Host and host-site specificity of bat flies (Diptera: Streblidae and Nycteribiidae) on Neotropical bats (Chiroptera)

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Abstract: Ectoparasite host specificity can be influenced by factors such as the degree of host isolation and ectoparasite mobility. Host-site specificity can result from factors such as proximity to mates, competition, and host grooming behaviour. Ectoparasitic bat flies on bats from the Lamanai area of Belize were collected from hosts captured in mist nets to determine host specificity and host-site specificity. Bat grooming behaviour was also recorded and quantified. From 455 bats (25 species in five families), 773 bat flies (32 species in two families) were collected. Of 32 bat fly species, 25 were only found on 1 bat species, 6 were found on 2 species of the same genus, and 1 was found on 2 species of different genera (the latter appearing to be an accidental association). Specificity of the bat flies tended to follow the taxonomy of the bat hosts, not the ecological isolation of the host species, since bat species that often roost in polyspecific groups did not share bat fly species. Mobility of the bat flies was not related to host specificity. Host-site specificity of bat flies occurred for either fur or membrane on the host, and long hind legs and ctenidia appear to be morphological adaptations for living in fur. Bat grooming behaviour was consistent with the assumptions of a simulation model, which suggested that host grooming could be responsible for host-site segregation of bat flies.

Résumé : Des facteurs, tels que le degré d'isolement de l'hôte et la mobilité de l'ectoparasite, peuvent influencer la spécificité d'hôte des ectoparasites. La spécificité de site sur l'hôte peut résulter de facteurs comme la proximité des partenaires sexuels, la compétition et le comportement de toilettage de l'hôte. Afin de déterminer la spécificité d'hôte et la spécificité de site sur l'hôte, nous avons prélevé dans la région de Lamanai au Belize des mouches stréblides et nyctéribiides, ectoparasites de chauves-souris, chez des hôtes capturés au filet japonais. Nous avons aussi noté et quantifié les comportements de toilettage. Nous avons récolté 773 mouches (32 espèces appartenant aux deux familles) chez 455 chauves-souris (25 espèces appartenant à cinq familles). Des 32 espèces de mouches, 25 se retrouvent sur une seule espèce de chauve-souris, 6 sur 2 espèces du même genre et 1 sur 2 espèces de genres différents (cette dernière association paraît être fortuite). La spécificité des mouches semble reliée à la taxinomie des chauves-souris hôtes et non pas à l'isolement écologique des hôtes, puisque des espèces de chauves-souris qui partagent souvent les mêmes perchoirs plurispécifiques n'ont pas les mêmes espèces d'ectoparasites. La mobilité des mouches n'est pas reliée à la spécificité d'hôte. La spécificité de site des mouches se manifeste pour la fourrure ou pour la membrane de l'hôte et les longues pattes postérieures et les cténidies des mouches semblent être des adaptations morphologiques pour la vie dans la fourrure. Le comportement de toilettage chez les chauves-souris est en accord avec les présuppositions du modèle de simulation qui avance que le toilettage de l'hôte peut être responsable de la ségrégation des mouches ectoparasites dans des sites particuliers sur les chauves-souris.

[Traduit par la Rédaction]

Introduction

Host specificity and host-site specificity of ectoparasites generally reflect morphological, behavioural, and physiological characteristics of ectoparasites and hosts. Variability in roosting preferences and ectoparasite fauna make tropical bats good candidates for investigating the influence of host and parasite ecology on ectoparasite specificity. We selected bat flies (Diptera: Streblidae and Nycteribiidae) for this study because they pupate on the surface of the host's roost, and thus are highly dependent on the roost for reproduction. Although early studies of bat fly host specificity concluded that bat flies were heteroxenous (capable of infesting many species in many genera) (e.g., Jobling 1949; Theodor 1957), others stressed that these studies often resulted in erroneous associations because they relied on museum specimens or were by-products of other research (e.g., Wenzel et al. 1966; Marshall 1976; Marshall 1981, 1982*a*). More recent studies of bats and bat flies in Panama (Wenzel et al. 1966) and the New Hebrides (Marshall 1976) used techniques to prevent contamination of specimens and concluded that bat flies were highly host specific. With a sample of more than

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12 000 bat flies, Wenzel et al. (1966) reported that 55% of the streblids collected in Panama were monoxenous (only found on one host species), 15% were monoxenous but were occasionally found on other species as a result of accidental associations, 13.5% were stenoxenous and were found on host species of the same genus, and only 15% were oligoxenous and found regularly on hosts of different genera. These results demonstrated that although most bat flies were highly specific, there was variability in specificity that could be due to differences in bat fly or host morphology and behaviour.

Ectoparasite mobility can be an important factor in determining host specificity. Parasites with restricted mobility are more likely to be host-specific because they are less capable of finding new hosts than highly mobile parasites (Wenzel et al. 1966; Marshall 1976, 1981). Feather mites have highly restricted mobility and are usually host specific, but they will colonize non-host feathers if placed in contact with them (Bridge 2002). Parasites that complete their entire life cycle on the host (host-limited parasites) are highly dependent on the host for reproduction and are more specific than those that spend part of their life cycle off of the host (Wenzel and Tipton 1966; Marshall 1976, 1981). In general, these two factors are closely related because host-limited ectoparasites tend to also be restricted in mobility, but exceptions can occur if the isolated nature of the host maintains specificity despite mobile free-living stages of the parasite (Hafner et al. 2000; Wenzel and Tipton 1966). Bat flies are relatively uniform in terms of their dependence on the host because all bat flies develop as larvae within the female, pupate on the surface of the host's roost, and live as adults on the host's body. They can differ in their mobility, however, because some species have functional wings, whereas others lack them. No nycteribiids can fly, whereas about 80% of streblid species have functional wings (Whitaker 1988).

