Sex biases in parasitism of neotropical bats by bat flies (Diptera: Streblidae)

Bruce D. Patterson[*][1], Carl W. Dick[*] and Katharina Dittmar[*][†]

[*] Department of Zoology, 1400 S. Lake Shore Dr., Field Museum of Natural History, Chicago, IL 60605-2496, USA
[†] Department of Biological Sciences, State University of New York at Buffalo, 109 Cooke Hall, Buffalo, NY 14260, USA
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Abstract: We describe levels of parasitism of ectoparasitic bat flies (Hippoboscoidea: Streblidae) on male and female bats from an extensive Neotropical survey. The collection resulted from coordinated vertebrate-parasite surveys undertaken by the Smithsonian Venezuelan Project (SVP) from 1965–1968, which sexed 24 978 bats of 130 species. Streblid parasites were recovered from 6935 individuals of 87 bat species, but only 47 species were captured frequently enough ($\geq$ 20 infested individuals) to permit reliable estimates of streblid parasitism on males and females. Well-sampled species included 39 phyllostomids, four mormoopids, two noctilionids, one natalid and one molossid. Prevalence of streblid parasitism (proportion of individuals infested) of male and female bats was generally not significantly different, and averaged 0.34 across infested species. In species-level analyses assessed against captures, significant sex differences in infestation levels were noted in six species; all had mean prevalence below 0.5 and females were parasitized disproportionately in each. Sex differences in total numbers of flies were noted in 21 species, and in 16 of these, females carried disproportionately heavy loads. Sex differences were also found for eight species of bat in the number of fly species infesting an individual; seven of eight showed heavier female parasitism. In analyses weighted by infestation levels, sex differences in total number of flies were found in only 12 species, with seven showing excessive parasitism of females, and no species showed sex differences in the number of fly species infesting them. These significant biases were not associated with sexual size dimorphism among the bat species. Generally higher levels of parasitism among female bats accords with theory, given their generally higher survivorship and enhanced probabilities of lateral and vertical transmission of host-specific parasites, but contrasts with patterns shown by many other parasitic arthropods. Future analyses should target social groupings of bats, not passively sampled foragers, to better address the mechanisms responsible for this pattern.

Key Words: Chiroptera, ectoparasites, Neotropics, parasitism, sex ratios, Venezuela

INTRODUCTION

Competitors, predators and parasites all may serve to limit rates of increase and act as important checks on the distribution, abundance and fitness of organisms. Although competition theory has been an important component of community ecology for half a century (Hutchinson 1959, MacArthur 1972), and predation is now universally regarded as a major structuring force (Berger *et al.* 2001, Terborgh 1988), we have much to learn about the importance and roles of parasitism (Morand *et al.* 2006, Packer *et al.* 2003, Thompson 1999). Richer empirical documentation offers tests of theoretical alternatives and points towards new mechanisms of interaction (Poulin 2007).

Bats (Order Chiroptera) are highly abundant and diverse in Neotropical forests. In places such as Guyana's Iwokrama Forest, about two-thirds of all mammals (86 of 130 species) are bats (Lim & Engstrom 2004). Neotropical bats are also impressively abundant, and their biomass can equal that of all other mammal species combined (Tuttle 1983). Their ecological success has been traced to their utilization of diverse trophic strategies, roosting structures, locomotory patterns and sensory modalities (Kalko 1997, Patterson *et al.* 2003). Their ecological importance as pollinators, seed dispersers and insectivores extends beyond primary trophic linkages to exert numerous indirect effects on forest health and vitality (Heithaus 1982, Myers 1992). Bats also have remarkably diverse social systems, living in groupings

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[1] Corresponding author. Email: bpatterson@fieldmuseum.org

that range from small family groups to aggregations of millions (Wilkinson 2003). Such ecological variation may cause bat species to differ dramatically in their susceptibility to different biological controls, as well as in the prevalence and intensity of parasitism. For example, the permanence and exposure of their roosting sites is known to correlate significantly with both the prevalence and intensity of parasitism on Neotropical bats (Patterson *et al.* 2007).

