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Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats

Hannah M. ter Hofstede* and M. Brock Fenton

York University Biology Department, 4700 Keele Street, Toronto, Ontario, Canada M3J 1P3

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Abstract

Evidence suggests that behavioural defences, such as habitat selection and grooming behaviour, have evolved in animals in response to the costs associated with ectoparasites. Bat fly and mite densities were compared among wild-caught bats in Belize with different roosting preferences (cavity, foliage, or both), and grooming behaviour was analysed for bat species with high and low ectoparasite density. Ectoparasites of bats were removed using forceps, and bat grooming behaviour was recorded with a camcorder. Because bat flies pupate on the surface of host roosts, bats that use cavity roosts (a sheltered environment for the pupae) were predicted to have higher densities of bat flies than those that use foliage (exposed environment). Cavity-roosting species generally had higher densities of bat flies and mites, although the relationship was more evident for bat flies. The grooming behaviour of bats was predicted to differ among species with high or low ectoparasite densities. Although there was no difference in the frequency of grooming behaviours for individuals with and without bat flies, there were differences in grooming behaviour at the species level. Bat species with high ectoparasite densities scratched more than those with low ectoparasite densities. These results suggest that ectoparasite densities and grooming behaviour are related to roosting preferences in bats.

Key words: ectoparasite defence, habitat selection, grooming, Chiroptera, bat flies

INTRODUCTION

Ectoparasites can reduce the fitness of their hosts, either in terms of survival or reproductive success, and these fitness costs favour the evolution of host behavioural defences (Hart, 1992). Avoidance and removal of ectoparasites are two behavioural strategies animals use to reduce these costs. Hosts can avoid ectoparasites by living in habitats that are unsuitable for the parasite, and evidence of habitat selection as a defence against ectoparasites has been reported for a variety of animals (Hart, 1992). Habitat selection can occur over very short time periods, involving individual animals moving from locations with high to low ectoparasite abundance (caribou: Downes, Theberge & Smith, 1986; cliff swallows: Brown & Brown, 1992; great tits: Christe, Oppliger & Richner, 1994; badgers: Butler & Roper, 1996). Habitat selections could also occur on an evolutionary timescale as species become adapted to particular habitats owing to the fitness benefits associated with low ectoparasite abundance. Costs and benefits of particular habitats influence the evolution of behavioural traits, and low parasite abundance in certain habitats has been linked to less time spent grooming for various species (birds: Cotgreave & Clayton, 1994; elk: Mooring & Samuel, 1998; bovids: Mooring, Benjamin *et al*., 2000).

Grooming is another, but not mutually exclusive, means by which animals can reduce ectoparasite densities. Studies on the role of grooming in ectoparasite control have demonstrated increased host grooming with increased ectoparasite abundance and increased ectoparasite abundance following the prevention of host grooming (impala: Mooring, McKenzie *et al*., 1996; pigeons: Clayton *et al*., 1999; cats: Eckstein & Hart, 2000). Although grooming can be effective at controlling ectoparasites, it is a costly behaviour (water loss: Ritter & Epstein, 1974; decreased vigilance: Mooring & Hart, 1995; hair loss: Mooring & Samuel, 1999; energy expenditure: Giorgi *et al*., 2001). The evolution of a dominant strategy in a host species, either avoidance or removal, depends on whether the benefits outweigh the costs.

