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ORIGINAL PAPER

Cimex pipistrelli (Heteroptera, Cimicidae) and the dispersal propensity of bats: an experimental study

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Abstract Previous results have shown frequent movements of crevice-dwelling bats between different shelters. Low roost fidelity of some dwelling bat species reduces the reproductive success of ectoparasites. The question of whether high densities of bat bugs (*Cimex pipistrelli*) represent a cost for crevice-dwelling bats (*Pipistrellus pygmaeus*), resulting in roost switching, has been examined. Sessions in a volary equipped with two bat boxes were carried out. One of the boxes was loaded with ectoparasites (low and high densities), the other served as a control and new roost for bats, which left the loaded box. Differences in the level of bat self-grooming, movements inside experimental boxes, and leaving the boxes between experiments with bat bugs and controls were significant. Allogrooming was observed only in few cases; therefore, the hypothesis of cooperation among individual bats in defense against bat bugs was rejected. Experiments with artificial parasitation, when bugs were added to a bat roost, showed that leaving a confined roost infested by bat bugs, i.e., roost switching, is a natural reaction of crevice-dwelling bat species, which reduces parasite load.

Introduction

Behavioral responses of hosts during their exposure to parasites usually reduce the effects of costly parasitism (Moore 2002). Field and experimental research has demonstrated that nest ectoparasites can reduce reproductive success of their hosts (Loye and Carroll 1991; de Lope and Moller 1993; Richner et al. 1993; Christe et al. 1996). Some birds have shown sensitivity to costs associated with parasites and the ability to discriminate levels of possible infestation and to choose less soiled nests (Barclay 1988; Opplinger et al. 1994; Rendell and Verbeek 1996). Low roost fidelity observed in many dwelling bat species significantly reduces the reproductive success of ectoparasites such as bat flies (Reckardt and Kerth 2006) or bat bugs (Bartonička and Gaisler 2007). However, up to the present, studies on the life history of bat ectoparasites have mainly dealt with species and their ontogenetic stages, which live on their hosts' bodies permanently (mites, e.g., Giorgi et al. 2001; nycteribiids, e.g., Reckardt and Kerth 2006, 2007; streblids, Gannon and Willig 1995).

As a result, the relations between bat species roosting in crevices and their ectoparasites living in the same shelters but mostly without physical contact with their hosts are unclear and often based only on speculation. Reckardt and Kerth (2007) showed that roost switching of *Myotis bechsteinii* between seasons can be explained as bat adaptive behavior to the life cycle of bat flies, i.e., their emergence from puparia. Roost switching during one season is well-known in pipistrelles, and seems to be an anti-parasite strategy with respect to roost parasites such as bat bugs (Bartonička 2007). Bartonička and Gaisler (2007) showed that the absence of bats in satellite roosts during the lactation period, coupled with high temperatures and natural mortality of parasites, reduced the number of bat bugs in bat boxes to less than half the initial number. Whereas bat bugs are common not only in fissure-like roosts but also in spacious shelters such as attics of building, we observed that some bat species (e.g., *Myotis myotis*) can reduce the load of parasitation by movements within such large roosts (Bartonička and Gaisler, unpublished observation).

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Little is known about parasite-induced behavior of bats within the roost, e.g., grooming. In this paper, I tested whether self-grooming or allogrooming can serve to reduce the parasite load. An experimental test of the hypothesis that high parasite load increases the probability of roost switching in crevice-dwelling bats is presented. In particular, the level and type of grooming and movement behavior with respect to different levels of parasitation, survival rate, and sucking success of bat bugs during laboratory infestation of bats are reported. Based on this new data, I discuss possible co-evolutionary responses between bat bugs and parasite-induced bat behavior, sucking success of bugs, and energy loss caused by roost switching.