The ecological isolation of the host can also influence the specificity of ectoparasites; wide-ranging hosts will come into contact with more animals and habitats and be exposed to more potential ectoparasites than ecologically isolated hosts (Wenzel and Tipton 1966; Marshall 1981). In Panama, Wenzel and Tipton (1966) found that the opossum (*Didelphis marsupialis* Linnaeus, 1758) had the largest number of ectoparasite species, a few of which were characteristic of marsupials but none that were monoxenous, reflecting the species' large range in Central America and its generalist nature. Competition among ectoparasites may result in increased specificity, although evidence that competition is a factor for ectoparasites is difficult to obtain. Competition could explain why one host usually does not support two or more closely related species (Marshall 1976), but the naturally low abundance of ectoparasites does not suggest competition for space or food on the host (Waage 1979), although abundance necessary for competition is usually not known. Several authors have described morphological and behavioural adaptations of ectoparasites apparently specialized for one host, and such specialization may maintain host specificity even when barriers to transmission are removed (Overal 1980; Tompkins and Clayton 1999).

The host is the ectoparasite's habitat (Bush et al. 1997), and there may be parasite specialization for particular sites or locations on the host. Specialization on a body area can only occur if there is variability among areas on the body of the host, so a complex body surface may be a prerequisite for host-site specificity. Previous extensive surveys (Wenzel and Tipton 1966; Marshall 1981) revealed that birds, which have a more complex body covering than mammals, tended to have more site-specific ectoparasites. In body surface complexity, bats represent an intermediate group between birds and most mammals because large areas of the body are composed of either naked skin (wing and tail membranes) or fur (bodies). These areas of bats provide two distinctly different habitats for ectoparasites, making specialization between these two areas possible.

Host-site specificity in ectoparasites can be caused by intraspecific factors (i.e., proximity to mates), competition, or host defences (Wenzel and Tipton 1966; Rohde 1979; Waage 1979; Marshall 1981). Rohde (1979) suggested that the chances of finding a mate were enhanced by specializing on one location on the host's body, but Rohde worked primarily with monogenean ectoparasites of marine fish, which were highly restricted in their mobility. Bat flies can move easily and quickly over the entire body of their host (Overal 1980; Fritz 1983), so specializing on fur or membranes should not enhance the ability of a bat fly to find a mate. Competition among ectoparasite species for resources is another possible cause of site specificity, but the evidence is anecdotal. For example, Lewis et al. (1967) noticed when two species of cattle-biting lice, *Linognathus vituli* (Linnaeus, 1758) and *Bovicola bovis* (Linnaeus, 1758), were present on a single cow at the same time, one species congregated on the lower body areas and the other on the upper body areas, but when each one was the sole ectoparasite on the host, they both infested all areas of the body evenly.

Host grooming behaviour may be responsible for ectoparasite site segregation. Host grooming is generally considered a major cause of mortality for most ectoparasites (Marshall 1981), providing selective pressure for the evolution of ectoparasite site specificity. Studies of the role of grooming in ectoparasite control have demonstrated either increased host grooming with increased ectoparasite abundance or increased ectoparasite abundance following the prevention of host grooming for a wide variety of animals (Bell et al. 1962; Lewis et al. 1967; Bennett 1969; Brown 1972, 1974; Mooring et al. 1996; Clayton et al. 1999; Eckstein and Hart 2000). Bats spend a considerable portion of their day grooming as evidenced by time budget analyses of roosting bats (Burnett and August 1981; Winchell and Kunz 1996; Fleming et al. 1998). Some studies have reported that bats with many mites or bat flies groom more than those with few ectoparasites (Wilkinson 1986; Giorgi et al. 2001). Waage (1979) proposed that increased host grooming in response to increased ectoparasite abundance can lead to decreased feeding opportunities for each individual parasite. If two parasite species living on the same host are similar then the species most capable of avoiding host grooming may out-compete the other, resulting in competitive exclusion. If, however, both parasite species are somewhat different in morphology or behaviour, they may become specialized for different areas on the host's body, dividing the defensive abilities of the host and reinforcing the use of separate locations. This hypothesis about the cause of host-site segregation among ectoparasites has been supported by data from a simulation model (Reiczigel and Rózsa 1998) and experimental studies (Rózsa 1993).

The purpose of this study was to investigate the degree of host specificity and host-site specificity of bat flies on bats at a site in Belize, Central America, and determine which factors could be responsible for these patterns. Previous studies of ectoparasite specificity has led us to four predictions: (1) the mobility of bat flies affects host specificity so that bat flies with functional wings would be less host specific than those with non-functional wings (Jobling 1949; Theodor 1957); (2) bats that tend to roost with other bat species (i.e., are not ecologically isolated) would have less specific bat flies than bats that tend to roost in monospecific groups; (3) bat flies would demonstrate specificity for fur or membrane, and these bat flies should have different morphological characteristics; and (4) if host grooming behaviour is responsible for host-site specificity, it should be consistent with the assumptions of the simulation model created by Reiczigel and Rózsa (1998).

