unteraltertheim	1	–	13–14	19–23
New versus old used in previous years	Blutsee	7	6	16–18	116–123
	Guttenberg2	–	–	27–35	51–52
	Höchberg	1	–	14–16	36–38
	Unteraltertheim	1	–	13–14	19–23

PROC GENMOD, distribution binomial; SAS Institute, Cary, NC).

Relationship between the roosting behaviour of the bats and the life cycle of the bat flies

We analysed long-term data on roost occupation in the Blutsee colony that were collected during the regular roost monitoring every summer between 1994 and 2002 (total of 833 census days). Using the available information on the life history of *B. nana* (Reckardt and Kerth 2006), we tested whether the bats adapted their roosting behaviour to the life cycle of the bat flies. For every year from 1994 to 2002, we assumed that each roost was infested with puparia from its first occupation by the bat colony in each year. The deposited puparia then metamorphosed and became contagious after 30 days; from this time onwards, each puparium was assumed to have remained contagious throughout the summer, but with an age-dependent emergence probability (Reckardt and Kerth 2006). We assumed that the infestation intensity (number of puparia in a roost) was significantly correlated with the intensity of roost use by the bats (Reckardt and Kerth 2006). Roost use intensity (bat days) was defined as the sum of daily numbers of bats that occupied a given roost. The number of adult females in the Blutsee colony ranged from 13 to 31 between 1994 and 2002 (mean 19), and the number of boxes ranged from 77 to 123 in the respective years (mean 88).

To test if female Bechstein's bats take the contagiousness of *B. nana* puparia into account when selecting among previously used roosts, we compared roost use intensity before and after puparia in a roost became contagious [generalised linear model (glm)1: SAS 9.0, PROC GENMOD, distribution binomial, year included as blocking factor, independent variable: bat days; dependent variable: between day 1 and day 29 and between day 30 and day 129 after the first occupation in a year]. Additionally, we tested if the rate at which roosts were re-occupied depended on the emergence probability of the puparia in the roost (glm2: PROC GENMOD, distribution Poisson, year included as blocking factor, independent variable: emergence probability of puparia dependent on time since deposition; dependent variable: mean number of roosts that were re-occupied per 10-day period since the first occupation in a year).

To analyse if the bats take the infestation intensity of roosts into account when selecting among contagious roosts, we compared roost use intensity (which positively correlates with infestation intensity, Reckardt and Kerth 2006) during the period of bat fly metamorphosis with the probability that the roost was re-occupied once puparia were contagious (glm3: PROC GENMOD; distribution binomial, year included as blocking factor; independent

variable: bat days between day 1 and day 29 after the first occupation in a year; dependent variable: roost occupied or not occupied later than 29 days after the first occupation in a year). We also compared roost use intensity of the re-occupied roosts before and after puparia became contagious (glm4: PROC GENMOD; Poisson distribution, year included as blocking factor; independent variable: bat days between day 1 and day 29 after the first occupation in a year; dependent variable: bat days between day 30 and day 129, the end of the breeding season).

Results

Roost selection experiment

The bats occupied (used as a day-roost) one or both boxes in 21 of the 27 pairs that contained old and recently used boxes (i.e. boxes with a high probability of being infested with contagious bat fly puparia). Within these 21 occupied pairs, the bats significantly preferred new (parasite-free) boxes to old (contagious) boxes (binomial tests: all occupied boxes $P = 0.036$; only the first occupied box per pair $P = 0.027$; Fig. 1a). Four out of the 21 pairs containing recently used old boxes were occupied before puparia in the old box were contagious; in all four cases the bats choose the new box.

The bats also occupied 11 of the 15 box pairs comprising old boxes that had only been used in previous years by the bats and thus only contained puparia that were no longer contagious. Within these 11 box pairs no preference for new (parasite-free) boxes versus old (infested but not-contagious) boxes was observed (binomial tests: all occupied boxes $P = 1$; only the first occupied box per pair $P = 1$; Fig. 1b).