Materials and methods

Volary sessions and equipment

Only adult female bugs of the *Cimex pipistrelli* Jenyns 1839 group were selected for the experiments. Until the beginning of experimental sessions, bat bugs were kept in darkness at low temperature (15°C, humidity 70%) when their survival without food was longest (Jones 1930; Johnson 1941 observed in *Cimex lectularius* Linnaeus 1758). Sessions were held in a volary (3×3×2.5 m) equipped with two bat boxes and under standard microclimatic conditions (temperature 25°C, humidity 70%). The soprano pipistrelles (*Pipistrellus pygmaeus* Leach 1825) used in the experiment were netted in the roof of a brick building housing a pheasantry at the village of Vranovice (48°57′50″ N; 16°37′51″ E), Czech Republic where a large colony of this species was situated. Only 20 females were kept in captivity simultaneously. The bats were fed each day after a session and had access to water enriched with vitamins. All bats were returned to their original colony after the sessions. During captivity, the light regime was natural and the air condition is stable. The boxes were equipped with thermometers and hygrometers (HOBO, Onset Computer Corporation, software BoxCar 3.7); they provided the only roosting space to bats in the volary. Both bat boxes were equipped with a camera (SONY DCR SR 52E) to monitor the bat behavior; another camera was installed on a tripod in the middle of the volary. Bat bugs were last fed 1 week prior to the beginning of the experiments (first release of the bugs into the appropriate box) (Hase 1917; Adkins and Arant 1959).

Other ectoparasites were removed from all bats before the first session. Bats inhabited the volary 1 week before the first session. Each session started 2 h before sunset, when bats were still in torpor, thus avoiding mutual disturbance. Only infrared light was applied during the observations. *C. pipistrelli* sample was divided into two experimental groups with different numbers (20, 50) of bat bugs. Only one bat box was infested by bat bugs, the other was bug-free unless the bats themselves carried the parasites into it.

At the beginning of each session, bugs were applied directly into the box via a small hole using a glass tube. Video sequences were recorded during 1 h after application of the bugs. One day after a session with addition of bugs to the roost, a control was carried out with an identical bat group and started 2 h before sunset. In control sessions, video recordings were made 120–60 min before sunset. After each session, all bugs were removed from the boxes, and their numbers, feeding status, and visible injuries were reported.

The bats were captured, handled, and temporarily kept in captivity under license numbers 922/93-OOP/2884/93 and 137/06/38/MK/E/07 of the Ministry of Environment of the Czech Republic. The author has been authorized to manipulate with free-living bats according to the certificate of competency number 104/2002-V4 (section 17 of the law number 246/1992).

Experimental groups and observed behavior

Video sequences lasting 1 h recorded the level of allogrooming and self-grooming, the number of bat movements within the box, and the number of bats leaving the box. The experiments were carried out with early pregnant, post-lactating, lactating females, and newly fledged young. Video sequences were recorded of two different bat assemblages: (1) early pregnant or post-lactating females (ten individuals in each session, 20 session pairs—experiment and control) and (2) age-mixed groups (five lactating females and their five young, ten session pairs).

Statistical analysis

All variables showed a normal distribution (Kolmogorov–Smirnov test). Statistica for Windows 7.0 (StatSoft, Tulsa, OK, USA) was used for data analyses. Paired *t* tests were used to check the differences between the level of grooming and movements of bats under experimental and control conditions. *T* tests were used to test differences in the numbers of sucked (clearly visible blood in the abdomen)/ unsucked (no blood mark in the abdomen) bat bugs found on bats, which stayed inside/left. The Bonferroni correction was applied if multiple tests were used for the same data set.

Materials

In all, I carried out 20 experiments (half with 20 and half with 50 bugs) and 20 controls without bugs. In the volary, I also tested ten age-mixed (five adult and five newly fledged young) bat groups and ten controls without bugs. To quantify the level of grooming, the number of movements and the condition of bat bugs (unsucked/sucked, lost, dead, on/off the bat body), 3,600 min of video records were examined.

Results

Level of grooming

All variables showed a normal distribution (Kolmogorov–Smirnov test); therefore, mean values were used. Paired *t* tests were used to check the differences between the level of self-grooming and allogrooming and the movements of bats in the experiments (with bugs) and in the controls (no bugs). The differences in the level of self-grooming ($t=7.65$, $p<0.001$, $n=20$), movements inside experimental boxes ($t=5.40$, $p<0.001$, $n=20$), and bats leaving between experiments ($t=5.98$, $p<0.001$, $n=20$) and controls were statistically significant (Fig. 1). Allogrooming was observed only in a few cases and differences were not significant ($t=2.02$, ns, $n=20$).