The purpose of this study was to determine if ectoparasite densities and grooming behaviour are related to habitat selection (in the form of roost preferences) in bats (order Chiroptera). Bat flies (order Diptera, families Streblidae and Nycteribiidae) and mites (order Acarina,

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*All correspondence to present address: H. M. ter Hofstede, Biology Department, University of Toronto at Mississauga, 3359 Mississauga Road North, Mississauga, Ontario, Canada L5L 1C6. E-mail: hhofsted@utm.utoronto.ca

families Spinturnicidae and Macronyssidae) are common ectoparasites of neotropical bats. Bats take refuge in roosts by day, and various bat species use roosts ranging from hollows (e.g. underground, in trees or in buildings) to crevices and foliage (Kunz, 1982; Kunz & Lumsden, 2003). Bat flies develop as larvae within the female fly, which deposits a third instar larva on the surface of the roost (Marshall, 1982). The larva immediately pupates, and when the adult emerges, it seeks a host (Marshall, 1982). Mites, however, are host-limited, completing their entire life cycle on the body of the host (Christe, Arlettaz & Vogel, 2000). These two life cycles vary in dependence on the roost of the bat: the reproductive success of bat flies (i.e. the pupal stage) depends on the roost of the host, whereas the reproductive success of mites, in comparison, is relatively independent of the host's environment.

The developmental biology of bat flies led to the hypothesis that bat flies are better adapted to bats roosting in cavities than those roosting in foliage because cavities provide a more protected environment for pupae than exposed (foliage) roosts (Jobling, 1949; Theodor, 1957; Wenzel, Tipton & Kiewlicz, 1966). Therefore, we predicted that cavity-roosting bat species would have greater bat fly densities than foliage-roosting species, but mite density should not be influenced by roost type. The differences in grooming behaviour among species with different roosting preferences and ectoparasite densities was also investigated. Given the assumption that ectoparasites are costly to their hosts, bat grooming behaviour was predicted to correspond with ectoparasite density at the species level.

MATERIALS AND METHODS

Study area

Data were collected from April to August 2001 at the Lamanai Archaeological Reserve (LAR) and the Lamanai Field Research Center (LFRC) in Belize, Central America. The LAR and LFRC are located along the west bank of the New River Lagoon (17°46′N, 88°39′W) within the Orange Walk District of Belize. The LAR, a 385-ha reserve of broadleaf deciduous forest, has an average daily temperature of 27 °C and an annual rainfall of 1480 mm (Lambert & Arnason, 1978). There are yearly cycles of rainfall; the dry season runs from *c*. January to June and the wet season from June to December (Lambert & Arnason, 1978).

Capturing bats and collecting ectoparasites

Bats were captured in 12 × 2 m mist-nets set at ground level along trails in the LAR. Nets were opened around dusk (18:00–20:30, average 18:45) and closed after about 10 bats had been captured for processing (19:00–23:45, average 21:10). On 2 occasions, 3 *Carollia perspicillata* were caught in their roosts using a hand-net, 1 in a chultun (an underground chamber built by the Maya) and 2 in a tunnel within a Maya temple. These individuals were included in the statistical analysis with individuals caught in mist-nets because the mean number of ectoparasites between the 2 methods of capture was similar. The nets were tended continuously, bats being removed as soon as possible after capture. While a bat was removed from the net and searched for parasites, a cloth bag was held around as much of the body as possible to reduce the number of ectoparasites that could escape. To prevent contamination of samples, bats were placed in separate cloth bags before processing. Forceps were used to remove all ectoparasites observed on the bats and they were preserved in vials of 70% ethanol. After a bag was used for a bat, it was washed and inspected before reuse to ensure the correct assignment of ectoparasites to bats. Usually ectoparasites were collected at the time of capture, whether the host bat was released immediately or held in captivity for recording grooming behaviour. Sometimes when bats were held for the grooming study, however, only the mites were removed, whereas the bat flies were counted and left on the body, so that bats grooming with and without bat flies could be videotaped. All bats were released at the site of capture, either that night or the next. Bat fly species are reported in ter Hofstede, Fenton & Whitaker (2004). Mites belonged to families Spinturnicidae and Macronyssidae, but were not identified to species. The following information was also recorded for each bat: sex, age (adult or juvenile), forearm length (mm), body mass (g), and reproductive condition (pregnant, lactating, non-reproductive).

