

Parasitol Res (2006) 98: 237–243
DOI 10.1007/s00436-005-0051-5

ORIGINAL PAPER

Karsten Reckardt · Gerald Kerth

The reproductive success of the parasitic bat fly *Basilia nana* (Diptera: Nycteribiidae) is affected by the low roost fidelity of its host, the Bechstein's bat (*Myotis bechsteinii*)

Received: 4 August 2005 / Accepted: 28 September 2005 / Published online: 10 December 2005
© Springer-Verlag 2005

Abstract We studied the reproductive ecology of the bat fly *Basilia nana* on free-ranging colonial female and solitary male Bechstein's bats (*Myotis bechsteinii*) during one reproductive season. The reproduction of *B. nana* took place from April to September, and the production of puparia in bat roosts was high. The metamorphosis of the flies took a minimum of 30 days, and at least 86% of the puparia metamorphosed successfully. However, only about 30% of flies from puparia deposited in female roosts and 57% of flies from puparia deposited in male roosts emerged in the presence of Bechstein's bats and were thus able to survive. The significantly higher emergence success of bat flies in male roosts was caused by the higher roost fidelity of the solitary males compared with the social females. Our results indicate that bats can control the reproductive success of bat flies by switching and selecting roosts.

Introduction

Host–parasite interaction is of high interest to evolutionary biologists. Parasites develop mechanisms to increase their fitness by exploiting the resources of their hosts. Hosts, in turn, attempt to maximise their own fitness by minimising the negative effects of parasite infestation. This leads to a co-evolutionary arms race between the parasite and the host, formulated in the “red queen hypothesis” (Van Valen 1973; Lively 1996).

Bat flies (Nycteribiidae and Streblidae), common and widespread ectoparasites of bats (Theodor 1967), attracted attention early on because of their interesting life cycle

(Schulz 1938; Ryberg 1947; Löhr 1953). The females of these holometabolous insects deposit their larvae on the wall of their host's roosts, where they pupariate and metamorphose independently of their hosts. After metamorphosis, the imagoes emerge only in the presence of a potential host (Ryberg 1947; Marshall 1971). Bat flies are wingless and are thus unable to actively search for their hosts.

The definite costs that bat flies impose on their hosts are unknown. However, ectoparasites can increase the costs of reproduction (Møller 1993; Bize et al. 2004), cause energetic costs (Giorgi et al. 2001), evoke the risk of disease transmission (Durden et al. 2004; Bowman et al. 1997) and may negatively influence growth and development (Fitze et al. 2004). Infestation with louse flies (Hippoboscidae) has negative effects on the condition of birds (Blanco et al. 2001), and similar effects can be assumed for bat flies, which are closely related to louse flies but infest bats instead of birds.

Low roost fidelity, observed in many bat species (Lewis 1995), could significantly reduce the reproductive success of bat flies and may thus have evolved as a parasite-avoiding behaviour. Bats that adapt their roosting behaviour to the life cycle of their parasites could avoid or reduce infestation with bat flies that have completed metamorphosis and are able to emerge from their puparia. To evaluate if roost switching indeed is effective in terms of parasite avoiding, substantial information about the reproductive biology of the bat flies is required. However, we lack crucial knowledge about the life history of bat flies. Furthermore, most of the scarce data that we have on the reproduction of bat flies stems from laboratory studies (Hase 1931; Schulz 1938; Ryberg 1947; Leong and Marshall 1968; Marshall 1970).

Lack of field data is probably a consequence of the difficulty to observe puparia of bat flies in their natural habitat, bat roosts in crevices or tree holes. As a consequence, little is known about the reproductive activity of bat flies, e.g. how many puparia an imago produces, which proportion of puparia is infectious, how long flies are able to survive in their puparium after metamorphosis, how fast flies can emerge from puparia after a host entered the roost

K. Reckardt (✉) · G. Kerth
Verhaltensbiologie, Zoologisches Institut,
Universität Zürich,
Winterthurerstrasse 190,
8057 Zurich, Switzerland
e-mail: reckardt@zool.unizh.ch
Tel.: +41-1-6355277
Fax: +41-1-6355490

and which signals trigger the emergence of bat flies from metamorphosed puparia.

Here, we present detailed field data on the reproductive biology of a bat fly species (*Basilina nana*, Diptera: Nycteribiidae). We investigated the reproductive activity and emergence success of bat flies and the developmental time and survival rate of puparia under natural conditions, in our case, in a female colony and in solitary males of the Bechstein's bat (*Myotis bechsteinii*, Chiroptera: Vespertilionidae).