We counted the number of puparia in 26 of the 42 old boxes by hand before we used them in the experiment. All of these boxes were infested with puparia, but their infestation intensity varied. As expected, the number of puparia per old box was significantly positively correlated with the bat days prior to the experiment (glm; recently used boxes $n = 12$, $\chi^2 = 12.15$, $P < 0.001$; boxes used in previous years $n = 14$, $\chi^2 = 16.39$, $P < 0.0001$). The probability that a recently used *old* box was occupied after the start of the experiment was significantly negatively correlated with both its number of puparia (glm; $n = 12$, $\chi^2 = 4.67$, $P < 0.05$) and its bat days before the experiment (glm; $n = 12$, $\chi^2 = 13.44$, $P < 0.0005$). No such correlation was found for the old boxes used in previous years (glm; puparia $n = 14$, $\chi^2 = 1.20$, ns; bat days $n = 14$, $\chi^2 = 0.20$, ns).

The bats occupied 18 of the 21 box pairs at new locations and 14 of the 21 box pairs at old locations. The
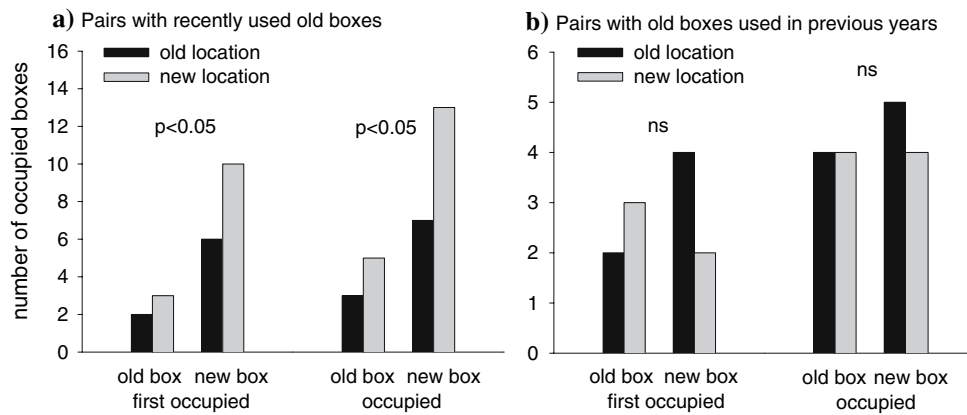
Fig. 1 a, **b** Results of the roost selection experiment: number of boxes occupied by the female Bechstein's bats as a function of whether they contained bat fly puparia (*old box*) or not (*new box*) and whether the box pairs were placed at old or at new locations. The parasites were likely to be contagious in the old boxes that had been recently used, whereas the parasites in the old boxes used in previous years were not contagious during the experiment. *First occupied* only the first occupied box per pair, *occupied* all occupied boxes of the experimental pairs. For the significance tests of new versus old boxes data from new and old locations were pooled

difference was not statistically significant (binomial test $P = 0.60$, ns; Fig. 1). The preference for the new boxes within the pairs that comprised the recently used and thus contagious old boxes was similar at new and at old locations (Fig. 1); however, due to the reduced sample size, it was no longer statistically significant if tested separately for both locations.

Relationship between the roosting behaviour of the bats and the life cycle of the bat flies

In accordance with our predictions, roost use probability was negatively correlated with the age-dependent contagiousness of the puparia. Roost use was significantly greater during the 29 days following a roost's first occupation of the year (glm1 $n = 318$ roosts over 9 years, $\chi^2 = 60.55$, $P < 0.0001$). Additionally, the probability that a previously used roost was re-occupied by the bats during the same breeding season was significantly negatively correlated with the age-dependent contagiousness of the puparia (glm2 $n = 6$ time periods, $\chi^2 = 6.82$, $P < 0.01$; Fig. 2).

Contrary to our predictions, the bats did not avoid re-occupying roosts that were most intensively used within the 29 days after their first occupation in any one year and which were thus most likely heavily infested with bat fly puparia. Roosts that were re-occupied when deposited puparia had become contagious had significantly more bat days during the first 29 days after the first occupation than roosts that were not re-occupied (glm3 $n = 318$ roosts over 9 years, $\chi^2 = 9.20$, $P < 0.01$). Moreover, roost use intensity before and after the puparia became contagious was significantly positively correlated (glm4 $n = 318$ roosts over 9 years, $\chi^2 = 17.52$, $P < 0.0001$).
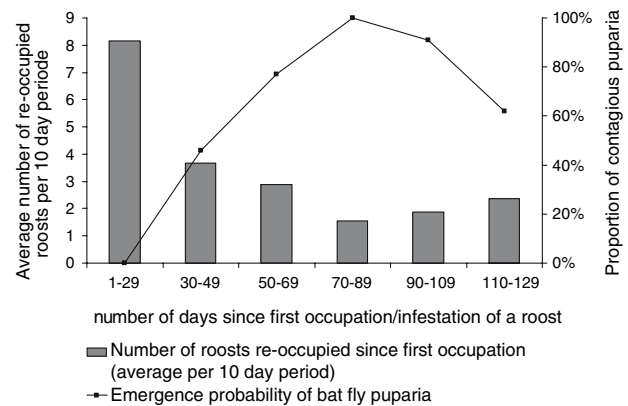