Bats are host to various parasites, both internal (Coggins 1988) and external (Whitaker 1988). The Chiroptera are second only to rodents in the number of families and species of ectoparasitic insect they host (Marshall 1981), their ectoparasites exhibit the highest degree of niche specialization, and more orders and families of ectoparasitic arthropod are exclusive to bats than to any other mammalian order (Wenzel *et al.* 1966). The most conspicuous ectoparasites are blood-sucking flies of the superfamily Hippoboscoidea (Marshall 1982). Traditionally classified into two families, Streblidae and Nycteribiidae (but see Dittmar *et al.* 2006), these obligate ectoparasites live only on bats, inhabiting the fur and flight membranes. Like all Diptera, bat flies must pupate or metamorphose to complete development. But unlike other flies, bat flies give birth to a single young that is already a third-instar larva and that immediately pupates. Deposition of larvae and pupation typically happen in or near the bat's roost, and weeks later, the newly emergent flies must relocate a host bat (Dick & Patterson 2006). Despite the decoupling of host and parasite at every generation, bat fly species are strikingly host specific (Dick 2007, Dick & Patterson 2007). A recent survey of bat flies on Paraguayan bats determined that 87% of 31 streblid species were restricted to a single bat species; the remaining 13% occurred on closely related host species (Dick & Gettinger 2005).

The fitness costs of bat fly parasitism are not well understood. By definition, parasites are symbionts that derive benefit from the host at some expense to it (Roberts & Janovy 2000). But it can be difficult to distinguish the effects of parasitism on host condition from the effects of host health on the virulence of the parasites (Bize *et al.* 2008). Actual energetic costs of bat fly parasitism remain poorly defined, but the flies take blood meals up to eight times per hour and typically die after being separated from their hosts for only several hours (Fritz 1983). Heightened grooming rates, reduced resting time, and elevated metabolism are all consequences of higher mite infestations of European bats (Giorgi *et al.* 2001). Both species co-occurrence analyses and host-choice experiments suggest that the number of flies on a given host bat are limited (Dick & Dick 2006, Tello *et al.* 2008). Hosts spend more time grooming as fly numbers increase (Overal 1980), and grooming is thought to be a major source of fly mortality (Marshall 1981). As many as six

bat fly species may coexist on a single host bat (Wenzel 1976), although one to three species is more typical. In cases of multiple infestation, fly species partition the bat's fur and flight membranes and exhibit highly structured ecomorphology (Dick 2005). Bat flies are not currently known to transmit disease pathogens or other parasites.

Despite great variation in bat social systems and their daily and seasonal aggregations, few studies have examined sex differences in bat fly parasitism, and these have produced equivocal results. Neither abundance nor prevalence of bat fly parasitism varied with the sex of bulldog bats (*Noctilio leporinus*) in southern Brazil (Moura *et al.* 2003) or Paraguay (Presley 2007). A study in São Paulo, Brazil yielded ambiguous results, with some fly species more abundant on female bats and others more abundant on males (Bertola *et al.* 2005). In Minas Gerais, Brazil, the most abundant bat fly (*Trichobius joblingi*) was found at higher intensity and prevalence on male hosts (Komeno & Linhares 1999) but in São Paulo this species was differentially found on females (Bertola *et al.* 2005). The only study to date to offer a fauna-wide assessment of infestations by sex was of Paraguayan bats, where females were generally more heavily infested than males (Presley & Willig 2008). Because Paraguay straddles the Tropic of Capricorn and its modest-sized bat fauna contains both tropical and temperate elements (López-González 2004), we decided to assess the generality of this pattern using surveys of hyperdiverse tropical bat faunas and their associated bat flies.

METHODS

The Smithsonian Venezuela Project (SVP) was conducted from 1965–1968 and was one of the largest coordinated surveys of vertebrates and their ectoparasites ever conducted. That effort sampled 38 213 mammals representing 270 species, including 24 979 sexed bats of 133 species. Most mammals were captured and held in individual paper bags, fumigated with ether, and their parasites collected in 70% ethanol (Handley 1976). All mammals were identified and curated by Charles O. Handley at the National Museum of Natural History (USNM). Host names were recently reviewed using computerized records of the National Museum of Natural History to revise names in accordance with subsequent taxonomic revisions and re-identifications. Thus, host identifications are accurate, consistent, and can be re-evaluated, all critical attributes for host-parasite studies (Poulin 1998, Wenzel *et al.* 1966).

Bulk parasite samples were collected and organized by individual host. At the Field Museum of Natural History (FMNH), Rupert L. Wenzel sorted, identified and enumerated the streblid bat flies (Diptera: Streblidae). Collections included 36 663 streblids, representing 22

genera and 116 species; two genera and 45 species were new to science (Wenzel 1976). Records analysed here consisted of the number of a given bat fly taxon recovered from a host individual; such aggregations have been termed an 'infrapopulation' in earlier parasite surveys (Bush *et al.* 1997). Multiple records were used for bat individuals that hosted two or more species of flies. We excluded SVP records not catalogued at the USNM (and hence lacking re-confirmed identifications), as well as those that lacked bat or bat fly identifications, gender specifications, or counts of parasite abundance. A total of 24 979 bats, representing 133 species in nine families, was sampled for parasitic bat flies.