Based on our data, we briefly discuss the possible co-evolutionary interactions between the life cycle of *B. nana* and the roost-switching behaviour of its host, the communally breeding Bechstein's bat. Frequent roost switching requires a great effort of coordination between female colony members (Kerth and Reckardt 2003) and is likely to affect central life history traits like group stability, individual associations among colony members and colony structure (Lewis 1996). Thus, parasitic bat flies could have great influence on the social structure of their hosts.

Materials and methods

Study species and study site

B. nana is an ectoparasite of several European bat species, primarily of those belonging to the genus *Myotis* (Hürka 1964). Bat flies are wingless and inhabit exclusively the fur of their hosts. We know from laboratory studies that, on average, every 9 days, females briefly leave their hosts to deposit a single larva on the wall of their host's roost. The puparium needs, on average, 30 days to metamorphose. In central Europe, reproduction seems to take place only in summer, as no winter records of puparia are known (Schulz 1938; Ryberg 1947—*B. nana* recorded as *B. nattereri* at that time).

Bechstein's bats represent an important, if not the primary, host of *B. nana* (Hürka 1964). Other Nycteribiidae species are not known from Bechstein's bats. Bechstein's bats live in deciduous forests in Europe. Females of this species are strictly philopatric and form nursery colonies of about 15 to 50 bats (Kerth 1998; Kerth et al. 2000). In central Europe, nursery colonies are formed by the end of April, and the females stay in the breeding habitat until September (Kerth 1998). The home range fidelity of nursery colonies is high, but within their home range, females switch very frequently between different roosts (Kerth et al. 2000, 2002). Nursery colonies use up to 50 roosts during one breeding season (Kerth and König 1996, 1999). In contrast, male Bechstein's bats live solitarily and switch roosts less often than females do (Kerth 1998; Kerth and Morf 2004).

From April to September 2002, we observed the reproductive phenology of *B. nana* in a nursery colony of Bechstein's bats, the "Blutsee" colony. This colony lives in a deciduous forest near the city of Würzburg (Germany). In

2002, it comprised 18 adult females and ten juveniles of both sexes. Colony members almost exclusively used bat boxes as day roosts (box type: Schwegler 2FN, Germany; Kerth 1998). Tree holes, the natural roosts of this species, are rarely used by the Blutsee colony. Bat boxes can be opened and checked for the presence of bat fly puparia. In addition to the female colony, seven male Bechstein's bats, as well as other mammals (e.g. *Apodemus* sp., Rodentia: Muridae; *Glis* sp., Rodentia: Gliridae), also used the bat boxes as roosts during the study period.

Monitoring the roost occupancy of bats and parasite infestation of boxes

The area that bats of the Blutsee colony use for roosting is small (about 0.5 km²). Since 1993, all bat boxes hanging in this area have been checked for the presence of Bechstein's bats at least two to three times per week during summer (Kerth 1998; Kerth et al. 2002). In summer 2002, about 150 bat boxes were available for the bats in this area. Many of them had been used by the colony for several years. In April 2002, before the bats returned to their summer habitat from hibernation, we counted the past years' remains of *B. nana* puparia in all boxes. Afterwards, we cleaned all boxes to eliminate every visible trace of puparia deposited in previous years.

From April 25 to September 17, we checked all bat boxes daily for the presence of Bechstein's bats. All 18 adult females of the Blutsee colony and the seven males present in the area were marked with passive integrated transponder (PIT) tags (Kerth and König 1996). This allowed us to individually identify roosting bats with a PIT-tag reader without opening the boxes and disturbing the bats. After the bats had left a box, we opened it and quantified and marked by felt pen all newly deposited puparia of *B. nana*. If a box had already been infested before, we also quantified the number of previously marked puparia from which flies had emerged during the presence of the bats. With this method, we were able to monitor the development of deposited puparia individually.

Metamorphosis and contagiousness of puparia

We used the natural roost-switching behaviour of the bats to estimate the duration of the metamorphosis and the contagiousness of the puparia. In each reoccupied bat box, we quantified the proportion of emerged puparia in relation to their age. The age of a puparium was calculated as the number of days between the date that a puparium was deposited in a roost and the date that a fly emerged from it. Since female Bechstein's bats generally stay a few days in each roost (on average, 3 days; Kerth and König 1999) before switching to the next, the day in the middle of each period that the bats stayed in a roost was used for the age calculation.