Roosting data

Roosting preference information was obtained from the literature for the bat species of which > 10 individuals were captured. Bat species were classified as cavity-roosting if individuals usually roost in enclosed structures such as caves, hollow trees, or human-made structures (such as mines, buildings, or bridges). Bat species were foliage-roosting if individuals usually roost under branches or leaves. Some bat species regularly use both roost types and were classified as both. This classification allowed for uncertainty in roosting preferences; although these bat species may be capable of using either roost type, they may not be using both roost types in this particular area. *Sturnira lilium* was 1 species that was known to use both roost types, based on a previous study in this area (Fenton, Vonhof *et al*., 2000).

Grooming data

Five frugivorous bat species of the family Phyllostomidae (7 *Artibeus intermedius*, 5 *Artibeus phaeotis*, 5 *Artibeus watsoni*, 15 *Glossophaga soricina*, and 12 *Sturnira lilium*; Table 2) were brought to the field centre at the end of each night and held in cylindrical wire cages covered with cotton cloths. To videotape grooming behaviour, 8-mm videotapes and a video camcorder (Canon ES2500)

Table 1. Sample sizes, mean body size measurements (FA, forearm length; M, body mass), roost type category and roosting information sources for bat species captured at Lamanai, Belize

		Mean ± SE		
Bat species	*n*	FA (mm)	M (g)	Roost type and roosting information sources
Artibeus intermedius Allen	21	66.5 ± 0.3	54.4 ± 1.4	Both: Reid, 1997
Artibeus jamaicensis Leach	39	60.4 ± 0.4	43.4 ± 1.1	Both: Villa-R, 1966; R. E. Goodwin, 1970; Foster & Timm, 1976; Morrison, 1979; Taboada, 1979; Kunz, August & Burnett, 1983; Kunz & McCracken, 1996; Ortega & Castro-Arellano, 2001
Artibeus lituratus Olfers	13	71.6 ± 0.5	71.3 ± 2.8	Both: G. G. Goodwin & Greenhall, 1961; Villa-R, 1966; Morrison, 1980; Dickerman, Koopman & Seymour, 1981; Simmons & Voss, 1998
Artibeus phaeotis Miller	58	38.4 ± 0.2	13.7 ± 0.3	Foliage: Timm, 1985, 1987
Artibeus watsoni Thomas	13	38.1 ± 0.2	11.4 ± 0.3	Foliage: Choe & Timm, 1985; Timm, 1987; Choe, 1997; Stoner, 2000
Carollia brevicauda Schinz	31	40.1 ± 0.4	16.0 ± 0.3	Cavity: Graham, 1988; Fenton, Bernard *et al*., 2001.
Carollia perspicillata Linnaeus	12	44.7 ± 0.3	21.4 ± 0.9	Cavity: G. G. Goodwin & Greenhall, 1961; Villa-R, 1966; Fleming, 1988; Graham, 1988; Cloutier & Thomas, 1992; Simmons & Voss, 1998
Desmodus rotundus E. Geoffroy	11	58.4 ± 0.5	34.1 ± 1.3	Cavity: G. G. Goodwin & Greenhall, 1961; Villa-R, 1966; Wimsatt, 1969; Greenhall *et al*., 1983; Wilkinson, 1985; Graham, 1988
Glossophaga soricina Pallas	65	35.7 ± 0.1	10.1 ± 0.1	Cavity: G. G. Goodwin & Greenhall, 1961; Villa-R, 1966; R. E. Goodwin, 1970; Graham, 1988; Simmons & Voss, 1998; Fenton, Bernard *et al*., 2001
Pteronotus parnellii Gray	12	57.1 ± 0.5	19.3 ± 0.8	Cavity: Taboada, 1979; Herd, 1983; Graham, 1988
Sturnira lilium E. Geoffroy	107	38.0 ± 0.1	15.8 ± 0.2	Both: G. G. Goodwin & Greenhall, 1961; Villa-R, 1966; Wohlgenant, 1994; Fenton, Vonhof *et al*., 2000