When comparing the session with 20 and 50 bugs, the differences were found in the level of self-grooming (*t* test, $t=-7.66$, $p<0.001$, $n_1=10$, $n_2=10$), movements ($t=-5.74$, $p<0.001$, $n_1=10$, $n_2=10$), and the number of bats leaving the boxes ($t=-4.04$, $p<0.001$, $n_1=10$, $n_2=10$), and no differences were found in the levels of allogrooming ($t=-0.16$, ns, $n_1=10$, $n_2=10$) (Fig. 1).

Bat movements and bugs

Bats with bugs stuck on their bodies were significantly more frequent among those that left a box than among those that stayed inside ($t=3.96$, $p<0.001$, $n_1=10$, $n_2=10$) (Fig. 2). Because bats started to move shortly after being bitten by a bug, the number of sucked bugs on bats that left the box did not differ even when different numbers of bugs were used in the session ($t=-1.80$, ns, $n_1=10$, $n_2=10$), whereas a higher number of bats left the more infested roost at the same time. The time of the last bat emerging from the box was longer at the higher level of parasitation ($t=-3.81$, $p<0.001$, $n_1=10$, $n_2=10$). On average, 1.3 (range 0–3) sucked bugs were found per bat leaving the box. Furthermore, a higher level of parasitation of juveniles than adult females was observed ($t=-4.70$, $p<0.001$, $n_1=5$, $n_2=5$) in both levels of parasitation (Fig. 3). The majority (89.9%) of bugs stuck on bats that left a box was recorded on juveniles, with a mean of 1.6 (1–3) bugs per bat. In all sessions (mixed and non-mixed-age bat groups together), only 0.43 (0–1) bugs per bat were recorded on adult females that left a box, resulting in 51% of the total number of bugs. Female bats were not stressed by the presence of bugs but were stressed by the bite of bat bugs after which they usually left the roost. Bat bugs were not able to suck on bats during their daily torpor because of the low body temperature, when bat body temperatures were around 24.1°C (±4.3°C).

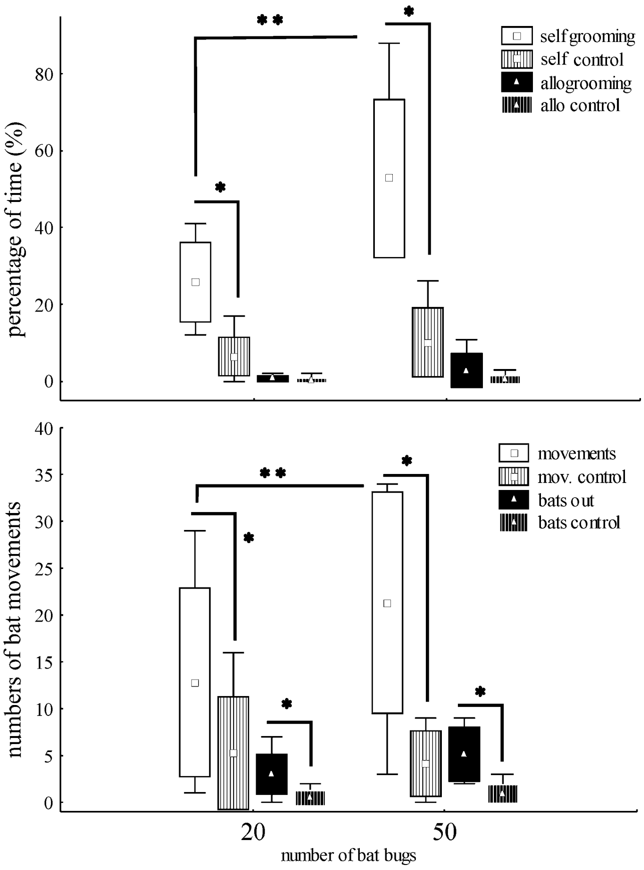

Fig. 1 Level of self-grooming, allogrooming, number of bat movements, and bats leaving bat box under different number of bat bugs. *One asterisk* (*) shows significant paired *t* tests ($p<0.001$) between the control (*self*, *allo*, *mov.*, and *bats control*) and experiment and *double asterisks* (**) significant *t* tests between level of grooming and number of bat movements under different number of bat bugs. Box–whisker plots (mean—central tendency, the standard deviation—*large box* and min–max range as *whiskers*). Bonferroni correction was applied ($p<0.012$)