Table 1 Number of bat flies found on colonial female and solitary male Bechstein's bats throughout summer 2002

	Female colony			Males
	May 8	August 5	September 5	Summer
Capture date	May 8	August 5	September 5	Summer
Number of bats present	18	28 ^a	22 ^a	–
Number of bats captured	15	28 ^a	18 ^a	7
Number of flies counted	9	16	21	0 to 3 per individual
Infestation intensity	0.6	0.57	1.17	0.78
Prevalence	0.4	0.39	0.72	0.42

^aNumber of bats, including juveniles, born in June/July 2002

Monitoring parasite infestation of bats

In 2002, we captured the bats of the Blutsee colony and counted the number of flies per individual three times (May 8, August 5 and September 5). For this purpose, we first searched gently the fur, using tweezers, for about 1 min and then blew through the fur for another minute. Since Bechstein's bats are considered an endangered species and are protected by law, we were not allowed to handle females in June and July, during late pregnancy and early lactation. Thus, no data on parasite infestation of females are available for that period. Males were captured repeatedly throughout the summer. In autumn 2002, we collected bat flies from the colony for accurate identification (Theodor 1954). *B. nana* was the only bat fly that we could observe in the study area.

Roost temperatures

To determine a possible relation between roost temperature and the emergence process of flies from their puparia, we placed temperature loggers (iButton DS1921L-F53, Maxim/Dallas Semiconductor Corp. USA) in a total of 86 bat boxes in the area of the Blutsee colony. Most loggers were placed in boxes that were used by Bechstein's bats in previous years and could thus be expected to become also day roosts in 2002. The loggers were glued with silicon to the roof of each bat box, the place where most of the puparia were deposited. Temperature was recorded every half hour. Loggers glued to the outside wall of a box were used to measure external temperature.

Emergence experiment

To test how long the flies are able to survive in their puparia and, particularly, whether they can survive winter, we took 16 infested bat boxes in October 2002 (after the bats had left the area but before the boxes experienced frost) and seven infested boxes in March 2003 (after they experienced frost below -10°C) from the Blutsee area to our laboratory in Zurich. We stored them at a temperature of 26°C and a humidity of ca. 40% and used them for emergence experiments. To induce emergence, we used house mice (*Mus domesticus*, Rodentia: Muridae) kept under laboratory conditions. We prepared two plastic boxes (about 500 cm^2) as cages and equipped each with one of the infested bat

boxes. In each cage, we released three house mice, which subsequently used the bat boxes as nesting places. We left the bat boxes for a maximum of 4 days (if not all puparia emerged earlier) in the cages and afterwards quantified the number of flies that had emerged due to contact with the mice. We selected 4 days of exposure because this is slightly above the average time that Bechstein's bats spend in a given roost.

Results

Infestation of the bats

In May 2002, we captured 15 out of the 18 females present in the Blutsee colony. The 15 bats were infested with a total of nine bat flies. Based on the assumption that the average infestation intensity of the remaining three bats was similar to that of the 15 captured ones, we estimated an infestation intensity of about 11 bat flies for the whole colony of 18 bats. The estimated values of infestation intensity based on the capture events in August and September were 16 and 26 bat flies, respectively, for the whole colony (Table 1). The mean infestation intensity of the seven male Bechstein's bats captured in 2002 was 0.78 flies per bat (Table 1). The mean infestation intensity did not significantly differ between the colonial females and the solitarily living males (Mann–Whitney *U* test, $U=84.5$, ns).

