

# Parasitism by bat flies (Diptera: Streblidae) on neotropical bats: effects of host body size, distribution, and abundance

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**Abstract** We examined the correlations between prevalence (proportion of infested individuals), mean intensity (number of parasites per infested individual), and the number of bat fly species parasitizing bats in Venezuela with host body mass, distribution, and abundance. Of 133 bat species sampled, 53 species in six families were captured frequently enough to allow estimation of their parasite loads. Over all species and six families, prevalence and mean intensity were uncorrelated with these variables, but the number of fly species was correlated with host body mass. Correlations of parasitism with body mass were strengthened among the 44 species of Phyllostomidae. Earlier studies showed that bat roosting habits influence their parasitism by bat flies with more permanent, enclosed roosts being with heavier parasitism. Multiple regressions of all measures of parasitism showed that roosting habits and host body mass, respectively, were the first variables to enter stepwise regressions, together accounting for 20–43% of the variation in measures of parasitism. Lack of correlation between proxies of distribution and abundance with parasitism is taken to indicate that proximate factors such as host-as-habitat, social groupings, and roost microhabitat take precedence over species-wide attributes like commonness and ubiquity.

## Introduction

In nature, populations can be influenced by competitors, predators, and parasites, acting as checks on distribution, abundance, and fitness. Competition theory has been central to community ecology for half a century (Hutchinson 1959; MacArthur 1972), and predation is now universally regarded as a major structuring force (Terborgh 1988; Berger et al. 2001). However, we are still learning about the importance and roles of parasitism (Thompson 1999; Packer et al. 2003; Morand et al. 2006). Richer empirical documentation of patterns aids the evaluation of alternative theories and may identify new mechanisms of interaction (Fenton et al. 2002; Altizer et al. 2003; Poulin 2007).

Bats (Mammalia: Chiroptera) are abundant and diverse in neotropical forests. In Peru's Manu Biosphere Reserve, one of the world's richest protected areas, 41% (92 of 222 species) of all documented mammal species are bats (Solari et al. 2006). The aggregate abundance of neotropical bats is equally impressive with biomass estimates equaling all other mammal species combined (Tuttle 1983). Their ecological success depends on the exploitation of diverse trophic strategies, roosting structures, habitats, movement patterns, and sensory modalities (Kalko 1997; Patterson et al. 2003), in turn enabled by the key innovations of flight and echolocation (Thewissen and Babcock 1992; Teeling et al. 2000; Simmons et al. 2008). Their ecological importance as pollinators, seed dispersers, and insectivores is transcendent, generating numerous indirect effects on forest health and vitality (Wilson 1989; Rainey et al. 1995). Bats have remarkably diverse social systems as well, living in groupings that range from small family groups to aggregations of millions (Hill and Smith 1984). Such ecological variation means that bat species should differ dramatically in their susceptibility to different biological controls.

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Bats are host to numerous internal (Coggins 1988) and external parasites, the most conspicuous being blood-sucking bat flies, Streblidae and Nycteribiidae (Marshall 1982). Traditionally regarded as two families (but see Dittmar et al. 2006), these obligate ectoparasites live only on bats, inhabiting the fur and flight membranes. Like other flies, bat flies must metamorphose to complete development. But unlike most other flies, bat flies give birth to a single young which is already at the third-instar larval stage and pupates immediately afterwards. Deposition and pupation of larvae typically happens in the vicinity of the bat's roost, and newly emergent flies must colonize a host bat (Dick and Patterson 2006). The intensity, prevalence, and evolutionary associations of bat fly parasitism all increase with the strength and durability of the bats' roost (ter Hofstede and Fenton 2005; Patterson et al. 2007). Despite the decoupling of host and parasite in each generation, bat fly species are strikingly host-specific. A recent survey of bat flies on Paraguayan bats determined that 87% of 31 streblid species were restricted to a single bat species (Dick and Gettinger 2005).