Materials and methods

Study area

Data were collected from 4 April to 4 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 forested reserve with many trails, was established for the preservation of a large Maya ruin. The reserve has an average daily temperature of 27 °C and an annual rainfall of 1480 mm (Lambert and Arnason 1978). There are yearly cycles of rainfall in this area; the dry season runs from approximately January to June and the rainy season from June to December. The vegetation in the LAR consists of broadleaf tropical deciduous forest (Lambert and Arnason 1978). To the west of the reserve is farmland, to the north is forest, and to the east is the New River Lagoon. Beyond the New River Lagoon to the east are large areas of savanna.

Collecting and identifying ectoparasites

Bats used in this study were cared for in accordance with the guidelines provided by the Canadian Council on Animal Care and the Animal Care Protocol of M.B.F. at York University. We captured bats in mist nets set along trails and over streams in the LAR. All mist nets were at ground level, measuring 12 m long and 2 m tall. We opened the mist nets around dusk (time from 1800 to 2030 and averaging 1845) and closed them after about 10 bats had been captured for processing (time from 1900 to 2345 and averaging 2110). On two occasions, we caught bats in their roosts using a hand net. One roost was a chultun (underground chamber built by the Maya) and the other a tunnel within a Maya temple.

We tended the mist nets almost continuously, removing bats as soon as possible after capture. While we removed a bat from the mist net and searched it for parasites, we held a cloth bag 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 to await processing. We used forceps to remove all ectoparasites observed on the bats and preserved the ectoparasites in vials containing 70% ethanol. We recorded the location on the body of the bat (fur or membrane) from which we captured each bat fly, and we inspected the bag after releasing each bat to look for ectoparasites that left the bat during processing. After a bag was used for a bat, we washed it before using it again to ensure 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 to record grooming behaviour. For approximately half of the bats held for the grooming study (24 of 51), only the mites were removed, while the bat flies were counted and left on the body, so we could videotape bats grooming with and without bat flies.

We identified bat flies to species using keys for Neotropical bat flies (Wenzel et al. 1966; Wenzel 1976; Guerrero 1993, 1994*a*, 1994*b*, 1995*a*, 1995*b*, 1996, 1998; Miller and Tschapka 2001). Specimens were deposited in the Indiana State University mammalian ectoparasite collection at Terre Haute. To determine if certain morphological features were associated with living in fur or on membranes, we categorized bat flies by three features: (1) presence or absence of functional wings, (2) presence or absence of a ctenidium (a row of spines on the body of the fly), and (3) length of the hind leg (measured from the articulation with the body to the end of the last tarsal segment). In long-legged bat flies, hind legs were longer than the body and head as measured from photographs of one specimen per species. Bat flies were designated as host-site specific if ≥70% of individuals were removed from either fur or membrane based on the required percentage necessary for the average sample size for all bat fly species (mean = 34 bat flies per bat species, SE = 6.5) to be found significantly different from 50% (equally distributed on fur and membrane) using the binomial test.

Collecting grooming data

Some bats were brought to the field centre at the end of each night and held overnight in cylindrical wire cages covered with cotton cloths or left hanging in bags. To videotape grooming behaviour, we used 8-mm videotapes and a video camcorder (Canon ES2500). We placed bats in a bat observation box (BOB) for videotaping. The BOB was 0.61 m high with a 0.30 m square base; two adjacent sides were made of wood and two of Lexan® polycarbonate. A wooden rod placed diagonally from one wooden side to the other, approximately 0.15 m from the top, functioned as a perch for the bat. The camcorder was placed on a tripod in front of one Lexan® polycarbonate side and a lamp was shone through the other.

All videotaping was conducted by day in a quiet room. A bat was placed on the perch in the BOB while one person was present to observe it, and the video camera was set to record. If bats did not groom spontaneously, they were offered sugar water from a syringe and pieces of fruit to stimulate grooming. For bats with bat flies, we counted the number of bat flies on the bat at capture and prior to putting it in the BOB for videotaping. After videotaping, we removed the bat from the BOB and immediately collected all the bat flies using the same protocol as before.

We transferred footage of bats grooming from 8-mm to VHS videotapes and used the capture feature of VideoWave version 4 (RealNetworks, Inc. 2000) to convert the video component of the VHS videotape to MPEG-2 format. We used VideoWave software to view the MPEG files with an accuracy of 33 ms, the duration of a single frame. We described and classified all grooming events seen on the video files for each bat videotaped and recorded the start and end times of grooming behaviours within the video to calculate durations.

Data analysis

We used SPSS version 10 (SPSS Inc. 1999) to analyze the data. Terminology relating to measurements of parasite variables follows Bush et al. (1997). Specifically, site, location, or habitat refers to the area on the body of the host used by the parasite. Prevalence refers to the total number of host individuals infested with bat flies divided by the total number of host individuals examined and is expressed as a percentage.

Results

Host–ectoparasite associations

We captured 455 bats belonging to 32 species in six families (Table 1). Twelve species had sample sizes >10, and captures were dominated by three species with sample sizes >50 (*Sturnira lilium*, *Artibeus phaeotis*, and *Glossophaga soricina*) (Table 1). We identified 773 bat flies belonging to 32 species in two families collected from 25 bat species in five families (Table 2). All bat species that lacked bat flies had sample sizes <5 (Table 1). Four bat fly species could not be identified and may represent new species (*Neotrichobius* sp. from *Artibeus toltecus*, *Basilia* sp. from *Rhogeessa aeneus*, *Paradyschiria* sp. from *Tonatia evotis*, and *Trichobius* sp. from *Carollia perspicillata* and *Carollia brevicauda*). The *Trichobius* sp. from *Carollia* spp. appears to be a form that is similar to *Trichobius dugesioides* and *Trichobius anducei* Guerrero, 1998; the latter being a species documented for *C. perspicillata* (Guerrero 1998). The majority of bat species infested with bat flies was infested with one bat fly species (Fig. 1). Bat species infested with more than one bat fly species usually had two “dominant” bat fly species (dominant referring to sample sizes >3); for four of five bat species with more than two bat fly species, the third and fourth bat fly species were only represented by one or two specimens (Table 1). *Glossophaga soricina* was the exception because it was infested with three bat fly species in relatively large numbers (Table 1).