We used *G*-tests to evaluate differences in proportionality between several measures of parasitism on male and female bats. Each fly has the opportunity to colonize either a male or female host, so that departures from equal proportions can be tested directly with this statistic if those decisions are assumed to be statistically independent. To avoid spurious effects of small sample size, we restricted tests to 47 bat species with ≥ 20 individuals infested with streblid flies. We tested differences between male and female infestations (non-zero counts of the number of bat flies on a given bat), the total number of flies (summed infestations), and number of fly infrapopulations (the number of bat fly species comprising an infestation). Two different sets of expectations were used to assess observed values of these variables: capture frequencies (fractions of male and female bats in captures sampled for ectoparasites) and infestation frequencies (proportions of males and females among those bats bearing streblid flies). Thus, if twice as many female bats of a given species were captured as males, 'proportionate to capture' tests expected twice as many females to be infested. 'Proportionate to infestation' tests used expectations based on sex ratios of infested individuals. To control experiment-wide errors at $P < 0.05$ in a survey involving so many independent tests, we used both Bonferroni ($\alpha < 0.00106$) and Sidak adjustments ($\alpha < 0.00109$) to assess the significance of individual tests (http://www.quantitativeskills.com/sisa/index.htm), although some would argue this conservative treatment raises the risk of ignoring some biologically significant differences (Moran 2003). We tabulated actual *G* statistics to allow readers to apply their own standard of significance.

Sexual size dimorphism of these species was estimated by Linares (1998), who judged 15 of 46 species (*Dermanura glauca* was not evaluated) to show notable dimorphism. We evaluated whether significantly biased loads were associated with sexual dimorphism using a binomial test, where 'success' was defined as larger infestations on the larger sex, 'trials' were defined as the significantly dimorphic bat species (n = 15), and the hypothetical probability of success was equal to the

proportion of bat species with significantly biased parasitic loads. Our alpha values report the probability of finding as few or fewer agreements between significant sex bias and appreciable sexual dimorphism as were actually observed.

RESULTS

Bat flies were recovered from 6935 bats, representing eight of nine families and 89 of the 133 bat species captured (Appendix 1). Streblid flies were recovered from all sampled species of Mormoopidae, Noctilionidae, Natalidae and Furipteridae, most species of Phyllostomidae, and select species of Emballonuridae, Molossidae and Vespertilionidae. No streblids were recovered from 11 individuals of one species of Thyropteridae, *Thyroptera tricolor*. Over all bat species, mean prevalence (proportion of infested individuals) averaged 27.8% (28.5% for females, 26.9% for males). Forty-seven species were captured frequently enough (≥ 20 infested individuals) to permit reliable estimates of streblid parasitism on males and females; prevalence among well-sampled species averaged 33.9% (36.4% for females, 31.4% for males).

Both captures and infestations were biased towards females (Appendix 1). Females comprised 53.2% of captures and 54.6% of infestations over all species, and values for well sampled species were comparable (50.9% and 54.6%, respectively). The excess of infested females in both groupings is significant in tests of proportionality between captures and infestations: $G = 67.8$ for all species and 99.8 for well-sampled species (both P < 0.0001).

Relative to capture frequencies, bat fly infestations of males and females in most species did not differ. However, six species showed disproportionately high infestations of females (Table 1; all P < 0.05 after Bonferroni correction). In no species were males infested more heavily than females. The intensity of parasitism also differed between sexes in 21 of the 47 species (Table 1). In five cases, males carried disproportionately heavy loads, whereas in 16 cases, females hosted significantly more flies than males. Finally, eight species showed significant sex differences in the number of fly infrapopulations supported by males and females, including all six of the species with prevalence differences (Table 1). In seven of the eight species, females supported significantly more species of bat flies than males.

Most of these sex differences in parasitism appear to be consequences of differential infestation. When fly loads of males and females are compared relative to levels of infestation for each sex, 12 species show significant differences between sexes (Table 1); in seven, females carried heavier loads whereas in five, males did. No species carried unbalanced infrapopulation loads after adjusting for differential infestation frequencies (Table 1).

Table 1. Tests for sex differences in bat fly parasitism. *G* statistics and the predominating sex are highlighted where deemed significant (P < 0.05) using Sidak's Bonferroni adjustment for experiment-wide error rates (P < 0.00109 in individual tests). Tests assess infestations, the total number of flies, and the number of fly infrapopulations against expectations based on capture frequencies (first three columns) and based on infestation frequencies (final two columns).