The fitness costs of bat fly parasitism are not well-understood or quantified (Bender 2000). However, flies take blood meals many times a day and typically die after being separated from their hosts for just a few hours (Fritz 1983). Behavioral studies indicate that fly numbers may be limiting; host-choice experiments indicate that the density of conspecifics determines the attractiveness of hosts to colonizing bat flies (Dick and Dick 2006). Hosts spend more time grooming as fly density increases (Overall 1980; ter Hofstede and Fenton 2005), and host grooming is thought to be the chief source of fly mortality (Marshall 1981).

The prevalence and size of parasite loads have been correlated with host body size in many taxa because larger hosts offer a larger target to colonizers and more "habitat" to support them (Poulin and George-Nascimento 2007). Larger hosts may also be more likely to or accumulate them through higher consumption (of intermediate stages) or larger ranges (Perez-Orella and Schulte-Hostedde 2005; Poulin and George-Nascimento 2007). Large hosts may also groom at lower rates (Arneberg et al. 1998b). Besides affecting ectoparasite density, host body size may also influence the species richness of parasite assemblages (Guégan and Hugueny 1994). As many as six bat fly species can coexist on a single host bat (Wenzel 1976), typically partitioning the bat's fur and flight membranes. Dick (2005) determined that coexisting flies often represent discrete ecomorphs reflecting their differential host utilization modes (see also Tello et al. 2008). These factors led us to predict that parasite loads should be more frequent and heavier on larger species of bats, and larger species should support more coexisting fly species.

Parasite loads may also be influenced by the total abundance, aggregation, and ubiquity of the hosts (Poulin 1991; Arneberg et al. 1998a; Krasnov et al. 2002). Such variables affect the quantity and dispersion of resources available to parasites and can either facilitate or limit parasite transmissions. Other factors being equal, we would predict that common, widespread bats should be more frequently and heavily infested, particularly those that are locally abundant.

We sought to test these predictions with a country-wide investigation of one of the world's richest bat faunas. The diverse bat species of Venezuela offer a 19-fold size range and vary over two orders of magnitude in total captures and incidence among collecting localities. This variation offers meaningful explorations of hypotheses concerning parasitism.

## Materials and methods

The Smithsonian Venezuela Project (SVP) was conducted from 1965 to 1968 and represented one of the world's largest coordinated surveys of vertebrates and their ectoparasites. That effort sampled 38,213 individual mammals representing 270 species, including 24,979 sexed individuals of 133 species of bats. 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, Jr. at the National Museum of Natural History (USNM; Handley 1976). Host names were recently updated in accordance with subsequent taxonomic revisions and reidentifications. These features ensure accuracy, consistency, and repeatability, all vital to robust host-parasite studies (Wenzel et al. 1966; Poulin 1998).

Body masses for these species were gleaned from a variety of primary and secondary sources, including Emmons and Feer (1997), Nowak (1999), Patterson et al. (1996), Silva and Downing (1995), and Simmons and Voss (1998). Data on distribution and abundance were taken directly from the SVP database. Because most bats were collected passively in mist nets while foraging, their sample sizes are themselves proxies of commonness, albeit biased by the sensory abilities and locomotory modes of the bats and occasionally by the specialized collecting methods used to sample them. We indexed the distributional range of bat species in Venezuela by counting the number of specific localities in which each was taken. Because most bat species occur more-or-less widely outside Venezuela, spatially explicit measures of their in-country distribution would be meaningless. We derived a gauge of local abundance by dividing the total sample size of a species by its locality records, essentially the mean number of individuals taken where the species occurs. Linares (1998)

characterized the roosting habits of bat species in 23 roosting structures; Patterson et al. (2007) ranked these from 1 to 6 in order of increasing permanence and protection and presented a weighted summary value for species that occupy multiple roosts.

Bulk parasite samples were collected and organized by individual host. At the Field Museum of Natural History (FMNH), Dr. Rupert Wenzel sorted, identified, and enumerated the streblid bat flies (Diptera: Streblidae). The total included 36,663 streblids, representing 22 genera and 116 species; two genera and 45 species were newly described (Wenzel 1976). Records each consisted of an “infrapopulation” (Bush et al. 1997), individuals of a given parasite taxon collected from a host individual; multiple records were used for individual bats that hosted two or more species of flies. The number of infrapopulations equals the number of bat fly species that co-occur on the individual bat. We excluded SVP records not catalogued at the USNM (and hence lacking reconfirmed identifications), as well as those that lacked bat or bat fly identifications, gender specifications, or counts of parasites loads. A total of 24,979 bats, representing 133 species in nine families, were sampled for flies.