The majority of bat fly species (25 of 32) was monoxenous (Fig. 1). Six of seven bat fly species collected from more than one host species were stenoxenous (Table 2). One specimen of *Speiseria peytonae* collected from *A. phaeotis* was most likely an accidental association because *A. phaeotis* is not a normal host for this species and *Speiseria* spp. are good flyers and easily abandon bats in mist nets to land on any nearby bat (Wenzel et al. 1966).

Of the 20 bat fly species with sample sizes ≥5, 18 demonstrated site specificity for either fur or membranes (Table 2). For bat species with one dominant bat fly species, six out of seven bat fly species were fur specific (Table 3). In *S. lilium* and *Artibeus jamaicensis*, the genus *Aspidoptera* was membrane specific and the genus *Megistopoda* was fur specific (Table 3). The same pattern, consisting of one membrane-specific and one fur-specific species, appeared in other bat species (Table 3) with three exceptions. We collected two *Trichobius* species in relatively large numbers on the membranes of *G. soricina*, occasionally from the same location on the same individual bat. *Pteronotus parnellii* and *Trachops cirrhosus* both had one fur-specific species and one species with no host-site preference (Table 3). *Trichobius yunkeri* and *T. dugesioides* appeared to be the only “generalist” bat flies among these species.

Table 4 summarizes the number of bat fly species by morphological features (presence or absence of functional wings, ctenidia, and long hind legs) and host-site preference. Only bat fly species with sample sizes ≥5 were included to avoid basing conclusions on only a few specimens. Functional wings did not appear to influence host-site preference, and the two species that did not show host-site preference had functional wings. Ctenidia and long hind legs, however, were only present on species with a preference for fur. Based on the pattern seen in this table, we plotted the proportion of individuals found in the fur against a relative index of leg length (body length divided by hind-leg length) (Fig. 2). We did not test for a correlation on this data owing to the nonindependence of species as data points in statistical analyses, and the unresolved phylogeny of these families made phyllogenetically controlled tests impossible (Harvey and Pagel 1991). Given these limitations, an interesting pattern did emerge: bat fly species with relatively short hind legs were found less often in the fur than those with relatively long hind legs. Of the species found mostly in the fur, a gradient appeared with species possessing ctenidia having relatively short hind legs compared with those lacking ctenidia.

We observed some differences in behaviour between fur-dwelling and membrane-dwelling bat flies that were not quantified. Species with very long legs (e.g., *Megistopoda* spp., *Neotrichobius* spp.) tended to push up to the surface of the fur and walk over it when attempting to escape capture, whereas those with shorter legs (e.g., *Metelasmus* sp., *Strebla* spp.) usually pushed through the fur. Membrane-dwelling species generally moved slower than fur-dwelling species.

We tested for correlations between the number of bat flies for two dominant bat fly species on five bat species with suitable sample sizes to determine if the number of one bat fly species affected the number of another on a single bat. We found a significant negative correlation between the numbers of *Megistopoda proxima* and *Aspidoptera delatorrei* on *S. lilium* (Spearman’s rank correlation, $r_S = -0.299$, $p = 0.007$, $n = 81$). No significant correlations were found for *Megistopoda aranea* and *Aspidoptera phyllostomatis* on *A. jamaicensis* ($r_S = 0.166$, $p = 0.334$, $n = 36$) and *Trichobius parasiticus* and *Strebla wiedemanni* on *Desmodus rotundus* ($r_S = -0.131$, $p = 0.700$, $n = 11$), but the correlations for *T. dugesioides* and *S. peytonae* on *C. brevicauda* ($r_S = 0.347$, $p = 0.060$, $n = 30$) and *T. yunkeri* and *Nycterophilia parnelli* on *P. parnellii* ($r_S = -0.566$, $p = 0.055$, $n = 11$) were close to significant, interestingly in opposite directions.

Table 1. Summary of bat species and their ectoparasites at Lamanai, Belize.