Discussion

Fast ontogenesis of the roost ectoparasites allows them to increase their numbers rapidly soon after the roost occupation by bats (e.g., Usinger 1966). Brown and Brown (1986) described the impact of ectoparasites on hosts' fitness and the negative influence on the coloniality of hosts. Bugs of the family Cimicidae are important roost ectoparasites of bats. An increase in parasite density is usually caused by high starting parasite abundance in the

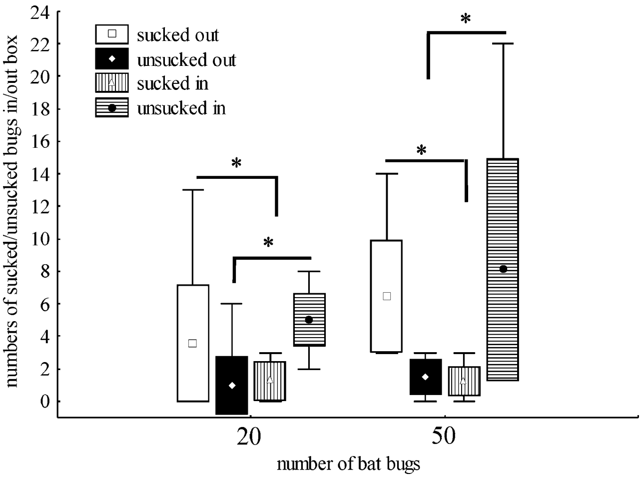

Fig. 2 Numbers of sucked/unsucked bat bugs found on bats that left or remained in the box during the sessions. *One asterisk* (*) shows significant *t* tests ($p<0.001$) among different bug groups. Box–whisker plots (mean—central tendency, the standard deviation—*large box* and min–max range as *whiskers*). Bonferroni correction was applied ($p<0.006$)

host's roost, low antiparasitic behavior and/or immunity reaction, optimal microclimate—microhabitats that are favorable for the parasite, decreased natal dispersal, and occupancy of the same roost for a long time (uninterrupted occupying of roosts by bats) (Brown and Brown 1986; Zahn and Rupp 2004). Resistance of bats against parasites can be influenced by sufficient nourishment; therefore, there are different numbers of parasites during the same time periods and in the same roosts (Christe et al. 2000). Frequent roost switching reduces the numbers of roost ectoparasites, namely, bugs in the abandoned roosts, which can be re-occupied later during the same or in the next season (Bartonička and Gaisler 2007). Although roost switching has been demonstrated as antiparasitic behavior, the phenomenon was not completely understood until now (cf. Lewis 1995; Vonhof and Barclay 1996; Brigham et al. 1997). It seems that parasitation is sufficiently important to be a cause of roost switching.

Ability to suck blood

It is well-known that the bugs spend only the time necessary for feeding on their host's body (Usinger 1966). At the beginning of each session, bat bugs orientated themselves in the experimental boxes quickly and they moved to the cluster of bats in daily torpor immediately. Marx (1955) suggests that the bed bug *C. lectularius* detects human hosts from as far as 1.5 m away through the use of heat cues, host kairomone(s), and/or CO_2. Temperature sensors on the antennae are capable of resolving differences of 1–2°C (Sioli 1937). Rivnay (1932) carried out an experimental study on host's preference of *C. lectularius* and found that a hungry bug can feed on all vertebrates whose body temperature exceeds ambient temperature by at least 3°C. The optimal blood temperature with respect to sucking in *C. lectularius* was found to be 37°C (Montes et al. 2002).