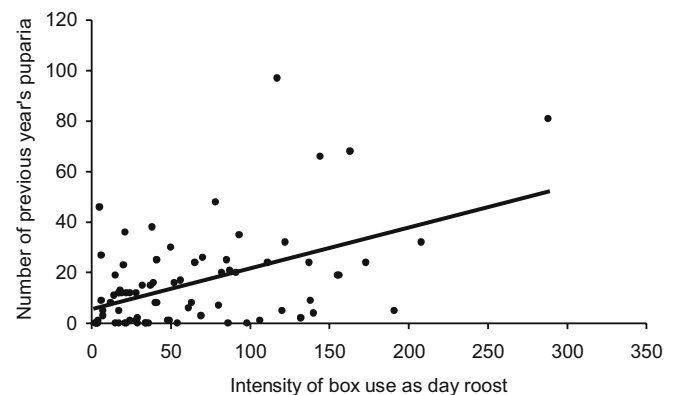
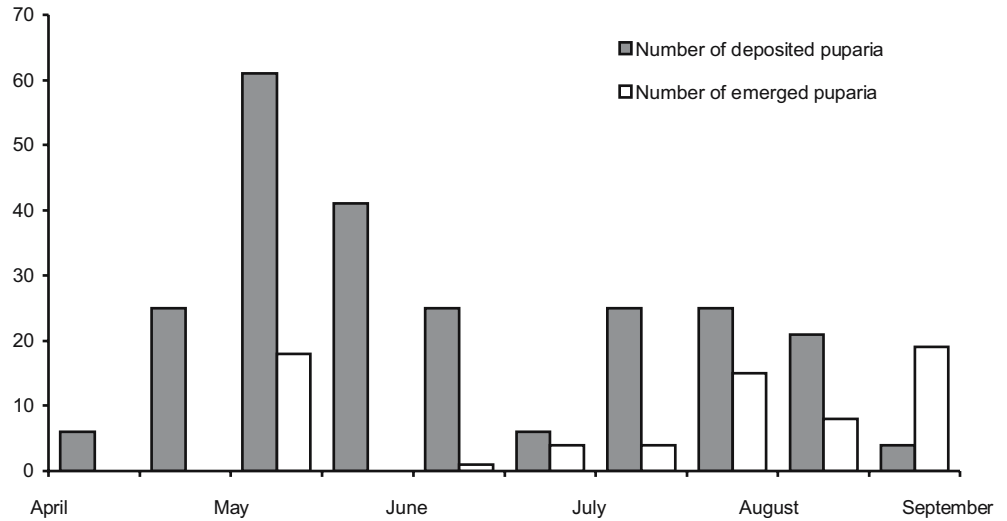


Fig. 1 Correlation between the intensity that bat boxes were used as day roosts between 1993 and 2001 and the number of remains of previous years' puparia found per box in spring 2002

Fig. 2 Reproductive activity of *B. nana* in the Blutsee colony. Number of deposited and emerged puparia in bat boxes used by the female colony during summer 2002



Reproductive activity of *B. nana*

In April 2002, before the bats returned to the Blutsee area, we found the remains of 1,262 puparia deposited in a total of 78 bat boxes in previous years. The number of puparia per box was significantly correlated with the intensity that these boxes were used as day roosts by the bats between 1993 and 2001. The intensity of roost use was calculated as the sum of daily numbers of bats using a particular bat box (Fig. 1; generalized linear model, SAS 8.1, proc genmod: $\chi^2=13.12, p<0.001$).

In 2002, the reproductive activity of bat flies in the female colony was highest at the end of May and the beginning of June. A second smaller peak appeared at the end of July and the beginning of August. In the first part of July, reproductive activity was clearly reduced. The emergence of bat flies took place in spring as well as in late summer and the beginning of autumn (Fig. 2).

In 2002, bat flies infesting the female colony deposited 233 puparia in 47 of the 49 bat boxes that were used as day roosts by members of the colony. During summer, 103 puparia (44%) later had contact with bats of the colony that

reoccupied 27 of the 47 infested boxes. Induced by the presence of the bats, 69 bat flies (30%) out of the 233 puparia deposited emerged and thus reinfested the colony (Fig. 3). Another 58 puparia emerged due to the presence of other mammals (e.g. *Apodemus* sp. and *Glis* sp.) in roosts that were not reoccupied by the bat colony. These bat flies did not survive since they could not infest an appropriate host.

The seven male Bechstein's bats living in the area used a total of only ten bat boxes as day roosts. Females used none of these boxes in 2002. In six of the ten bat boxes used by males, a total of 21 puparia were deposited by bat flies, which infested four of the seven males. Seventeen (81%) of these puparia later had contact with male Bechstein's bats, significantly more than in the females' roosts ($\chi^2=10.57, p<0.01$). Induced by contact with the males, 12 bat flies emerged out of the 21 deposited puparia (57%), again significantly more than in the females' case ($\chi^2=6.87, p<0.01$). However, the proportion of flies that emerged from only those puparia that had contact with a potential host after metamorphosis did not significantly differ between the female and male roosts ($\chi^2=0.11, ns$; Fig. 3).