Bat		Bat fly			
Family and species	*n*	Species	*n*	Number of bats infested	Prevalence (%)*
Phyllostomidae					
Artibeus intermedius Allen, 1897	21	*Paratrichobius longicrus* (Miranda-Ribeiro, 1907)	12	4	19
Artibeus jamaicensis Leach, 1821	39	*Megistopoda aranea* (Coquillett, 1899)	42	14	36
		Aspidoptera phyllostomatis (Perty, 1933)	9	7	18
		Metelasmus pseudopterus Coquillett, 1907	1	1	3
		Paratrichobius longicrus	1	1	3
		Unidentified	4	3	na
		All bat flies for *A. jamaicensis*	57	19	49
Artibeus lituratus Olfers, 1818	13	*Megistopoda aranea*	1	1	8
Artibeus phaeotis Miller, 1902	58	*Neotrichobius stenopterus* Wenzel and Aitken, 1966	14	12	21
		Speiseria peytonae Wenzel, 1976	1	1	2
		All bat flies for *A. phaeotis*	15	13	22
Artibeus toltecus Saussure, 1860	1	*Neotrichobius* sp.	3	1	na
Artibeus watsoni Thomas, 1901	13	*Neotrichobius stenopterus*	7	7	54
Carollia brevicauda Schinz, 1821	31	*Trichobius* sp.	55	17	55
		Speiseria peytonae	24	12	39
		Strebla guajiro (Garcia and Casal, 1965)	1	1	3
		Unidentified	4	4	na
		All bat flies for *C. brevicauda*	84	21	68
Carollia perspicillata Linnaeus, 1758	12	*Trichobius* sp.	15	8	67
		Speiseria ambigua Kessel, 1925	2	2	17
		Strebla guajiro	2	2	17
		All bat flies for *C. perspicillata*	19	9	75
Desmodus rotundus E. Geoffroy, 1810	11	*Trichobius parasiticus* Gervais, 1844	59	10	91
		Strebla wiedemanni Kolenati, 1856	21	8	73
		All bat flies for *D. rotundus*	80	11	100
Glossophaga soricina Pallas, 1766	65	*Trichobius uniformis* Curran, 1935	33	24	37
		Trichobius dugesii Townsend, 1891	22	21	32
		Strebla curvata Wenzel, 1976	11	5	8
		Unidentified	5	5	na
		All bat flies for *G. soricina*	71	31	48
Micronycteris microtis Miller, 1898	3		0		
Mimon cozumelae Goldman, 1914	1	*Mastoptera minuta* Costa-Lima, 1921 complex	4	1	na
Mimon crenulatum E. Geoffroy, 1810	2	Unidentified	3	1	na
Phyllostomus discolor Wagner, 1843	1	*Trichobius costalimai* Guimarães, 1937	2	1	na
Platyrrhinus helleri Peters, 1866	3	*Paratrichobius* sp.	3	1	na
Sturnira lilium E. Geoffroy, 1810	107	*Megistopoda proxima* (Séguy, 1926)	150	71	66
		Aspidoptera delatorrei Wenzel, 1966	94	41	38
		Unidentified	3	3	na
		All bat flies for *S. lilium*	247	82	77
Tonatia evotis Davis and Carter, 1978	1	*Paradyschiria* sp.	4	1	na
Tonatia saurophila Koopman and Williams, 1951	1		0		
Trachops cirrhosus Spix, 1823	4	*Trichobius dugesioides* Wenzel, 1966	24	4	na
		Strebla mirabilis Waterhouse, 1879	7	4	na
		Unidentified	1	1	na
		All bat flies for *T. cirrhosus*	32	4	na
Uroderma bilobatum Peters, 1866	9	*Paratrichobius dunni* Curran, 1935	4	3	33
Vampyressa pusilla Wagner, 1843	2		0		
Vespertilionidae					
Bauerus dubiaquercus Van Gelder, 1959	3		0		
Eptesicus furinalis d'Orbigny, 1847	3	*Basilia ortizi* Machado-Allison, 1963	6	2	na
Lasiurus ega Gervais, 1856	2		0		

Table 1 (*concluded*).

Bat		Bat fly			
Family and species	*n*	Species	*n*	Number of bats infested	Prevalence (%)*
Myotis elegans Hall, 1962	7	*Basilia anceps* Guimarães and Andretta, 1956	11	5	63
		Unidentified	2	2	na
		All bat flies for *M. elegans*	13	5	63
Myotis keaysi Allen, 1914	1	*Basilia anceps*	1	1	na
Rhogeessa aeneus Goodwin, 1958	15	*Basilia* sp.	29	11	73
		Unidentified	1	1	na
		All bat flies for *R. aeneus*	30	12	80
Emballonuridae					
Rhynchonycteris naso Wied-Neuwied, 1820	4		0		
Saccopteryx bilineata Temminck, 1838	2		0		
Mormoopidae					
Pteronotus parnellii Gray, 1843	12	*Trichobius yunkeri* Wenzel, 1966	46	9	75
		Nycterophilia parnelli Wenzel, 1966	47	8	67
		Trichobius sparsus Kessel, 1925	2	2	17
		Unidentified	13	3	na
		All bat flies for *P. parnellii*	108	12	100
Noctilionidae					
Noctilio leporinus Linnaeus, 1758	1	*Noctiliostrebla traubi* Wenzel, 1966	2	1	na
Molossidae					
Molossus ater E. Geoffroy, 1805	2	*Trichobius jubatus* Wenzel, 1976	2	1	na
Unknown species	5				
Total	455				

*Prevalence (percentage of bat species captured that was infested) is only reported for bat species with $n > 5$; na, not available.

Table 2. Bat fly species and their host and host-site preferences from Lamanai, Belize.

	Samples (*n*)			
Family and species	Membrane	Fur	Percentage from fur	Host species
Streblidae				
Aspidoptera delatorrei	78	9	10	*Sturnira lilium*
Aspidoptera phyllostomatis	6	2	25	*Artibeus jamaicensis*
Mastoptera minuta	4	0	na	*Mimon cozumelae*
Megistopoda aranea	2	39	95	*Artibeus jamaicensis, A. lituratus*
Megistopoda proxima	8	109	93	*Sturnira lilium*
Metelasmus pseudopterus	0	1	na	*Artibeus jamaicensis*
Neotrichobius sp.	0	3	na	*Artibeus toltecus*
Neotrichobius stenopterus	1	20	95	*Artibeus phaeotis, A. watsoni*
Noctiliostrebla traubi	2	0	na	*Noctilio leporinus*
Nycterophilia parnelli	1	46	98	*Pteronotus parnellii*
Paradyschiria sp.	4	0	na	*Tonatia evotis*
Paratrichobius dunni	1	3	75	*Uroderma bilobatum*
Paratrichobius longicrus	1	12	92	*Artibeus intermedius* or *A. lituratus, A. jamaicensis*
Paratrichobius sp.	0	3	na	*Platyrrhinus helleri*
Speiseria ambigua	1	1	na	*Carollia perspicillata*
Speiseria peytonae	1	23	96	*Artibeus phaeotis, C. brevicauda*
Strebla curvata	1	10	91	*Glossophaga soricina*
Strebla guajiro	0	3	na	*Carollia brevicauda, C. perspicillata*
Strebla mirabilis	0	7	100	*Trachops cirrhosus*
Strebla wiedemanni	0	21	100	*Desmodus rotundus*
Trichobius costalimai	2	0	na	*Phyllostomus discolor*
Trichobius dugesii	15	6	29	*Glossophaga soricina*