To avoid spurious effects of small sample size, we restricted comparisons to bat species with  $\geq 10$  infested individuals. We examined the differences between species in prevalence (proportion of sampled bats infested by streblids, tabulated in Patterson et al. (2007), mean intensity (count of all flies harvested from individual hosts), as well as the standard deviation (SD) and maximum of this count. We also examined the mean fly species (the number of bat fly infrapopulations comprising an individual’s infestation).

We used Spearman rank correlation,  $r_s$ , on untransformed variables because it lacks assumptions about the normality, homoscedasticity, and co-linearity of the varia-

bles. For parametric analyses, we first log-transformed the variables (except prevalence, which was logit-transformed) to approximate normality. Partial correlation analysis was used to assess correlations taking roosting habits into account, correlations designated by  $r_R$ . Stepwise multiple regression was used to assess covariation among dependent and independent variables. We included roosting habits in these analyses because earlier studies showed them to be strongly correlated with prevalence, mean intensity, and infrapopulation size (Patterson et al. 2007). All analyses were run with Statistica 6.0 (StatSoft 2003).

## Results

Although 91 species of bats met our documentation criteria and hosted streblid flies, 53 species belonging to six families were represented by at least 10 infested individuals (Table 3 of the Appendix). These included one emballonurid (*Peropteryx macrotis*), 44 phyllostomids, four mormoopids, two noctilionids, one natalid (*Natalus tumidirostris*), and one molossid (*Molossus rufus*). The number of samples for each bat species averaged 128 individuals (range 11 to 1,057 individuals) and their body mass averaged 25.9 g (5.6 to 95 g). On average, the bat samples were collected from 20.8 localities (three to 107 sites) with local abundances averaging 6.0 individuals (1.33 to 23.7) per site.

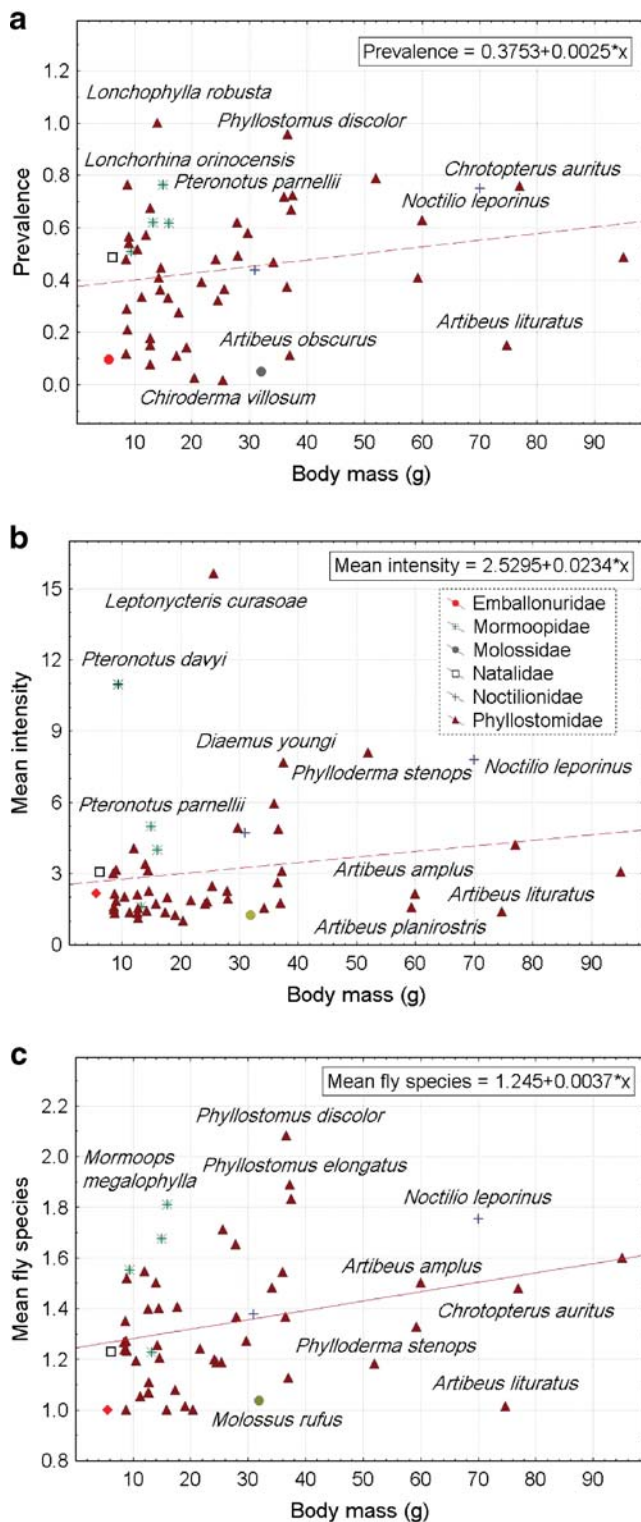
Prevalence of streblid parasitism averaged 44.1%, varying from 1.7% to 100%. Mean intensities of species averaged 3.1 flies (1 to 15.6), while the mean fly species per individual bat was 1.34 (1 to 2.08) species. Nearly equivalent variation was found among the 44 phyllostomid species, which averaged 26.7 g (8.5 to 95 g), 23.1 localities (three to 107 sites), and 5.3 individuals (1.33 to 23.7) per