In this study, although bugs were unable to suck on bats during the daily torpor because of low blood temperature, they were able to localize them and reach their bodies. This statement is illustrated by the observation of high locomotor activity of bat bugs on the bats' bodies without host reaction during the first 20 min of most experimental sessions. However, bug activity can cause the activation of the bats, which consequently leads to an increase of their body temperature and allows the bugs to suck. Differences in the availability of feeding are very important with respect to the timing of parasite pressure during the day. If bugs can feed on bats only when they are active, the parasite load of bat bugs will be highest during the short activity period before leaving and after returning to the roost when bats are not torpid. Also when bugs bite bats, the latter can leave the roost and transport bat bugs to a non-infested roost at a distance.

Antiparasitic behavior

Bats, when in torpor, were not stressed by the presence of the bugs themselves, but when woken up and stressed by the bug bites, they normally left the roost. The host's reactions to bug bites are probably caused by substances in the saliva (Valenzuela et al. 1995). Also, allergic response can often be present (Hecht 1930). Adaptive parasite-induced behavior (an effort to kill or eat ectoparasite, or to groom, fidget, and scratch) can decrease the level of successful sucking (Moore 2002). However, results from

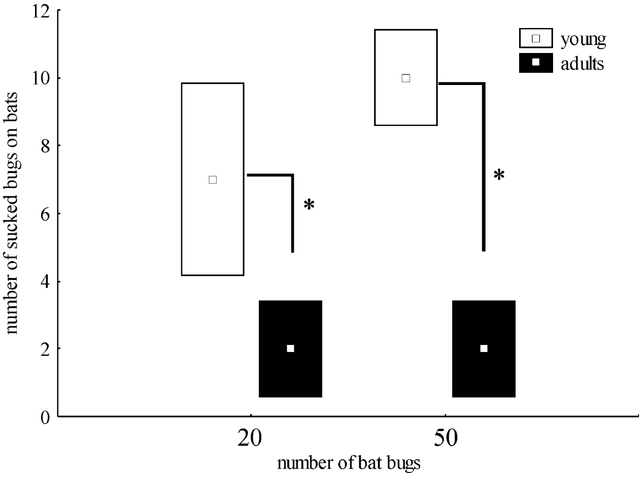

Fig. 3 Different levels of parasitation of juveniles and adult females. Bonferroni correction was applied ($p<0.012$)

the current volary experiments did not show any behavior, which might reduce the pressure of roost ectoparasites before the blood loss. Usinger (1966) notes that bats avoid eating bat bugs because of their intensive smell (an alarm pheromone); therefore, it can be expected that bats would not bite bugs during experimental sessions (cf. Overal and Wingate 1976). However, bat bugs were served periodically together with the common food (mealworm larvae, *Tenebrio molitor*; and crickets, *Gryllus assimilis*) to bats kept in the volary. Bats ate bugs without restraint and even during several days. Analyses of prey of *P. pygmaeus* also showed the presence of *Cimex* spp. body fragments in pellets (Bartonička et al. 2008). Despite the bats' ability to feed or to bite bat bugs, they refrain from doing so during experiments although it could prevent their blood loss.

Cooperation in grooming

Allogrooming (grooming of conspecifics) is one form of social behavior that can be observed in many social mammals (O'Brien 1993; Hart 1994; Mooring and Hart 1995; Gompper et al. 1997). It is suggested that allogrooming has both social and hygienic function. Bats groomed their colony mates mainly on the body parts that are difficult to reach. The hypothesis of cooperation among individual bats in defense against bat bugs has not been confirmed so far, though allogrooming was observed in other bat species, mainly between parents and offspring (Wilkinson 1986; Kerth et al. 2003; Willis and Brigham 2004). The same authors (i.e., Wilkinson 1986; Kerth et al. 2003) did not find significant positive correlation between the time a bat was groomed and the time it groomed itself, and allogrooming was very rare compared to self-grooming in their study. Also in my sessions, only a few allogrooming events were observed. Adult bats did not cooperate in defending each other against bat bugs; neither did the females defend their offspring, despite the higher level of parasitation of juveniles. A higher number of sucked bugs found on the young were also reported by Christe et al. (2000). On the other hand, there is no direct correlation between the number of bugs in the roost during lactation (non-fledging period of young) and first-year survival probability. Therefore, the breeding lifespan, which is usually used as the major indicator of fitness (in birds, e.g., Brown and Brown 1998), should be determined between infested and non-infested roosts. Finally, it can be assumed that the two observed behavior modes, allogrooming and self-grooming, do not serve exactly the same purpose. I suggest that in pipistrelles, self-grooming is used to remove ectoparasites (bat bugs), whereas allogrooming serves mainly for social functions.