were used. Bats were placed in an observation box for videotaping. The observation box was 0.61 m high with a 0.30 m^2 base; 2 adjacent sides were made of wood and 2 of lexan polycarbonate. A wooden rod placed diagonally from 1 wooden side to the other, *c*. 0.15 m from the top, functioned as a perch for the bat. All videotaping was conducted by day in a quiet room. A bat was placed on the perch in the observation box while 1 person was present to observe it, and the video camera was set to record. If a spontaneous grooming bout did not occur within 5 min, the bat was fed sugar water. If it again did not groom in 5 min, it was fed a piece of fruit. These food items were given to stimulate grooming, not reward the bat, since only the first grooming bout for each animal was analysed. For bats with bat flies, the number of flies on the bat were counted before putting it in the observation box for videotaping. After videotaping, the bat was removed from the observation box and all the bat flies immediately collected using the same protocol as before.

Footage of bats grooming were transferred from 8 mm tape to VHS and the capture feature of VideoWave software (version 4) was used to convert the video component of the VHS tape to MPEG-2 format. VideoWave software was used to view the MPEG files frame-by-frame (30 frames/s). The following terminology was used to describe grooming behaviour: *a bout* refers to the entire time a bat is grooming and is considered to be over when 5 min has passed with no grooming activity; *an event* refers to the occurrence of 1 type of grooming behaviour, separated in time by other grooming behaviours or inactivity. For example, a scratching event could consist of 1 or more scratches followed by some other grooming behaviour, such as licking. All grooming events were described and classified for each bat videotaped and the start and end times of grooming events within the video were recorded to calculate durations.

Data analysis

SPSS (version 10) and SigmaStat (version 3.0) were used to analyse the data. To control for differences in body size among bat species, the number of ectoparasites/mm forearm length was used as a measure of ectoparasite density. Forearm length was less variable than body mass (Table 1), which fluctuates with reproductive status. Individuals from 3 bat species (*Carollia perspicillata*, *Desmodus rotundus* and *Pteronotus parnellii*) were so heavily infested with mites that not all of them could be collected using our methods. To avoid biased results by using data only from the few individuals for which all the mites could be collected, these 3 bat species were excluded from statistical comparisons relating to mite density (their data, however, are still included in the figures for comparison).

Two variables (frequency and duration) were compared for 2 grooming behaviours (scratching and licking). Scratching was always performed with the hind feet, not the thumbs. Frequency of scratching was measured as the number of scratching events during a grooming bout, not the number of individual scratches, and the same was true for licking. Duration was measured as the total duration of