	Proportionate to captures			Proportionate to infestations	
	Infestations G_{cap}	Total number of flies G_{cap}	Number of fly infrapopulations G_{cap}	Total number of flies G_{inf}	Number of fly infrapopulations G_{inf}
Anoura caudifer	1.68	0.02	1.68	2.93	0.00
Anoura geoffroyi	0.05	0.03	1.08	0.04	0.61
Anoura latidens	0.66	**13.0** ♂♂	0.30	5.18	0.12
Artibeus amplus	0.03	0.55	0.14	0.18	0.03
Artibeus lituratus	**12.0** ♀♀	**14.7** ♀♀	**12.9** ♀♀	0.09	0.01
Artibeus obscurus	0.18	0.07	0.01	0.11	0.27
Artibeus planirostris	**33.8** ♀♀	**151.9** ♀♀	**63.7** ♀♀	**18.9** ♀♀	2.35
Carollia brevicauda	1.77	**12.6** ♀♀	4.02	3.24	0.27
Carollia perspicillata	**37.2** ♀♀	**47.8** ♀♀	**35.4** ♀♀	0.54	0.27
Chrotopterus auritus	2.04	**16.4** ♂♂	0.14	**16.2** ♂♂	0.13
Dermanura glauca	0.06	0.13	0.13	0.43	0.01
Desmodus rotundus	6.72	**100.7** ♀♀	0.44	**157.7** ♀♀	0.14
Enchisthenes hartii	0.55	1.43	0.55	0.05	0.00
Glossophaga longirostris	9.64	10.36	**11.7** ♂♂	0.73	0.03
Glossophaga soricina	4.07	4.62	5.26	0.02	0.40
Leptonycteris curasoae	**61.2** ♀♀	**1194** ♂♂	**104.4** ♀♀	**18.3** ♂♂	0.12
Lionycteris spurrelli	0.39	2.00	0.07	5.48	0.18
Lonchophylla robusta	0.00	3.04	0.03	3.04	0.03
Lonchorhina aurita	5.11	**34.6** ♀♀	4.57	5.13	0.01
Lonchorhina orinocensis	2.01	0.11	0.02	0.12	0.03
Lophostoma brasiliense	0.74	0.71	0.71	1.71	0.05
Lophostoma silvicolum	0.00	3.17	0.20	2.79	0.14
Macrophyllum macrophyllum	5.59	**20.0** ♀♀	9.91	0.47	0.05
Micronycteris minuta	2.27	0.80 ♀♀	3.11	**14.8** ♀♀	0.00
Phylloderma stenops	0.77	**11.5** ♀♀	1.81	0.48	0.15
Phyllostomus discolor	0.07	**47.0** ♀♀	2.62	**36.6** ♀♀	1.56
Phyllostomus elongatus	5.04	**125.7** ♀♀	4.92	**79.0** ♀♀	0.75
Phyllostomus hastatus	6.46	**22.8** ♀♀	3.07	1.75	0.05
Platyrrhinus aurarius	0.34	3.85	0.91	1.18	0.06
Platyrrhinus helleri	0.02	0.08	0.01	0.01	0.06
Platyrrhinus umbratus	0.37	0.73	0.10	3.04	0.12
Sturnira erythromos	0.08	0.00	0.00	0.13	0.11
Sturnira lilium	**27.1** ♀♀	**136.5** ♀♀	**32.9** ♀♀	**26.6** ♂♂	0.80
Sturnira ludovici	6.92	**19.0** ♀♀	**12.6** ♀♀	0.36	0.44
Sturnira tildae	**10.2** ♀♀	**19.9** ♀♀	**18.2** ♀♀	0.54	0.31
Trachops cirrhosus	0.34	0.14	0.45	0.52	0.00
Trinycteris nicefori	2.07	8.08	2.44	0.73	0.00
Uroderma bilobatum	0.04	0.13	0.01	0.02	0.01
Vampyressa pusilla	0.02	0.43	0.02	0.63	0.00
Mormoops megalophylla	0.85	9.84	8.09	0.42	2.47
Pteronotus davyi	4.06	**135.1** ♂♂	0.03	**121.2** ♂♂	0.00
Pteronotus gymnonotus	0.29	0.27	0.11	1.61	0.08
Pteronotus parnellii	3.21	**20.2** ♀♀	0.96	**58.8** ♀♀	0.20
Noctilio albiventris	4.03	0.00	0.55	0.10	0.76
Noctilio leporinus	0.09	**71.4** ♂♂	0.03	**54.3** ♂♂	0.05
Natalus tumidirostris	0.25	**29.2** ♀♀	0.05	**19.5** ♀♀	0.58
Molossus rufus	1.18	0.39	1.49	0.39	0.01