**Table 1** Rank correlation coefficients ( $r_s$ ) between ecological attributes of bats and parasitism by bat flies

	Sample size	Localities	Local abundance	Roosting habits	Body mass	Prevalence	Mean intensity	SD intensity	Maximum intensity	Mean fly species
Sample size	–	0.76*	0.68*	0.11	0.10	0.11	0.06	0.09	0.36*	0.28*
Localities	0.83*	–	0.07	–0.07	0.23	0.02	0.01	0.04	0.25	0.14
Local abundance	0.69*	0.23	–	0.16	–0.04	0.16	0.05	0.08	0.27	0.25
Roosting habits	0.14	0.13	0.00	–	–0.31*	0.41*	0.53*	0.49*	0.48*	0.47*
Body mass	0.08	0.17	0.01	–0.23	–	0.19	0.23	0.24	0.26	0.30*
Prevalence	0.03	0.02	0.08	0.40*	0.22	–	0.69*	0.66*	0.59*	0.70*
Mean intensity	–0.05	0.00	–0.09	0.52*	0.33*	0.72*	–	0.98*	0.88*	0.74*
SD intensity	–0.03	0.02	–0.07	0.49*	0.32*	0.67*	0.98*	–	0.93*	0.75*
Maximum intensity	0.26	0.26	0.16	0.54*	0.29	0.59*	0.86*	0.91*	–	0.77*
Mean fly species	0.21	0.14	0.19	0.51*	0.31*	0.68*	0.74*	0.72*	0.74*	–

Analyses of all bat species ( $n=53$ ) are given above the diagonal, and those for phyllostomids only ( $n=44$ ) are given below the diagonal

\* $P<0.05$



**Fig. 1** Parasitism and body mass: **a** prevalence and body mass ( $r_s = 0.19$ ; n.s.); **b** mean intensity and body mass ( $r_s = 0.23$ ; n.s.); **c** fly species and body mass ( $r_s = 0.30$ ;  $P < 0.05$ )

site. Phyllostomids had a mean prevalence of 43.2% (1.7% to 100%), mean intensity of 2.86 (1 to 15.6) flies, and mean fly species of 1.32 (1 to 2.08) species (Table 3 of the Appendix).

#### Body mass

Over all 53 species, body mass was not correlated with prevalence or with mean intensity and its corollaries ( $P > 0.05$ ; Table 1), but it was found to be loosely correlated with mean number of fly species ( $r_s = 0.30$ ,  $P < 0.05$ ). Most measures of parasitism were strongly and positively correlated, so that species that tended to have higher prevalence had higher intensities (with higher SDs and maximums) and hosted more fly species. The mean number of fly species was significantly correlated with all other variables in the analysis, including sample size, roosting habits, and body mass (Fig. 1; Table 1).