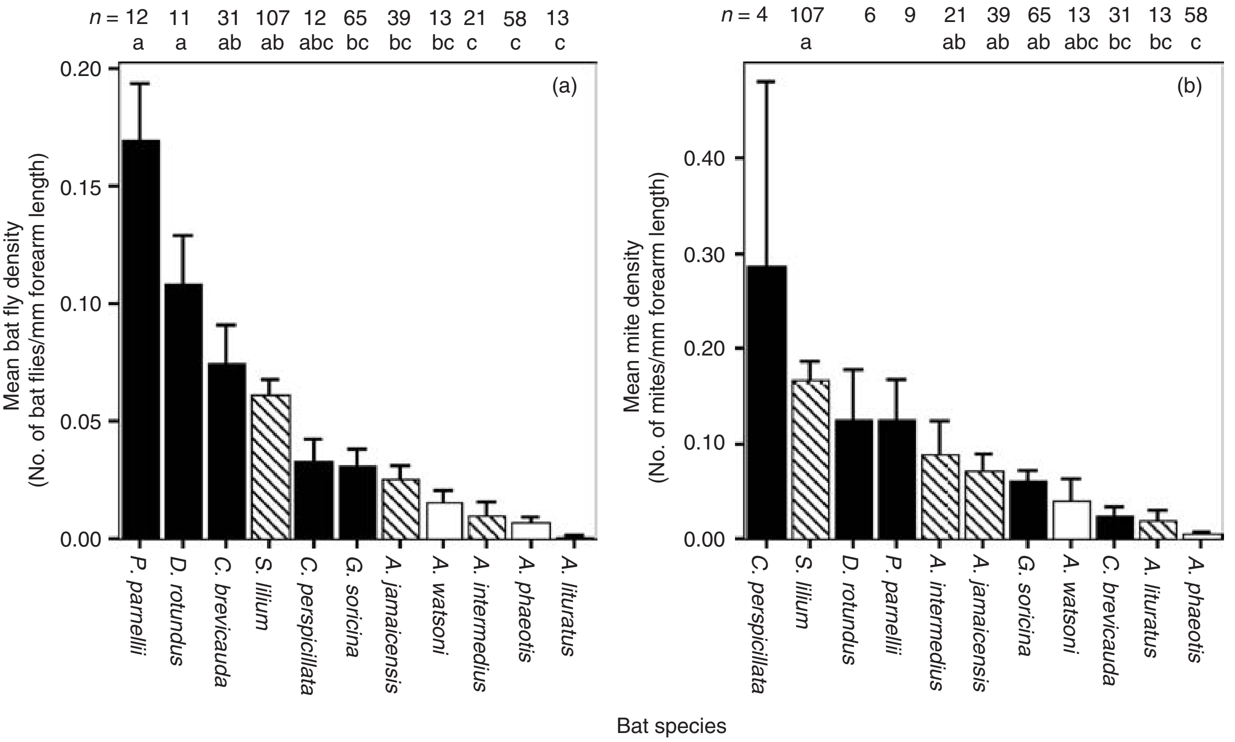

Fig. 1. Mean ectoparasite density for 11 bat species captured at Lamanai, Belize: (a) mean bat fly density; (b) mean mite density. Black bars, cavity-roosting species; hatched bars, species that roost in both cavities and foliage; white bars, foliage-roosting species. Different letters above the bars represent significant differences (species lacking letters were excluded from statistical analysis). Error bars are 1 SE.

each grooming behaviour (chewing, scratching or licking) per bout (s). To allow for parametric statistical tests, these data were transformed by adding 3/8 to each value and taking the square root, recommended for data with many small numbers (especially zeros) and with correlating means and variances (Zar, 1999).

RESULTS

Roost preferences and ectoparasite density

More than 10 individuals of 10 Phyllostomidae and one Mormoopidae (*P. parnellii*) were captured. Five species were designated as cavity-roosters, two species as foliage-roosters, and four species as regularly using both roost types (Table 1). The density of bat flies and mites compared among bat species included all parasite species combined for each group. Both mean bat fly density (Kruskal–Wallis test: $H_{10} = 119.7$, $P < 0.001$; Fig. 1a) and mean mite density (Kruskal–Wallis test: $H_7 = 101.2$, $P < 0.001$; Fig. 1b) differed significantly between some bat species. Cavity-roosting species generally had higher densities of both ectoparasites, although the relationship was more evident for bat flies than for bat mites.

Grooming behaviour

Grooming bouts often occurred after the bat drank sugar water (41), whereas grooming bouts after eating fruit (25) and spontaneous grooming bouts (22) occurred less often. This distribution was representative of what occurred within each species as well. The most common grooming behaviours were licking, scratching and chewing the hind claws. Bats licked by rubbing their tongues in short strokes over the surface of the body, and they directed licking mostly to the membranes (usually the wings, but also the tail membrane). Bats scratched repeatedly and rapidly, hanging by one foot and pulling the claws of the other foot through the fur like a comb. Bats usually scratched the fur, only occasionally scratching the wings. Chewing the hind claws consisted of bringing the hind claws to the mouth and scraping the claws over the lower incisors. Bats chewed the thumb claw and licked the thumbs in the same manner.