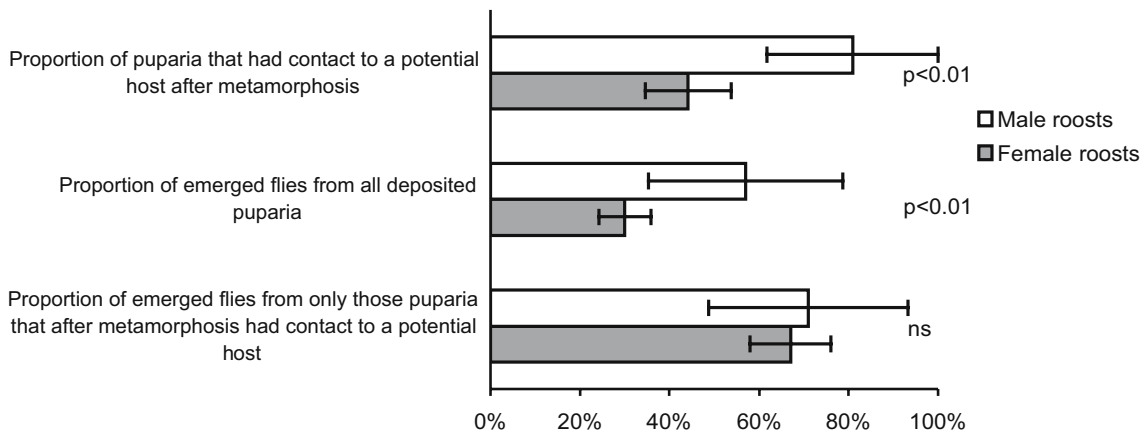


Fig. 3 Emerging success of *B. nana* in roosts used by male and female Bechstein's bats. Error bars: $\pm 95\%$ confidence interval

Table 2 Proportion of flies emerging from puparia under natural and under experimental conditions

Conditions puparia experienced	Natural conditions in the Blutsee colony					Experimental conditions					
						Only above zero			Also below zero		
Temperatures puparia experienced	1–29	30–49	50–69	70–89	90–109	110–200	200–300	300–400	400–500	300–400	400–500
Age of puparia (days)											
Number of puparia in contact with a host	34	24	13	5	11	2	31	6	8	4	21
Number of flies emerged through contact	0	11	10	5	10	2	17	4	6	0	0
Proportion emerged (%)	0	46	77	100	91	100	55	67	75	0	0

Nineteen puparia that we found in bat boxes in 2002 were of uncertain origin. Most likely, bat flies infesting male or female Bechstein's bats that were temporarily resting alone or in very small groups and were therefore overlooked during our roost monitoring also deposited these 19 puparia.

Metamorphosis and contagiousness of puparia

In our study area, no puparium emerged earlier than 30 days after deposition. This was obviously the minimum number of days that *B. nana* needed for metamorphosis. About 50% of flies emerged when in contact with Bechstein's bats 30 to 49 days after the puparium was deposited. The proportion of emerging flies reached a maximum of 100% between 70 and 89 days after deposition and decreased again afterwards (Table 2). The maximum number of days between deposition and emergence that we were able to observe in the field was 109 days. However, the potential maximum number of days that puparia could survive is much longer. In our laboratory, we observed emergence from puparia 457 days after they were deposited if brought in contact with house mice. Nevertheless, puparia that previously had experienced frost (below -10°C) in their natural habitat during winter 2002/2003 did not emerge later under laboratory conditions (Table 2).

We examined the minimum proportion of contagious puparia by quantifying the proportion of emerging flies in the 28 bat boxes that were reoccupied by a potential host 30 days after the puparia were deposited (the minimum number of days for a metamorphosis to take place). In 15 boxes reoccupied by Bechstein's bats, flies emerged from 36 out of the 53 deposited puparia (68%). In 13 boxes reoccupied by mammals other than Bechstein's bats (e.g. *Apodemus* sp. and *Glis* sp.), flies emerged from 58 out of the 94 deposited puparia (62%). The difference in the proportion of emerging flies between roosts reoccupied by Bechstein's bats and roosts reoccupied by other mammals was not significant (Mann–Whitney *U* test, $U=73.5$, ns).

In three infested boxes that were reoccupied twice by mammals (Bechstein's bats did not reoccupy infested boxes twice), altogether, 18 flies out of 21 puparia emerged (86%). This suggests that after metamorphosis, flies in at least 86% of the puparia are alive and capable of infesting a host.