Significantly biased parasite loads were not obviously related to sexual size dimorphism. Fifteen species show significant sexual size dimorphism (Table 1); the 23 species showing at least one significant bias in parasitism included seven where females were larger, 13 where the sexes were subequal, and three where males were larger. Although male biases were observed in *Noctilio leporinus*, where males are larger than females, they were also observed in *Pteronotus davyi* and *Leptonycteris curasoae* where the sexes are equal in size, and in *Chrotopterus auritus* and *Anoura latidens* where females are larger. Binomial tests determining whether the larger sex

Table 2. Binomial tests of association between sex-biased parasitism and sexual dimorphism in body size. The first three columns designate test parameters while the last tallies the probability that associations between the two are at random.

	Successes	Trials	P(success)	α
Proportionate to captures				
Infestations	2	15	0.13	0.69
Total number of flies	5	15	0.478	0.19
Number of fly infrapopulations	2	15	0.174	0.50
Proportionate to infestations				
Total number of flies	4	15	0.261	0.65
Number of fly infrapopulations	0	15	0	–

was significantly more heavily parasitized are tallied in Table 2; all four possible tests indicate that sex bias in parasitism and host size dimorphism are unrelated.

DISCUSSION

This extensive survey of a major neotropical bat fauna uncovered significant differences between sexes in levels of infestation and parasite loads involving streblid bat flies. In most cases and by most measures, tests showed females were more frequently and heavily parasitized. Despite some methodological differences and our analysis of a much richer fauna, this study confirms the main conclusions of Presley & Willig (2008) that female bats are generally more heavily infested by ectoparasites. Because it encompassed many more infested bat species (89 versus 19–22 species in Paraguay), surveyed many more bats (24 979 versus 2909 in Paraguay), and restricted analysis to a single family of parasites (versus 11 in Paraguay, where 55% of ectoparasites were macronyssid mites), this survey refines the sex-bias pattern and strengthens this conclusion.

Higher infestation of bat flies on female hosts is a result that contrasts with studies of other mammalian ectoparasites. Across many host–parasite systems, when the sexes are differentially infested, it is commonly males that exhibit higher parasite loads. A meta-analysis of sex differences in parasitism showed that biases tended towards male hosts, particularly where arthropod parasites were involved (Schalk & Forbes 1997). Male-biased infections by nematodes are also widespread and well documented in field studies (Poulin 1996). But at least one other group of bat ectoparasites, mites, also typically shows female-biased infestations (Christe *et al.* 2007, Whitaker *et al.* 2007).

Many bat species exhibit slight sexual dimorphism in body size, females in many species being 1–7% larger than males in linear dimensions (Ralls 1976). Other factors being equal, larger size means more 'habitat' for the parasite and perhaps larger refuges from host grooming. Although a third of the sampled species were sexually dimorphic in size, dimorphism was not associated with significant sex biases (Table 2). Elsewhere, size dimorphism was not a significant component of variation in Paraguayan bat fly infestations (Presley & Willig 2008). Sex differences in body size of these bat species are evidently minor compared to other ecological and behavioural differences affecting parasite loads.

Many factors – physiological, morphological, behavioural and social – may differentially expose either sex to parasitism, and the ecological diversity of bats makes them excellent subjects for teasing these variables apart. However, many relevant variables were not tracked in the SVP surveys, handicapping our ability to assess them. In fact, most bats sampled by SVP were captured with mist nets while they foraged, a technique that obscures their social groupings, associations, and roosts. As discussed below, physical, social and physiological contexts are vital for evaluating various explanations for parasite loads, so a number of interesting hypotheses could not be tested with these data. Future analyses of fly parasite loads in bats should focus on parasitism levels among individuals of known social groupings, preferably collected at the roost where inter-relationships of individuals could be assessed.

One class of explanations for sex bias in parasitism centres on immunological mechanisms. Immunocompetence has been proposed to explain the higher intensity of spinturnicid (wing mite) parasitism on reproductive and pregnant female bats versus non-reproductive females (Christe *et al.* 2000). High testosterone levels in males may be responsible for immunosuppression and lead to male-biased infestation patterns (Folstad & Karter 1992). Hormones may also influence the levels and seasonality of parasitic infestations independently of immunology, as rabbit fleas depend on the hormones of reproducing female hosts to complete their own ovarian maturation (Mead-Briggs & Rudge 1960, Rothschild & Ford 1964).