Bats either had or did not have bat flies during the grooming bout (Table 2). Two species had large enough sample sizes to test for the effect of bat flies on the frequency of scratching (*S. lilium*: eight with and four without bat flies; *G. soricina*: seven with and eight without bat flies). A two-factor analysis of variance (ANOVA), with bat species as factor one and the presence or absence of bat flies during the grooming bout as factor two, resulted in no interaction between factors ($F_{1,23} = 3.166$, $P = 0.088$) and no significant differences between species ($F_{1,23} = 2.185$, $P = 0.153$) or presence or absence of bat flies ($F_{1,23} = 3.944$, $P = 0.059$). Because there were no significant differences in scratching frequency between bats with or without bat flies, data for all bats observed were pooled for the following tests.

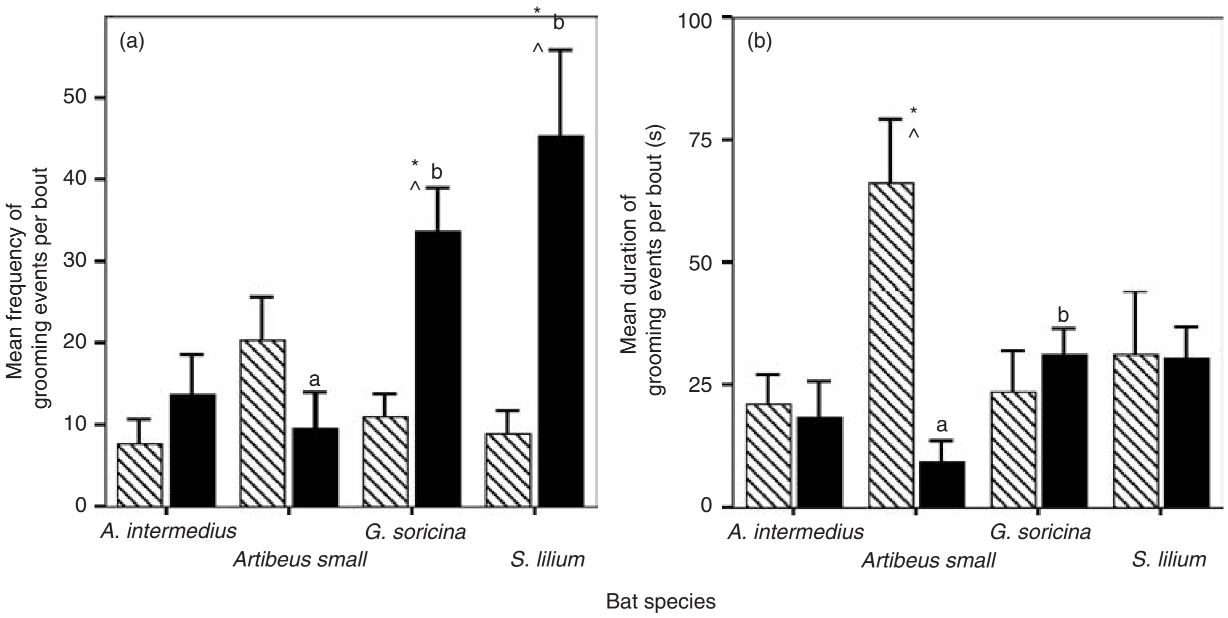

Fig. 2. Frequency and duration of licking (hatched bars) and scratching (solid bars) events for four bat species: (a) mean frequency of grooming events per bout (events/bout); (b) mean duration of grooming events per bout (s/bout). Error bars are 1 SE. *, significant differences between grooming behaviours within species; different letters, significant differences between species for a grooming behaviour.