Table 2 (*concluded*).

Family and species	Samples (*n*) Membrane	Fur	Percentage from fur	Host species
Trichobius dugesioides	15	9	38	*Trachops cirrhosus*
Trichobius jubatus	2	0	na	*Molossus ater*
Trichobius parasiticus	42	17	29	*Desmodus rotundus*
Trichobius sp.	53	10	16	*Carollia brevicauda, C. perspicillata*
Trichobius sparsus	0	2	na	*Pteronotus parnellii*
Trichobius uniformis	24	9	27	*Glossophaga soricina*
Trichobius yunkeri	21	23	52	*Pteronotus parnellii*
Nycteribiidae				
Basilia anceps	0	13	100	*Myotis elegans, M. keaysi*
Basilia ortizi	0	6	100	*Eptesicus furinalis*
Basilia sp.	0	27	100	*Rhogeessa aeneus*

Note: na, not available.

Table 3. Host-site preferences of bat flies for bat species with one, two, or three dominant bat fly species.

Number of dominant fly species	Host species	Bat fly species	Host-site preference
1	*Artibeus intermedius*	*Paratrichobius longicrus*	Fur
	Artibeus phaeotis	*Neotrichobius stenopterus*	Fur
	Artibeus watsoni	*Neotrichobius stenopterus*	Fur
	Carollia perspicillata	*Trichobius* sp.	Membrane
	Eptesicus furinalis	*Basilia ortizi*	Fur
	Myotis spp.	*Basilia anceps*	Fur
	Rhogeessa aeneus	*Basilia* sp.	Fur
2	*Artibeus jamaicensis*	*Megistopoda aranea*	Fur
		Aspidoptera phyllostomatis	Membrane
	Carollia brevicauda	*Speiseria peytonae*	Fur
		Trichobius sp.	Membrane
	Desmodus rotundus	*Strebla wiedemanni*	Fur
		Trichobius parasiticus	Membrane
	Pteronotus parnellii	*Nycterophilia parnelli*	Fur
		Trichobius yunkeri	None
	Sturnira lilium	*Megistopoda proxima*	Fur
		Aspidoptera delatorrei	Membrane
	Trachops cirrhosus	*Strebla mirabilis*	Fur
		Trichobius dugesioides	None
3	*Glossophaga soricina*	*Strebla curvata*	Fur
		Trichobius dugesii	Membrane
		Trichobius uniformis	Membrane

Grooming behaviour

We analyzed grooming behaviour of 51 bats from seven species (7 *Artibeus intermedius*, 3 *A. jamaicensis*, 5 *A. phaeotis*, 5 *Artibeus watsoni*, 4 *C. brevicauda*, 15 *G. soricina*, and 12 *S. lilium*). The most common grooming behaviours were licking, scratching, and chewing the hind claws. Bats regularly alternated between scratching the fur and chewing the hind claws and either behaviour could start a grooming sequence. Bats used different grooming behaviours for different areas of their bodies. With data from all bats pooled, fur was groomed significantly more by scratching (mean duration = 42.6 s, SE = 5.7) than licking (mean duration = 1.9 s, SE = 0.5; Wilcoxon's signed-rank test: $Z = -5.968$, $p < 0.001$, $n = 51$). The opposite was true for grooming wings, which were groomed more by licking (mean duration = 36.9 s, SE = 9.1) than scratching (mean duration = 4.4 s, SE = 2.0; Wilcoxon's signed-rank test: $Z = -4.688$, $p < 0.001$, $n = 51$).

Discussion

Except one likely accidental association, the bat fly species we collected were either monoxenous or stenoxenous, indicating a high degree of host specificity and supporting previous reports (Wenzel et al. 1966; Marshall 1976). The prediction that flightless species would be more host specific

Fig. 1. (*a*) Number of host bat species by number of bat fly species per host and (*b*) host specificity of bat flies given as the number of bat fly species with one or two host species for bat flies collected at Lamanai, Belize.