Movement of bats and number of bugs

The emergence time of the last bat from the experimental box was shorter when a lower number of bat bugs were applied. A comparison of the number of bugs adhering to bats that left the bat box under low and high parasite load shows that bats react to one of the first bug bites and, when changing position and self-grooming is unsuccessful, they leave the box. Thus, the emergence time can correlate with changing (increasing) the success of bugs to find bats with body temperatures suitable for sucking and, at the same time, with a higher level of self-grooming. Consequently, the bats disturb each other and indirectly induce an increase in the body temperature of adjacent bats. As a result, these bats can also be attacked by bat bugs because of their higher body temperature. Experiments with artificial parasitation, when bugs were added to the roost manually, show that leaving confined roost occupied by a high number of ectoparasites is a natural reaction of crevice-dwelling bat species. However, vacation of the roost is not always needed; bats prefer changing location within the roost in case this strategy helps to reduce the parasite load. Therefore, further studies are needed in species occupying more spacious roosts, which allow effective changes of position.

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References

Adkins TR, Arant FS (1959) A technique for the maintenance of a laboratory colony of *Cimex lectularius* L. on rabbits. J Econ Entomol 52:685–686

Barclay RMR (1988) Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). Auk 105:53–60

Bartonička T (2007) Bat bugs (*Cimex pipistrelli*, Heteroptera) and roost switching in bats. Ber Naturforsch Ges Oberlausitz 15:29–36

Bartonička T, Řehák Z, Andreas M (2008) Diet composition and foraging activity of *Pipistrellus pygmaeus* in a floodplain forest. Biologia 63:1–7

Bartonička T, Gaisler J (2007) Seasonal dynamics in the numbers of parasitic bugs (Heteroptera, Cimicidae): a possible cause of roost switching in bats (Chiroptera, Vespertilionidae). Parasitol Res 100:1323–1330

Brigham RM, Vonhof MJ, Barclay RMR, Gwilliam JC (1997) Roosting behaviour and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). J Mammal 78:1231–1239

Brown RC, Brown WB (1986) Ectoparasitsm as a cost of coloniality in cliff swallows (*Hirundo pyrrhonata*). Ecology 67:1206–1218

Brown CR, Brown MB (1998) Fitness components associated with alternative reproduction tactics in cliff swallows. Behav Ecol 9:158–171

Christe P, Opplinger A, Richner H (1996) Begging, food provisioning, and nestling competition in Great Tit broods infested with ectoparasites. Behav Ecol 7:127–131

Christe P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). Ecol Lett 3:207–212

de Lope F, Moller AP (1993) Female reproductive effort depends on the degree of ornamentation of their mates. Evolution 47:1152–1160

Gannon MR, Willig MR (1995) Ecology of ectoparasites from tropical bats. Environ Entomol 24:1495–1503

Giorgi MS, Arlettaz R, Christe P, Vogel P (2001) The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). Proc R Soc Lond B 268:2071–2075

Gompper ME, Gittleman JL, Wayne RK (1997) Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim Behav 53:781–797

Hart BL (1994) Behavioural defense against parasites: interaction with parasite invasiveness. Parasitology 109:139–151

Hase A (1917) Die Bettwanze *Cimex lectularius* L.: ihr Leben und ihre Bekämpfung. Monogr Angew Entomol Z Angew Entomol Beiheft 4:1–144