Table 2. Summary of grooming experiments for bat species, with number of bat flies during grooming bout and sample sizes

Species	No. of bat flies during grooming bout	No. of bats
Artibeus intermedius	0	6
	1	1
Artibeus small	0	8
	1	2
Glossophaga soricina	0	8
	1	5
	2	1
	3	1
Sturnira lilium	0	4
	1	2
	2	2
	3	1
	4	1
	5	2

Comparing grooming variables between and within species

Data for *A. phaeotis* and *A. watsoni* were pooled for the grooming tests (*Artibeus* small) owing to the physical similarity of these species, lack of difference in ectoparasite density (Fig. 1), similarity of roosting preferences (both are tent roosting species), and infestation by the same bat fly species (*Neotrichobius stenopterus*; ter Hofstede *et al*., 2004). A two-factor repeated measures MANOVA was run, with species as a between-subjects factor (four levels: *A. intermedius*, *Artibeus* small, *G. soricina*, and *S. lilium*) and grooming behaviour as a within-subjects factor (two levels: scratching and licking) for two variables (frequency and duration). There was a significant interaction between the two factors of the MANOVA (Pillai's trace: $F_{6,80} = 6.300$, $P < 0.001$); therefore, 20 pairwise tests were conducted to determine significant differences between and within bat species. Six significant differences were found (three between species and three within species; Fig. 2) after a Bonferroni correction for 20 tests ($\alpha = 0.0025$). Scratching, but not licking, differed significantly between species. The small *Artibeus* scratched significantly less frequently than *G. soricina* ($F_{1,40} = 10.929, P = 0.002$) and *S. lilium* ($F_{1,40} = 15.472$, $P < 0.001$). The small *Artibeus* also scratched for significantly less time than *G. soricina* ($F_{1,40} = 11.222$, $P = 0.002$). Both *G. soricina* ($F_{1,40} = 21.065$, $P < 0.001$) and *S. lilium* ($F_{1,40} = 35.011$, $P < 0.001$) scratched significantly more frequently than they licked, and the small *Artibeus* spent significantly more time licking than scratching ($F_{1,40} = 22.798$, $P < 0.001$).

DISCUSSION

Cavity-roosting species typically had higher ectoparasite densities than foliage-roosting species. *Sturnira lilium* had many bat flies for a species using both types of roosts (Fig. 1a). This could reflect a general lack of data about roosts used by *S. lilium* (Fenton, Vonhof *et al*., 2000) or a preference of *S. lilium* for cavity roosts. While the pattern of mite and bat fly density among species was generally similar, two species had very different densities of bat flies and mites. *Artibeus intermedius* had low mean bat fly density but relatively high mean mite density, while the opposite was true for *C. brevicauda*. The foliage-roosting species (*Artibeus* spp. and *S. lilium*) are most closely related to each other, followed by *Carollia* spp. and the rest of the cavity-roosting species (Wetterer, Rockman & Simmons, 2000), suggesting that roosting preference may map to phylogeny and also influence ectoparasite density.

Exposed roosts may not be ideal for the development of bat fly pupae (Jobling, 1949; Theodor, 1957; Wenzel *et al*., 1966), but decreased roost fidelity and smaller group sizes in foliage-roosting bats could also negatively affect ectoparasite populations. Timm (1987) suggested tent-roosting could help control ectoparasites. Foliage-roosting bats tend to switch roosts more often than cavity-roosting bats, perhaps because foliage roosts are ephemeral and abundant (Lewis, 1995). Lewis (1996) found that, similarly to the chamber-switching behaviour of the badger *Meles meles* (Butler & Roper, 1996), the amount of roost-switching in *Antrozous pallidus* correlated positively with the number of ectoparasites, and she believed roost-switching interrupts the life cycle of ectoparasites that spend part of their life cycle within the roost (e.g. bat flies). Roost-switching, however, would not reduce populations of permanent ectoparasites, such as mites. Ectoparasites with limited mobility generally increase in abundance with increasing host group size (Côté & Poulin, 1995), and Kunz (1976) found that the level of bat fly infestation increased with group size on roosting *Plecotus townsendii*. Foliage-roosting bats usually live in smaller groups than cavity-roosting bats (Kunz, 1982), so observed differences in ectoparasite abundance could reflect group size. The distribution of bat wing mites is not related to environmental variables, such as rainfall and vegetation (Sheeler-Gordon & Owen, 1999), perhaps making group size the most important factor for these ectoparasites.