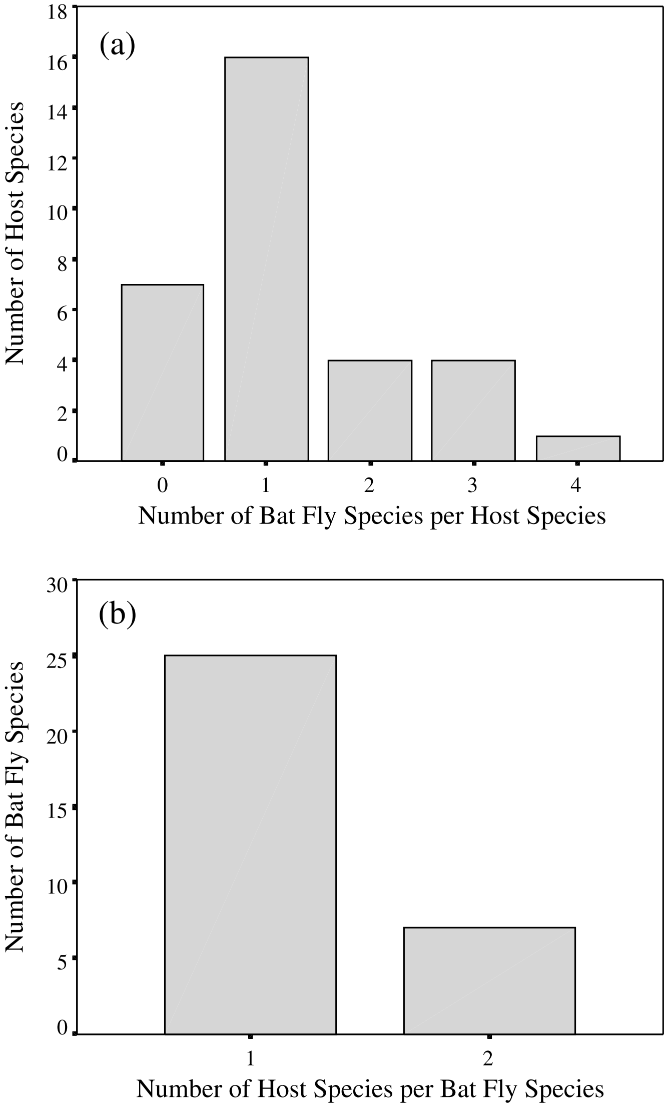


Table 4. Number of bat fly species (for species with $n > 5$) categorized by morphological feature and host-site preference.

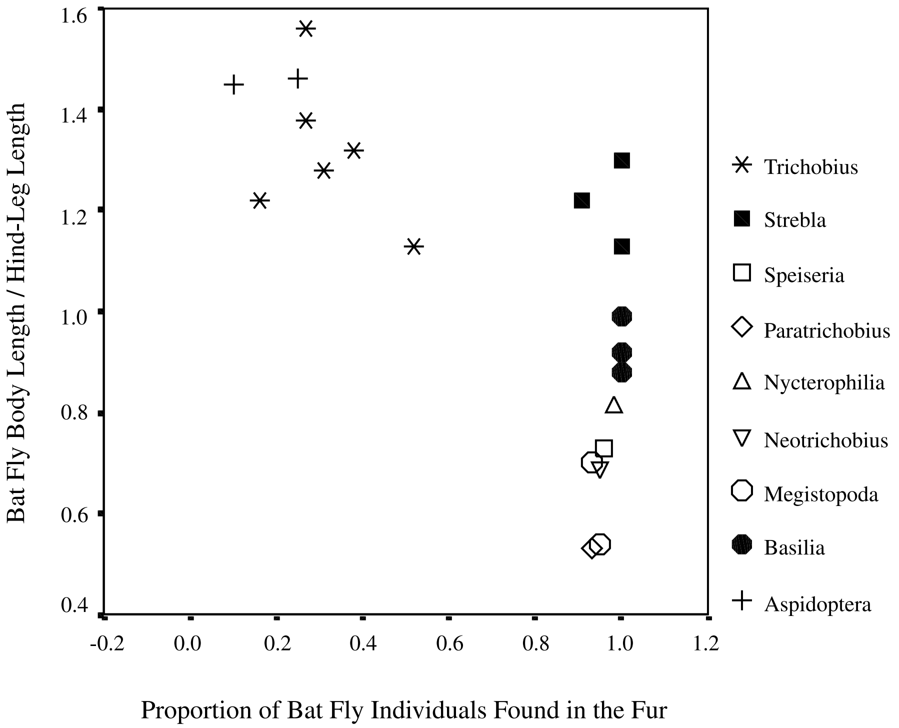
	Number of bat fly species by host-site preference			
Morphological feature	Fur	Membrane	No preference	Totals
Functional wings				
Present	6	4	2	12
Absent	6	2	0	8
Ctenidium				
Present	6	0	0	6
Absent	6	6	2	14
Long hind legs				
Present	9	0	0	9
Absent	3	6	2	11

than those that could fly was not supported by the data because bat flies found on more than one bat species were as likely to lack functional wings (three of six) as have them (three of six). Likewise, the hypothesis that ecologically isolated species would have more specific ectoparasites than those that live in polyspecific groups was not supported. Tent-roosting species generally roost in monospecific groups, yet *A. phaeotis* and *A. watsoni*, both tent-roosting species, shared a bat fly species (*Neotrichobius stenopterus*). Graham (1988) conducted a study of interspecific roosting associations of bat species in Peru and found that certain species often shared roosts with other species, such as *C. perspicillata*, *G. soricina*, and *D. rotundus*, whereas others rarely or never shared roosts like *Uroderma bilobatum*, a tent-roosting species. The species sharing the most roosts with other species were also found with the greatest number of different species (Graham 1988). Although most associations appeared to be neutral, there was a particularly close association between *C. perspicillata* and *G. soricina* (Graham 1988). In our study area in Belize, we observed a group of *C. perspicillata* roosting together with *T. cirrhosus*, but these two species of bats did not share a bat fly species and neither did individuals caught in the same roost. The bat fly species in our study appear to follow phylogenetic lines, and there is some evidence of co-speciation between the Streblidae and Neotropical bats (Patterson et al. 1998). Specificity in these species may be maintained by physiological or behavioural characteristics of their hosts (Wenzel et al. 1966; Marshall 1981), which are more likely to be similar among members of the same genus than among species of different genera using the same roost.