But many ecological factors are likely to influence sex-biased parasitism, and some of these may take precedence over immunological factors in explaining variation in levels of parasitism (Krasnov *et al.* 2005). Heavier loads on females could be attributable to differential roost-site selection by male and female bats (Zahn & Rupp 2004). Bats roosting in more permanent and enclosed shelters exhibit a higher prevalence, intensity and diversity of parasitism than bats that roost in exposed, transient structures (Patterson *et al.* 2007). Permanent roosts, such as caves, mines, and other large cavities, typically house larger colonies of bats than do ephemeral roosts such as tree leaves and smaller cavities (Kunz 1982). The permanence of bat roosts is also closely tied to the fidelity of bats roosting there (Lewis 1995), which in turn determines the dynamics of roost-switching. Roost-switching may serve as a behavioural strategy for

avoiding parasites altogether or reducing parasite loads (Reckardt & Kerth 2006, Timm 1987).

Females might select higher-quality roosts that attract larger numbers of bats, which in turn facilitate higher levels of infestation by making them more vulnerable to infestation (Krasnov *et al.* 2002, Zahn & Rupp 2004). However, the density of roosting bats is critical to transmission, as large roosts offer more space for bats to spread out, thus decreasing physical contact and the likelihood of parasite transfers (Dick *et al.* 2003). The colony-size effect has been observed to affect louse infestations of certain Galapagos birds, where amblyceran lice responded positively to an increase in the degree of host sociality (Whiteman & Parker 2004). Females in many bat species roost in dense maternity colonies (McCracken 1984); the dense crowding of these colonies helps to maintain high body temperatures needed for the rapid growth of juvenile bats but may also facilitate transmission of parasites to colony members. Bat flies are known to move between host individuals when they roost so closely together that their fur is touching (Overal 1980). Females in many species of mammals enjoy higher instantaneous survivorship rates and so might be a better prospect for a colonizing parasite or alternatively be more likely to accumulate a non-selective one.

Curiously, documented effects of bat aggregations seem to enhance their parasitism by streblids, not reduce it. Reductions might be expected if allo-grooming were widespread and important in controlling parasite loads (Wohland 2000). Although grooming may be the principal source of bat fly mortality (Marshall 1982) and appears to influence host-site selection by the flies (ter Hofstede *et al.* 2004), grooming behaviour itself does not predict parasitism levels in bats. In fact, harem male *Artibeus lituratus* in Venezuela spend half as much time during the day grooming as do harem females (Muñoz-Romo 2006), yet the male *A. lituratus* in our sample enjoyed significantly lower infestation levels (Table 1). Again, knowing the social affiliations of the bats sampled would help to illuminate the role of these variables and the behavioural, physiological and social conditions promoting susceptibility. Future field surveys should incorporate social biology into their experimental design.

ACKNOWLEDGEMENTS

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Appendix 1. Records of streblid bat flies on Venezuelan bats, by sex. Taxonomy follows Simmons (2005) except as discussed by Solari *et al.* (2006). Captures record all sexed, identified, and catalogued bats that were processed for ectoparasites, while infested bats reflect the number of those harbouring one or more streblid flies. Prevalence and mean intensity of all streblids calculated separately from male and female totals. Species marked with an asterisk were deemed to have been adequately sampled for statistical tests.

	Number of captured bats		Number of infested bats		Prevalence		Mean intensity	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Emballonuridae								
Cormura brevirostris	7	8	1	–	0.143	0	2.00	
Diclidurus albus	15	8	–	–				
Diclidurus ingens	3	–	–	–				
Diclidurus isabellus	7	21	–	–				
Diclidurus scutatus	12	2	–	–				
Peropteryx kappleri	30	23	3	–	0.1		1.33	
Peropteryx macrotis	128	83	16	2	0.125	0.024	1.94	4.00
Peropteryx trinitatis	21	40	3	2	0.143	0.05	3.00	2.00
Rhynchonycteris naso	68	78	1	2	0.015	0.026	1.00	1.00
Saccopteryx bilineata	214	118	1	1	0.005	0.008	4.00	1.00
Saccopteryx canescens	13	10	–	–				
Saccopteryx leptura	26	13	–	–				
Phyllostomidae								
Ametrida centurio	77	72	–	1	0	0.014		1.00
*Anoura caudifer	63	55	28	34	0.444	0.618	2.36	1.74
Anoura cultrata	3	3	–	1		0.333		2.00
*Anoura geoffroyi	85	86	55	58	0.647	0.674	2.96	2.90
*Anoura latidens	58	52	23	26	0.397	0.5	2.13	3.19
*Artibeus amplus	26	18	17	11	0.654	0.611	3.29	3.00
Artibeus concolor	91	29	–	–				
*Artibeus lituratus	520	376	101	39	0.194	0.104	1.40	1.46
*Artibeus obscurus	88	211	13	27	0.148	0.128	1.85	2.00

Appendix 1. Continued.