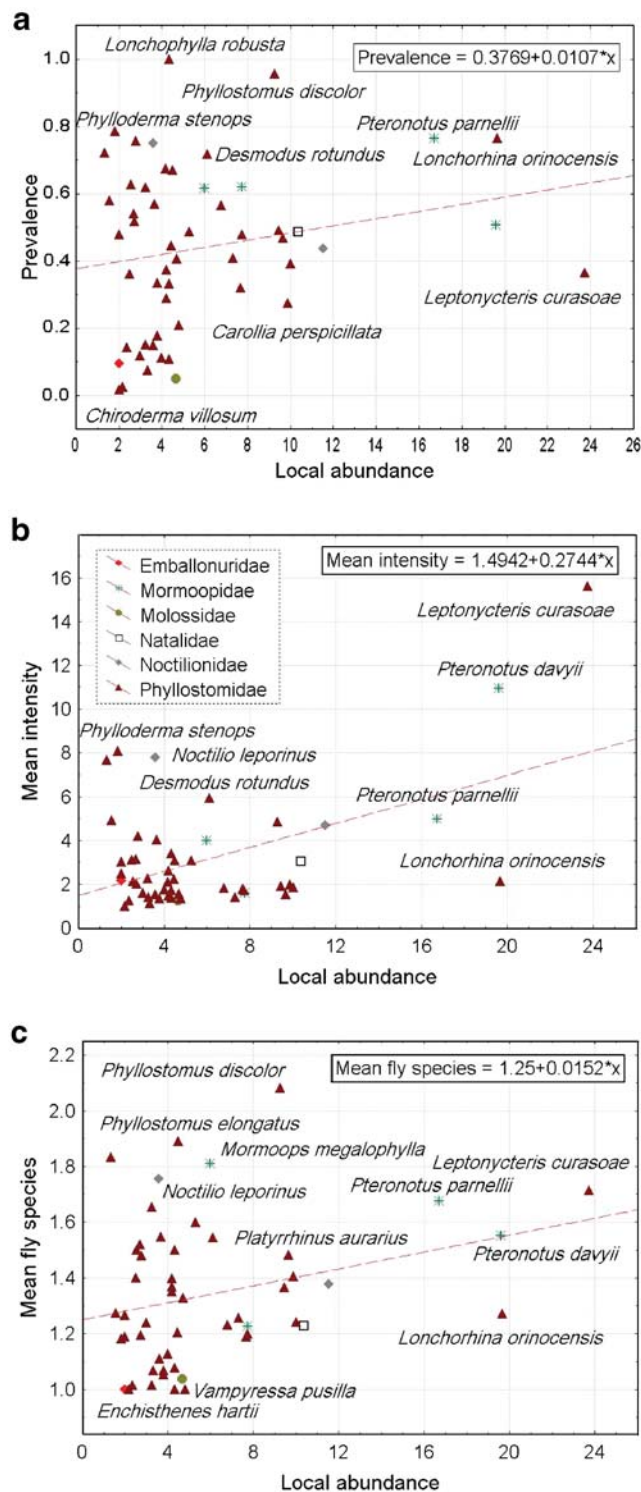
When comparisons are limited to 44 species of Phyllostomidae, correlations are somewhat strengthened. Body mass is not correlated with prevalence but correlates with mean intensity and its SD as well as mean fly species (all  $P < 0.05$ ). As before, measures of parasitism were all positively correlated, and mean fly species is strongly correlated to all other variables save sample size (Table 1).

Using partial correlations to control for the effects of roosting habits, body mass was positively and significantly correlated with all three measures of parasitism over all bat species: prevalence ( $r_R = 0.35$ ), mean fly load ( $r_R = 0.30$ ), and mean fly species ( $r_R = 0.45$ , all  $P < 0.05$ ). The latter variable was significantly and positively correlated with all others in the data set (all  $r_R > 0.43$ ), but prevalence and mean fly loads were uncorrelated ( $P > 0.05$ ). Among phyllostomids, after accounting for roosting habits, body mass was positively and significantly correlated with prevalence ( $r_R = 0.33$ ) and mean fly species ( $r_R = 0.44$ ) and nearly so with mean fly loads ( $r_R = 0.28$ ). Prevalence lost its correlation with mean intensity but was strongly correlated with mean fly species ( $r_R = 0.59$ ); as before, mean fly species was correlated with all other variables studied.