Differences in the grooming behaviour of bats at the species level reflected differences in mean ectoparasite density. Bats seem to defend themselves against ectoparasites through scratching, not licking, because bat species (*Artibeus* small) with the lowest mean density of bat flies scratched less per grooming bout than the two species with higher mean bat fly densities (*G. soricina* and *S. lilium*) and licked more than they scratched, while the opposite was true for *G. soricina* and *S. lilium*. Two studies found no skin reactions in response to bat fly bites on two species of neotropical bats (Overal, 1980; Fritz, 1983), suggesting that scratching is not a reaction to skin irritation. Scratching was predominantly directed toward the fur and licking towards the wing membranes (ter Hofstede *et al*., 2004). This difference in grooming behaviours reflects differences in host-site preference: mites were almost only found on the membranes, whereas 13 of 22 bat fly species preferred fur over membrane, and each bat species had at least one bat fly species that specialized on fur (ter Hofstede *et al*., 2004). This suggests that scratching is directed more towards bat flies than towards bat mites. Although stress owing to capture may have played a role in the behaviour of these animals, no specific difference in stress level between species was noticed. The fact that individuals with and without bat flies did not demonstrate a statistical difference in grooming behaviour could have been owing to the small number of bat flies used in the experiment (Table 2).

Vertically transmitted parasites, those passed from host parents to offspring, are hypothesized to be less harmful to their hosts than horizontally transmitted parasites, those that move easily among host individuals, because the fitness of vertically-transmitted parasites depends on the successful reproduction of their hosts (Clayton & Tompkins, 1994). This theoretical argument has been supported by experimental studies on several taxa (bacteria and bacteriophage: Bull, Molineux & Rice, 1991; fig wasps and nematodes: Herre, 1993; rock doves and ectoparasitic arthropods: Clayton & Tompkins, 1994). Bat flies pupate on the surface of the roost, and this life stage off the host provides an opportunity to seek new hosts. Observational studies of the movement of bat flies indicates that they move quickly and easily among bats in a group (Overal, 1980; Fritz, 1983), suggesting that bat flies should be considered horizontally transmitted ectoparasites. By comparison, mites generally require physical contact to be transmitted from one individual to another. Although it is possible for mites to move among unrelated bats roosting in physical contact, Christe, Arlettaz *et al*. (2000) found that mites increased in number on pregnant bats in colonies and then moved onto their offspring to reproduce. This suggests a vertical mode of transmission for mites. Perhaps bat flies are more costly than mites thus providing the selection pressure for the evolution of differences in grooming behaviour among bat species with different densities of bat flies. Bat flies have been recovered from the stomachs of some neotropical bats, and *A. jamaicensis* will consume streblids if offered them (Overal, 1980), but the absence of reports of bats grasping bat flies with their claws and eating them suggests that direct mortality of bat flies owing to grooming is rare. Scratching might function in some other way, such as forcing flies to move frequently so they have less time to feed, as observed for tabanid flies on horses (Waage & Davies, 1986).

Our data on bat flies and mites and published data on roost preferences provided support for the hypothesis that foliage-roosting corresponds with lower ectoparasite density than cavity-roosting. The analysis supports the prediction that high densities of bat flies are associated with sheltered roosts, whereas mites are less affected by roost conditions. Bats did not groom differently when bat flies were present or absent during a grooming bout, but there were differences in grooming behaviour at the species level. Specifically, scratching was more frequent in species with a high ectoparasite density.

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