Roost temperature and emergence

Increasing temperature due to roost occupation by the bats did not seem to have an influence on the emergence process of the bat flies. Average day temperature in the roosts significantly increased with the number of bats staying in the roost (Spearman rank correlation: $n_{\text{days}}=88$, $n_{\text{roosts}}=28$, $r_s=0.636$, $p<0.0001$). Nevertheless, the percentage of emerging flies from the puparia present in an occupied roost was not significantly correlated with the number of bats staying in the roost ($n_{\text{puparia}}=77$, $n_{\text{roosts}}=22$, $r_s=0.080$, ns), the number of days the bats were present in the roost ($n_{\text{puparia}}=77$, $n_{\text{roosts}}=22$, $r_s=-0.065$, ns) or the average roost temperature itself ($n_{\text{puparia}}=77$, $n_{\text{roosts}}=22$, $r_s=-0.241$, ns).

Discussion

Abandoning the host to lay eggs or deposit puparia can be risky for an ectoparasite when its active dispersal abilities are low. In this case, the survival of its offspring strongly depends on the behaviour of the host. As long as the host predictably returns to the same place, e.g. as in nesting songbirds, the parasite's strategy of depositing offspring in the host's roosts may be adaptive. The nests of songbirds provide an excellent breeding environment for ectoparasites, and many ectoparasitic arthropods, including mites, bugs, fleas and ticks, may have evolved specifically in such nest environments (Clayton and Moore 1997; Marshall 1981; Waage 1979). However, the strategy is risky when the host is highly mobile and unpredictable in its moving pattern.

The latter problem is faced by *B. nana*, which deposits its puparia in the roosts of the Bechstein's bat, a bat species that frequently switches its roosts (Kerth and König 1999; Kerth and Morf 2004). Frequent roost switching has been found in many bat species that use tree cavities as day roosts (Lewis 1995) and can also be observed in Bechstein's bats that roost in tree cavities instead of bat boxes (Kerth, unpublished data). Thus, roost switching is a natural behaviour of many bat species.

Low roost fidelity is thought to have, at least in part, evolved as a parasite-avoiding strategy (Lewis 1995). In our study site, the frequent roost switching of Bechstein's bats in fact led to the death of 70% of the puparia deposited in the roosts of female bats and 43% of the puparia deposited in the roosts of male bats. Our results show that

roost switching can be an effective strategy to reduce the reproductive success of bat flies infesting a bat colony.

Reproductive activity of *B. nana*

In accordance with Schulz (1938) and Archer and Cardinal (2001), our data show that bat flies reproduce in summer, between the end of April and the beginning of September, the breeding season of the host bats. The number of deposited puparia in May and June was surprisingly high (Fig. 2), particularly if we take into account that we estimated only 11 bat flies in the female colony shortly after it arrived from hibernation (Table 1). This can only be explained if we imply that adult bat flies, which survived the winter, reproduced very quickly in spring, with a much shorter interval between two successive births of a larva by a female than the previously reported 9 days (Schulz 1938). Intervals of 3 to 5 days between successive births were observed before in Nycteribiidae (in *Eucampsipoda sundaicum*, *Penicillidia actedona* and *P. sumatrensis*; Marshall 1971). An infestation of the female colony after it arrived from hibernation with bat flies emerging from puparia deposited in previous years is unlikely. Although our laboratory experiments showed that *B. nana* is able to survive in its puparium for more than 1 year, this was only the case when the puparia did not experience frost. Hence, puparia cannot survive the normal winter temperatures in central Europe (Table 2).

Our data suggest that at least two generations of bat flies exist per year: one generation that emerges in spring and reproduces during summer and autumn and one generation that emerges in autumn, survives the winter on their hosts and reproduces in spring. The longest life span of a bat fly imago observed in a laboratory was about 6 months (Schulz 1938; Marshall 1970), which indicates that overwintering imagos die not later than the following spring or summer. This could explain the low reproductive activity of flies at the beginning of July, the time when the overwintering flies probably have already died and the new generation has not yet emerged. Consequently, flies theoretically could disappear from the female colony during summer if bats could escape reinfestation by avoiding contact with infested bats or roosts previously used in the same year.

Metamorphosis and survival of puparia

Bat flies are obviously not able to decide in which roost to deposit their puparia. The strong correlation between the number of remains of puparia found in a box and the intensity bats used a box as a day roost between 1993 and 2001 confirms that the deposition of puparia mainly depends on the roost preferences of the host. The time when flies larviposit probably depends exclusively on an internal cycle and the developmental state of the larva. In the laboratory, Schulz (1938) observed that highly gravid

flies deposited their larvae even at unsuitable places when not provided with an appropriate surface.