	Number of captured bats		Number of infested bats		Prevalence		Mean intensity	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
*Artibeus planirostris	907	704	343	157	0.378	0.223	2.25	1.66
Carollia benkeithi	8	10	2	–	0.25	0	1.50	
*Carollia brevicauda	270	244	121	91	0.448	0.373	1.90	1.57
*Carollia perspicillata	2156	1854	647	418	0.3	0.225	2.73	2.81
Centurio senex	5	–	–	–				
Chiroderma salvini	16	14	3	3	0.188	0.214	1.00	1.00
Chiroderma trinitatum	49	18	–	1	0	0.056		1.00
Chiroderma villosum	549	157	8	8	0.015	0.051	2.25	3.63
Choeroniscus godmani	10	4	–	–				
Choeroniscus minor	2	1	–	–				
*Chrotopterus auritus	10	27	7	19	0.7	0.704	3.00	7.05
Dermanura cinerea	1	1	1	1	1	1	2.00	1.00
*Dermanura glauca	214	215	39	37	0.182	0.172	1.33	1.51
Dermanura gnoma	32	26	–	3	0	0.115		1.00
*Desmodus rotundus	442	399	272	264	0.615	0.662	10.7	7.47
Diaemus youngi	6	12	3	9	0.5	0.75	29.0	9.00
Diphylla ecaudata	3	8	–	–				
*Enchisthenes hartii	58	63	21	18	0.362	0.286	1.76	1.67
*Glossophaga longirostris	348	457	35	84	0.101	0.184	1.86	1.63
*Glossophaga soricina	426	411	129	103	0.303	0.251	1.98	1.95
Glyphonycteris sylvestris	1	2	–	–				
Lampronycteris brachyotis	1	2	–	1	0	0.5		3.00
*Leptonycteris curasoae	179	542	122	141	0.682	0.26	25.1	27.8
Lichonycteris degener	1	–	–	–				
*Lionycteris spurrelli	105	67	55	40	0.524	0.597	2.55	1.83
*Lonchophylla robusta	13	13	13	13	1	1	5.85	4.31
Lonchophylla thomasi	9	9	1	–	0.111		1.00	
*Lonchorhina aurita	46	76	21	20	0.457	0.263	4.95	3.50
*Lonchorhina orinocensis	83	163	60	118	0.723	0.724	2.77	2.68
*Lophostoma brasiliense	24	27	18	15	0.75	0.556	5.72	6.87
Lophostoma carrikeri	–	3	–	3	0	1		9.33
*Lophostoma silvicolum	24	18	15	11	0.625	0.611	4.27	3.00
*Macrophyllum macrophyllum	15	35	14	13	0.933	0.371	4.50	5.08
Mesophylla macconnelli	51	18	4	2	0.078	0.111	1.00	1.00
Micronycteris hirsuta	3	2	–	–				
Micronycteris megalotis	55	88	–	5		0.057		1.20
*Micronycteris minuta	36	31	12	18	0.333	0.581	5.50	2.67
Micronycteris schmidtorum	10	8	–	1		0.125		1.00
Mimon crenulatum	33	37	1	–	0.03		1.00	
*Phylloderma stenops	16	11	11	11	0.688	1	9.09	10.0
*Phyllostomus discolor	142	178	138	168	0.972	0.944	11.3	9.13
*Phyllostomus elongatus	58	60	50	42	0.862	0.7	7.66	3.33
*Phyllostomus hastatus	180	308	94	130	0.522	0.422	5.10	4.70
*Platyrrhinus aurarius	33	29	17	12	0.515	0.414	2.53	1.92
Platyrrhinus brachycephalus	1	3	–	1		0.333		1.00
*Platyrrhinus helleri	382	367	30	30	0.079	0.082	1.17	1.20
*Platyrrhinus umbratus	104	117	35	34	0.337	0.291	1.83	2.44
Platyrrhinus vittatus	4	6	3	4	0.75	0.667	3.00	1.25
Rhinophylla pumilio	42	16	13	6	0.31	0.375	1.54	1.17
Sphaeronycteris toxophyllum	114	43	2	1	0.018	0.023	1.00	1.00
Sturnira bidens	13	3	5	–	0.385		1.60	
Sturnira bogotensis	2	2	1	–	0.5		1.00	
*Sturnira erythromos	44	67	11	15	0.25	0.224	1.36	1.53
*Sturnira lilium	1008	767	439	236	0.436	0.308	2.51	1.89
*Sturnira ludovici	117	205	69	78	0.59	0.38	2.12	1.97
*Sturnira tildae	118	93	74	30	0.627	0.323	2.54	2.80
Tonatia saurophila	8	11	3	8	0.375	0.727	1.33	8.13
*Trachops cirrhosus	172	182	52	49	0.302	0.269	3.44	3.71
*Trinycteris nicefori	101	87	8	13	0.079	0.149	1.63	2.15
*Uroderma bilobatum	366	273	41	32	0.112	0.117	1.24	1.28
Uroderma magnirostrum	243	122	9	4	0.037	0.033	1.00	1.00
Vampyressa bidens	53	63	4	2	0.075	0.032	1.00	1.00