Like Linhares and Komeno (2000) in Brazil, we found a negative correlation between the numbers of the genera *Megistopoda* and *Aspidoptera* on *S. lilium*, suggesting that competition could be a factor affecting their distribution. Competition, however, is not the only possible explanation for this relationship. Although specializing on a particular site on the host may not help a highly mobile ectoparasite locate mates, finding an individual host with members of its species could. Conspecific bat flies may congregate on the same host individuals to increase their chances of finding a mate, hence, producing an effect similar to competition whereby individuals tend to be found more often with conspecifics than with individuals of other species. Future studies could focus on teasing apart these two competing hypotheses by exposing captive colonies of healthy bats to species one and two separately and together to determine if this clumped distribution is maintained in the absence of the other species or enhanced by the presence of the other species. Bat fly species on four other bat species did not show this negative correlation, although *P. parnellii* was close to significant, and bat flies on *C. brevicauda* had a positive association, suggesting that competition is not a factor for many species in this community.

With the exception of *T. yunkeri* and *T. dugesioides*, all bat fly species we collected were fur or membrane specific. Long hind legs and the presence of a ctenidium appear to be morphological adaptations of bat flies living in fur, and these two features compensate for each other. Fur-living species with ctenidia have shorter legs than fur-living species lacking ctenidia. Ctenidia may function as organs of attachment

Fig. 2. Scatterplot of leg length index (body length/hind-leg length) plotted against the proportion of individuals collected from the fur for each bat fly species with sample sizes ≥5. Solid symbols represent flies with ctenidia, whereas open symbols and asterisks represent flies without ctenidia.



(Humphries 1967; Theodor 1957), although more convincing evidence suggests that they prevent abrasive damage by fur to sensitive joints (Marshall 1980). The inability to escape the abrasive action of fur during locomotion on the bat could be responsible for the evolution of ctenidia on fur-living bat flies with relatively short legs, whereas species with long hind legs could walk over the fur to escape abrasion. Membrane-specific species, on the other hand, may have short legs to help them cling to the smooth surface of the membrane.

Although the assumptions of Reiczigel and Rózsa's (1998) simulation model were designed to fit data on birds and lice, they are well suited to the data collected here on bats and bat flies. Each simulation began with one host species and two ectoparasite species, like our data showing that bats tended to have two dominant bat fly species. The model provided the two generalist ectoparasites with two distinctly different body areas on the host, corresponding to fur and membrane on bats. Grooming behaviour was assumed to differ between these two body areas, and bats in this study groomed the fur mostly through scratching and the membranes mostly through licking. Bats may be restricted to scratching the fur because most furred areas cannot be reached by licking, and scratching the wings may be avoided because it could damage the bare skin. The most effective evasive behaviours for the ectoparasites were assumed to differ between the two body areas and, although differences in speed were not quantified for bat flies, fur-dwelling bat flies tended to move more quickly than membrane-dwelling bat flies (Linhares and Komeno 2000; Ross 1961). These data could indicate that it is best to avoid scratching by fast movement and to avoid licking by hiding in folds of membrane. Differences in the mobility of bat flies are mirrored by differences in morphology, with fur-living species having longer hind legs than membrane-living species (Fig. 2). Simulations (run for 300 generations and replicated 200 times) produced two outcomes: (1) one parasite species went extinct or (2) the two species became specialized for different locations on the host's body (Reiczigel and Rózsa 1998). Based on the similarities between our data and this model, we believe that grooming is one possible cause of bat fly host-site specificity.

Reiczigel and Rózsa's model was also based on the assumption that grooming is effective at killing or otherwise removing ectoparasites. An abundance of anecdotal information suggests that this is the case for bats and bat flies. Although Fritz (1983) did not observe bats reacting to bat flies, he did not quantify behaviours. Bats held in captivity usually lose their bat flies within a few days, apparently as result of grooming (Kunz 1976). Overal (1980) placed 40 *Megistopoda* bat flies on 10 caged *A. jamaicensis* and later found 13 dead or damaged at the bottom of the cage, presumably victims of grooming behaviour. Overal (1980) discovered bats readily ate streblids when streblids were offered to them, a behaviour also documented by Marshall (1982*b*) for the bat *Megaderma spasma* (Linnaeus, 1758) and a polyctenid ectoparasite in Malaysia. Out of six bat flies placed on three unrestrained *Artibeus cinereus* (Gervais, 1856), only one was present after 5 days, whereas all remained if the bats were restrained from grooming; thus, indicating that the loss of bat flies in the first experiment was most likely the result of the grooming behaviour of the host instead of some other factor (Overal 1980). These observations, combined with evidence that bats in colonies with high bat fly abundance groom more than those in colonies with low bat fly abundance (Wilkinson 1986), suggest that bat grooming is a behavioural defence against bat flies and possibly other ectoparasites too.

Our data demonstrated that bat flies are highly host specific and that ecological isolation of hosts and bat fly mobility are not major factors in determining bat fly specificity. The majority of bat flies was host-site specific for either fur or membranes reflecting morphological specializations, namely leg length and the presence or absence of a ctenidium. Host grooming behaviour was consistent with the assumptions of a simulation model (Reiczigel and Rózsa 1998), suggesting that host-mediated competition caused by host grooming could be responsible for host-site segregation in bat flies.

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