The emergence of flies strongly depended on the behaviour of the host too. It took place independently of the number of bats that occupied an infested roost or the number of days that the bats spent in the roost. If Bechstein's bats reoccupied an infested roost after the flies had passed their metamorphosis, emergence was almost certain. In Bechstein's bats, males show higher roost fidelity than females do (Kerth 1998; Kerth and Morf 2004). As a result, puparia deposited in roosts used by male Bechstein's bats had a probability to emerge and reinfest Bechstein's bats that was twice as high as that of puparia deposited in females' roosts. The significantly higher proportion of flies that emerged in male roosts, however, only resulted from the significantly higher proportion of puparia that, after metamorphosis, had contact with the males relative to the females (Fig. 3). The proportion of flies that emerged from only those puparia that had contact with a potential host after metamorphosis was similar, regardless whether the host was a female colony member or a single male. This result shows that the reproductive success of the bat flies indeed depends on the roost fidelity and roost-selection behaviour of the host.

Why do bat flies not go locally extinct?

The production of puparia by bat flies is a phylogenetic constraint that makes flies susceptible to an effective behavioural defence by their hosts. The frequent roost switching of Bechstein's bats, especially of the females, significantly reduced the reproductive success of *B. nana*. The bat flies seemed to compensate for low roost fidelity in their hosts through the production of high numbers of puparia, which infested nearly every roost used by the female bats.

Theoretically, females could completely avoid previously used roosts. In that case, *B. nana* would die out locally since reinfestation during summer would be unlikely due to the social isolation of the female colonies (Kerth et al. 2002). However, under natural conditions, the number of suitable roosts might be too small to avoid reoccupation of the same roost during one breeding season. Moreover, some roosts might provide special conditions of temperature and humidity that outweigh the disadvantages of bat fly infestation. In addition, Bechstein's bat colonies regularly split into subgroups that use different roosts (Kerth and König 1999). Thus, even if the number of suitable roosts was high enough, reoccupation might occur because individuals of a colony might have only partial information on which roosts have been previously used by other colony members. Why the Bechstein's bats did not totally avoid reoccupation of roosts infested with contagious puparia remains unknown. However, it ensured reinfestation with a new generation of bat flies.

The deposition of puparia in the host's roosts provides this wingless and thus normally contact-transmitted ecto-

parasite with the possibility of horizontal transmission between hosts without direct body contact. During summer, Bechstein's bat colonies live isolated from both other female colonies and solitary males. Female Bechstein's bats of different colonies, even if they live in close proximity, do not use the same bat boxes as day roosts (Kerth et al. 2002). Therefore, direct exchange of bat flies between different nursery colonies is impossible. However, exchange of bat flies between male and female Bechstein's bats that subsequently use the same roosts (Kerth, unpublished data) is possible. As a result, transmission of bat flies through males, which move between colonies (Kerth et al. 2000; Kerth and Morf 2004), is likely. Thus, the deposition of puparia in the host's roosts may allow bat flies to partially counteract the negative effects that the social isolation of Bechstein's bat colonies has on their dispersal opportunities.

Acknowledgements We thank D. Dechmann, A. Ross-Gillespie, B. König and D. Turner for helpful comments on the manuscript. We are grateful to N. Bansac and S. Rauchfuss for their assistance in the field, to G. Lexa for leasing her apartment and to B. König for her constant support. The handling, marking and observation of Bechstein's bats were done under license from the nature conservancy department of the government of Lower Franconia. We gratefully acknowledge its support and that of the local department of forestry. This work was supported by the Swiss National Science Foundation (SNF; 31-59556.99).