Hecht O (1930) Hautreaktionen auf die Stiche blutsaugender Insekten und Milben als allergische Erscheinungen. Zentralbl Haut Geschl Krankh 44:241–255

Johnson CG (1941) The ecology of the bed-bug, *Cimex lectularius* L., in Britain. J Hyg 41:345–361

Jones RM (1930) Some effects of temperature and humidity as factors in the biology of the bedbug (*Cimex lectularius* Linn.). Ann Entomol Soc Am 23:105–119

Kerth G, Almasi B, Ribi N, Thiel D, Lüpold S (2003) Social interactions among wild female Bechstein‘s bats (*Myotis bechsteinii*) living in a maternity colony. Acta Ethologica 5:107–114

Lewis SE (1995) Roost fidelity of bats: a review. J Mammal 76:481–496

Loye JE, Carroll SP (1991) Nest ectoparasite abundance and cliff swallow colony site selection, nestling development, and departure time. In: Loye JE, Zuk M (eds) Bird–parasite interactions. Oxford University Press, Oxford, UK, pp 222–241

Marx R (1955) Über die Wirtsfindung und die Bedeutung des artspezifischen Duftstoffes bei *Cimex lectularius* Linné. Zeitschr Parasitenk 17:41–73

Montes C, Cuadrillero C, Villela D (2002) Maintenance of a laboratory colony of *Cimex lectularius* (Hemiptera: Cimicidae) using an artificial feeding technique. J Med Entomol 39:675–679

Moore J (2002) Parasites and the behavior of animals. Oxford series in ecology and evolution. Oxford University Press, New York

Mooring MS, Hart BL (1995) Differential grooming rate and tick load of terrestrial male and female impala. Behav Ecol 6:94–101

O'Brien TG (1993) Allogrooming behaviour among adult female wedge-caped capuchin monkeys. Anim Behav 46:499–510

Opplinger H, Richner H, Christe P (1994) Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success of the great tit (*Parus major*). Behav Ecol 5:130–134

Overal WL, Wingate LR (1976) The biology of the bat bug *Stricticimex antennatus* (Hemiptera: Cimicidae) in South Africa. Ann Natal Mus Pietermaritzb 22:821–828

Reckardt K, Kerth G (2006) The reproductive ecology of the bat fly *Basilia nana* (Diptera: Nycteribiidae) is affected by low roost fidelity of its host, the Bechstein's bat (*Myotis bechsteinii*). Parasitol Res 98:237–243

Reckardt K, Kerth G (2007) Roost selection and roost switching of female Bechstein's bats (*Myotis bechsteinii*) as a strategy of parasite avoidance. Oecologia 154:581–588

Rendell WB, Verbeek NAM (1996) Old nest material in nestboxes of tree swallows: effects on reproductive success. Auk 98:142–152

Richner H, Opplinger A, Christe P (1993) Effect of an ectoparasite on reproduction in great tits. J Anim Ecol 62:703–710

Rivnay E (1932) Studies in tropisms of the bedbug *Cimex lectularius* L. Parasitology 24:121–136

Sioli H (1937) Thermotaxis und perzeption von Wärmestrahlen bei der Bettwanze (*Cimex lectularius* L.). Zool Jahrb Physiol Morphol Tiere 58:284–296

Usinger RL (1966) Monograph of cimicidae (Hemiptera–Heteroptera). Entomological Society of America. Thomas Say Foundation, New York

Valenzuela JG, Walker FA, Ribeiro JMC (1995) A salivary nitrophorin (nitric-oxide-carrying hemoprotein) in the bedbug *Cimex lectularius*. J Exp Biol 198:1519–1526

Vonhof MJ, Barclay RMR (1996) Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. Can J Zool 74:1797–1805

Wilkinson GS (1986) Social grooming in the common vampire bat, *Desmodus rotundus*. Anim Behav 34:1880–1889

Willis CKR, Brigham RM (2004) Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, *Eptesicus fuscus*, conform to the fission–fusion model. Anim Behav 68:495–505

Zahn A, Rupp D (2004) Ectoparasite load in European vespertilionid bats. J Zool Lond 262:383–391