Appendix 1. Continued.

	Number of captured bats		Number of infested bats		Prevalence		Mean intensity	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
*Vampyressa pusilla	85	30	18	6	0.212	0.2	1.22	1.67
Vampyrodes caraccioli	18	5	1	–	0.056		1.00	
Vampyrum spectrum	2	3	–	–				
Mormoopidae								
Mormoops megalophylla	18	55	13	29	0.722	0.527	7.62	7.03
Pteronotus davyi	101	115	46	54	0.455	0.47	11.8	20.7
Pteronotus gymnonotus	25	25	14	17	0.56	0.68	2.29	1.65
Pteronotus parnellii	218	201	139	146	0.638	0.726	9.68	7.06
Pteronotus personatus	2	2	1	1	0.5	0.5	2.00	1.00
Noctilionidae								
Noctilio albiventris	300	165	127	71	0.423	0.43	6.46	6.34
Noctilio leporinus	47	37	33	28	0.702	0.757	10.4	17.4
Furipteridae								
Furipterus horrens	–	6	–	1		0.167		
Thyropteridae								
Thyroptera tricolor	5	6	–	–				
Natalidae								
Natalus tumidirostris	56	117	29	54	0.518	0.462	5.07	3.06
Molossidae								
Cynomops abrasus	2	–	–	–				
Cynomops greenhalli	–	1	–	–				
Cynomops paranus	2	–	–	–				
Cynomops planirostris	119	49	–	–				
Eumops auripendulus	5	–	–	–				
Eumops bonariensis	11	6	–	–				
Eumops dabbenei	1	–	–	–				
Eumops glaucinus	59	19	2	1	0.034	0.053	1.00	1.00
Eumops hansae	1	1	–	–				
Molossops mattogrossensis	7	11	–	–				
Molossus aztecus	92	60	–	–				
Molossus bondae	17	4	–	–				
Molossus molossus	215	109	2	–	0.009		1.00	
Molossus rufus	241	150	20	8	0.083	0.053	1.20	1.50
Molossus sinaloae	4	1	–	–				
Nyctinomops laticaudatus	122	95	1	1	0.008	0.011	1.00	1.00
Promops centralis	1	–	–	–				
Promops nasutus	2	2	–	–				
Tadarida brasiliensis	5	3	–	–				
Vespertilionidae								
Eptesicus andinus	9	3	–	–				
Eptesicus brasiliens	39	25	–	–				
Eptesicus diminutus	1	1	–	–				
Eptesicus furinalis	6	10	–	–				
Eptesicus fuscus	1	3	–	–				
Eptesicus montosus	24	12	–	–				
Histiotus montanus	1	3	–	–				
Lasiurus blossevillii	2	5	–	–				
Lasiurus cinereus	5	3	–	–				
Lasiurus ega	9	10	–	–				
Myotis albescens	54	30	–	–				
Myotis keaysi	30	23	5	2	0.167	0.087	1.80	1.00
Myotis nesopolus	8	18	–	1		0.056		1.00
Myotis nigricans	71	76	1	–	0.014		1.00	
Myotis oxyotus	5	4	2	1	0.4	0.25	1.00	1.00
Myotis riparius	15	4	–	–				
Rhogeessa minutilla	129	93	1	–	0.008		5.00	
Rhogeessa tumida	16	8	–	–				
Grand Total	13285	11694	3790	3145	0.285	0.269	3.72	3.61
Total for adequately sampled species	10128	9783	3689	3068	0.364	0.314	3.92	3.80