Fig. 2 Relationship between the roosting behaviour of female Bechstein's bats and the contagiousness of *Basilia nana* bat fly puparia in their roosts. The rate that roosts were re-occupied after their first occupation in a year was significantly negatively correlated with the age-dependent emergence probability (contagiousness) of the puparia. Data on the life cycle of *B. nana* are from Reckardt and Kerth 2006; roost use data are from the Blutsee colony. All data were collected between 1994 and 2002 and years were pooled

Discussion

Our field study provides both experimental and correlative evidence that female Bechstein's bats adapt their roosting behaviour to the life cycle of the parasitic bat fly *B. nana* in order to decrease their contact with puparia of this parasite in their roosts. Our data suggest that the bats selected their day-roosts as a function of the infestation of a roost as well as the contagiousness of the puparia in a roost. The observed re-occupation of previously intensively used and presumably heavily infested roosts indicates that the bats also took other criteria beside parasite infestation into account when selecting roosts.

In the field experiment, female Bechstein's bats largely avoided boxes that were highly likely to contain contagious bat fly puparia (old boxes that had been recently used; Fig. 1a). Non-contagious boxes that had been used in previous years and only contained dead puparia (Reckardt and Kerth 2006) were occupied with the same probability as new boxes that contained no puparia at all (Fig. 1b). Box pairs at new locations were not significantly preferred over pairs at old locations, and the preference for the non-contagious boxes was similar at both locations. Thus, in accordance with our predictions, the location of the box pairs and the infestation history of the box in previous years had no significant influence on the roost selection of the bats.

The observed avoidance of contagious boxes at new locations (Fig. 1) indicates that the bats were not just remembering the location of their previous roosts but were also able to recognise recently used roosts directly. This ability may be important in order to reduce contact to bat fly puparia, since female Bechstein's bat colonies often split into subgroups that use different roosts. Although such subgroups do not remain stable, and the females permanently mix up and form new subgroups (Kerth and König 1999), not every individual in a colony might be informed about all day-roosts used by its colony mates. Discrimination against recently occupied but unfamiliar roosts may also protect the females from accidental occupations of roosts previously used by solitary males, which can occupy and infest roosts in the roosting areas of female colonies (Kerth and Morf 2004; Reckardt and Kerth 2006).

Our experiment does not allow conclusions to be drawn on the proximate mechanisms that assisted the females in distinguishing between contagious and not contagious roosts. However, we assume that the bats may use the smell of fresh urine and bat droppings as an indicator of a possible infestation of the roosts, since only recently used boxes – but not boxes used in previous years – were avoided during the experiment. This clue would provide reliable information on infestation risk, as almost all (96%) occupied roosts become infested with bat fly puparia (Reckardt and Kerth 2006). A similar mechanism has been supposed to avert yellow baboons from using sleeping groves infested with infective ova and larvae of intestinal parasites (Hausfater and Meade 1982).

The avoidance of the recently used boxes is in agreement with both the parasite avoidance and the predator avoidance hypothesis. The accumulation of fresh bat droppings indicates a possible infestation of a roost with parasites, but it could also attract predators to roosts. However, the predator avoidance hypothesis is not in agreement with the result that new locations (sites unknown to predators) were not preferred over old locations.

The analysis of our long-term observational data indicates that the roosting behaviour of the bats was adapted to the life cycle of the bat flies (Fig. 2). The bats used roosts most intensively within the first 29 days after the first occupation in a year when all puparia deposited in the roosts were still undergoing metamorphosis and roosting was safe in terms of bat fly infestation (glm1). Once the puparia became contagious, roost use dropped significantly. If roosts were re-occupied, the bats largely avoided them at times when they were likely to contain highly contagious puparia. The observed correlation between the contagiousness of the bat fly puparia in a roost and the probability that this roost was re-occupied (Fig. 2; glm2) indicates that the bats are able to remember the location of previously used roosts and to assess the contagiousness of the bat fly puparia deposited there.