References

- Archer MS, Cardinal BR (2001) Seasonal reproduction and host infestation rates for Nycteribiids of the large bentwing bat. *Med Vet Entomol* 15:452–454
- Bize P, Roulin A, Tella JL, Bersier JF, Richner H (2004) Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *J Anim Ecol* 73:1080–1088
- Blanco G, De la Puente J, Corroto M, Baz T, Colas J (2001) Condition-dependent immune defence in the Magpie: how important is ectoparasitism. *Biol J Linn Soc* 72:279–286
- Bowman AS, Coons LB, Needham GR, Sauer JR (1997) Tick saliva: recent advances and implications for vector competence. *Med Vet Entomol* 11(3):277–285
- Clayton DH, Moore J (1997) Host–parasite evolution: general principles and Avian models. Oxford University Press, Oxford
- Durden LA, Polur RN, Nims T, Banks CW, Oliver JH (2004) Ectoparasites and other epifaunistic arthropods of sympatric cotton mice and golden mice: comparisons and implications for vector-borne zoonotic diseases. *J Parasitol* 90(6):1293–1297
- Fitze PS, Clobert J, Richner H (2004) Long-term life-history consequences of ectoparasite-modulated growth and development. *Ecology* 85 (7):2018–2026
- 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 Biol Sci* 268:2071–2075
- Hase A (1931) Über die Lebensgewohnheiten einer Fledermausfliege in Venezuela; *Basilisa bellardii* RONDANI (Fam Nycteribiidae–Diptera Pupipara). *Z Parasitenkd* 3:220–257
- Hürka K (1964) Distribution, bionomy and ecology of the European bat flies with special regard to the Czechoslovak fauna (Dip, Nycteribiidae). *Acta Univ Carol Biol* 1964(3):167–234
- Kerth G (1998) Sozialverhalten und genetische Populationsstruktur bei der Bechsteinfledermaus (*Myotis bechsteini*). Wissenschaft und Technik Verlag, Berlin
- Kerth G, König B (1996) Transponder and an infrared-video camera as methods in a field study on the social behaviour of Bechstein's bats (*Myotis bechsteini*). *Myotis* 34:27–34
- Kerth G, König B (1999) Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteini*). *Behaviour* 136:1187–1202
- Kerth G, Morf L (2004) Behavioural and genetic data suggest that Bechstein's bats predominately mate outside the breeding habitat. *Ethology* 110(12):987–999
- Kerth G, Reckardt R (2003) Information transfer about roosts in female Bechstein's bats: an experimental field study. *Proc R Soc Lond B Biol Sci* 270:511–515
- Kerth G, Mayer F, König B (2000) Mitochondrial DNA (mtDNA) reveals that female Bechstein's bats live in closed societies. *Mol Ecol* 9:793–800
- Kerth G, Safi K, König B (2002) Mean colony relatedness is a poor predictor of colony structure and female philopatry in the communally breeding Bechstein's bat (*Myotis bechsteini*). *Behav Ecol Sociobiol* 52:203–210
- Leong MC, Marshall AG (1968) The breeding biology of the bat-fly *Eucampsipoda sundaicum* THEODOR, 1955 (Diptera: Nycteribiidae). *Malay Nat J* 21:171–180
- Lewis SE (1995) Roost fidelity of bats—a review. *J Mammal* 76 (2):481–496
- Lewis SE (1996) Low roost-site fidelity in pallid bats: associated factors and effect on group stability. *Behav Ecol Sociobiol* 39:335–344
- Lively CM (1996) Host–parasite coevolution and sex—do interactions between biological enemies maintain genetic variation and cross-fertilization? *Bioscience* 46(2):107–114
- Löhl H (1953) Fledermaus-Fliegen. *Nat Volk* 83:182–185
- Marshall A (1970) The life cycle of *Basilisa hispida* THEODOR 1967 (Diptera: Nycteribiidae) in Malaysia. *Parasitology* 61:1–18
- Marshall AG (1971) The ecology of *Basilisa hispida* (Diptera: Nycteribiidae) in Malaysia. *J Anim Ecol* 40:141–154
- Marshall AG (1981) The ecology of ectoparasitic insects. Academic, London
- Møller AP (1993) Ectoparasites increase the cost of reproduction in their hosts. *J Anim Ecol* 62:309–322
- Ryberg O (1947) Studies on bats and bat parasites. Bokförlaget Svensk Natur, Stockholm, Sweden
- Schulz H (1938) Über Fortpflanzung und Vorkommen von Fledermausfliegen (Fam. Nycteribiidae—Diptera, Pupipara). *Z Parasitenkd* 10:297–328
- Theodor O (1954) Nycteribiidae. In: Lindner E (ed.) Die Fliegen der paläarktischen Region, vol 12. Stuttgart, Germany, pp 1–43
- Theodor O (1967) An illustrated catalogue of the Rothschild collection of Nycteribiidae (Diptera) in the British Museum (Natural History). British Museum (Natural History), London, United Kingdom, pp viii, 1–506
- Van Valen L (1973) A new evolutionary law. *Evol Theory* 1:1–30
- Waage JK (1979) The evolution of insect/vertebrate association. *Biol J Linn Soc* 12:187–224