Overall, our results indicate that the infestation of Bechstein's bat colonies with parasitic bat flies is a major cause for roost switching and roost selection in this species. The bats recognised roosts that were recently occupied and thus most likely infested even if these roosts were unfamiliar. The overall roosting behaviour of the bats was also well correlated with the life cycle of the bat flies. The combination of these two factors makes it unlikely that the explanation of roost switching is primarily for reasons other than parasite avoidance, such as thermoregulatory benefits or predator avoidance. The reduction of bat fly reproductive success due to the roost switching of female Bechstein's bats (Reckardt and Kerth 2006) is therefore unlikely to be a mere side effect of the switching behaviour.

Ectoparasites other than bat flies are unlikely to cause roost switching in Bechstein's bats. The only ectoparasites besides bat flies that were regularly observed in the four studied Bechstein's bat colonies were wing mites (K. Reckardt and G. Kerth, unpublished data). Wing mites, however, are nymphiparous and live permanently on their hosts. Roost switching therefore does not affect their prevalence. Other potential ectoparasites that deposit their eggs in the roosts of the bats, such as fleas, were absent or extremely rare on Bechstein's bats (K. Reckardt and G. Kerth, unpublished data). The prevalence of bat flies among female Bechstein's bats was 50%, and mean colony infestation intensities ranged between 0.2 and 2.9 flies per bat (K. Reckardt and G. Kerth, unpublished data). These relatively low numbers of bat flies in the female colonies are a result of the roost switching behaviour of the bats (Reckardt and Kerth 2006) and thus do not indicate that the costs of an infestation with *B. nana* may be of little evolutionary significance for female Bechstein's bats.

The female bats took the contagiousness of puparia – but not the infestation intensity of the roosts – into account when re-occupying previously used roosts. Even though our experimental and long-term data suggest that female Bechstein's bats were able to recognise infested roosts, the

bats did not avoid the re-occupation of previously intensively used and, therefore, probably heavily infested contagious roosts. Contrary to our prediction, we even observed a positive correlation between roost use intensity at times when the roosts were not contagious and the probability that the roosts were re-occupied after the puparia became contagious (glm3). We assume that those roosts were re-occupied because they provided beneficial conditions (e.g. warm roost temperatures; Kerth et al. 2001) that outweighed the negative effects of the bat fly infestation. This assumption is supported by the result that roost use intensity during metamorphosis of the bat fly puparia was not only positively correlated with the probability that the roosts were re-occupied after they became contagious (glm3), but also with roost use intensity after the re-occupation (glm4). Roost competition with other species occupying bat boxes (e.g. dormice) cannot explain the re-occupation of infested roosts because the bats always had alternative boxes available.

Similarly to the nest choice of songbirds (Stanback and Dervan 2001), the roosting behaviour of female Bechstein's bats may reflect a trade-off between the negative effects of parasite infestation and beneficial qualities of roosts, such as advantageous microclimatic conditions (Kerth et al. 2001) No single factor can conclusively explain the high frequency of roost switching in Bechstein's bats, but the combination of parasite avoidance together with an improvement of microclimatic conditions may be a possible explanation.

Conclusions

The results of this study are in accordance with those from previous studies on mammals and birds that show a relationship between site selection/alternation and parasite infestation. The deposition of inactive instars in the nest of a bird, which would only rarely leave its unfledged young (Duffy 1983; Hart 1997), may be adaptive for parasites. However, the deposition of such instars in the home of a mobile host that can easily switch its living place may reflect a phylogenetic constraint. The life cycle of arthropod ectoparasites, particularly their metamorphosis, largely depends on external factors such as temperature and humidity (Marshall 1981; Bartonička and Gaisler 2007). Thus, the options for a parasite to extend or shift the period of contagiousness in the host's home may be limited compared to the options a mobile host has to adapt its roosting behaviour. Our results suggest that for mobile hosts, avoidance of infested places and switching behaviour can be effective defence strategies against parasites. This may apply to a wide range of species. Parasite avoidance thus should be considered in studies on habitat selection.

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