#### Distribution and abundance

Over all bats, there were strong correlations between sample size and the number of localities a bat was recorded at ( $r_s = 0.76$ ) and its local abundance ( $r_s = 0.68$ ). Sample size was also more weakly correlated with the maximum intensity of infestation ( $r_s = 0.36$ ) and mean number of fly species ( $r_s = 0.28$ ; all  $P < 0.05$ ; Fig. 2).

Among phyllostomids, correlations are undiminished between sample size and localities ( $r_s = 0.83$ ) and local abundance ( $r_s = 0.69$ ), but disappear between sample size and maximum intensity ( $r_s = 0.26$ ) and mean fly species ( $r_s =$



**Fig. 2** Parasitism and local abundance: **a** prevalence and local abundance ( $r_s=0.16$ , n.s.); **b** mean intensity and local abundance ( $r_s=0.05$ , n.s.); **c** mean fly species and local abundance ( $r_s=0.25$ , n.s.)

0.21; both  $P>0.05$ ). Within Phyllostomidae, no measure of parasitism is correlated with distribution or abundance measures. For both sets of bats, all are correlated with roosting habits (Table 1).

## Multivariate effects

Log-transformed variables for distribution, abundance, body size, and roosting habits were used as independent variables in stepwise regressions to predict five measures of parasitism: prevalence, mean intensity, SD intensity, maximum intensity, and mean fly species. In all five regressions, roosting habits was the first variable to enter, followed by body mass, both with high degrees of significance (all  $P<0.01$ ). Neither sample size nor number of localities was significant in any regression, and local abundance was the third variable in the regressions of maximum intensity ( $P<0.01$ ). Together, roosting habits and body mass account for 20.6% (prevalence) to 42.7% (mean fly species) of the variance in parasitism of these species (Table 2).

## Discussion

This extensive survey of parasitism in Venezuelan bats shows that body mass is not correlated with the prevalence or mean intensity of streblid parasitism. However, over six families of bats, body mass correlates with the number of fly species that individuals support, and correlations of body mass and parasitism are strengthened in analyses restricted to the 44 species of Phyllostomidae. Multivariate regression analyses show that this effect does not depend on covariation with roosting habits. Together, the two variables account for 20–43% of variation in parasitism by bat flies.

Body mass is an excellent proxy for host body size, which can influence its space use and density, metabolism, fecundity, and survivorship. Host size is thought to affect parasitism directly by affecting the amount of resource available to parasites. Larger host species may provide more space and a greater diversity of niches to parasites. Larger hosts are also more likely to accumulate parasites because they consume more food, range wider, and live longer (Poulin 1997). The analyses in Tables 1 and 2 show small but significant effects of body mass on parasitism.

Streblid bat flies are dispersal-prone parasites, and 79% of New World species are volant (Dick and Patterson 2007). They spend roughly a third of their life span as pupae, decoupled from their host, and must seek and colonize a host as a newly emergent adult (Dick and Patterson 2006). Consequently, they are far less dependent than dispersal-limited parasites (e.g., lice, wing mites, bat bugs) on physical, interpersonal contact of hosts in order to disperse horizontally.

Host body size ought to be more important for dispersal-limited parasites or parasites that never leave the host, simply because such parasites are limited to fewer host

**Table 2** Stepwise multiple regressions of measures of parasitism on variables of host ecology

Cells record the order of entry and level of significance for each regression coefficient and for the overall regression  
 \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

	Prevalence	Mean intensity	SD intensity	Maximum intensity	Fly species
Intercept	***		**		**
Roosting habits	1**	1***	1***	1***	1***
Body mass	2**	2***	2***	2***	2***
Local abundance				3**	
Localities					
Sample size					
$F_{3,47}$	5.3**	7.5***	7.6***	13.6****	13.4****
Adjusted $R^2$	0.206	0.348	0.345	0.43	0.427

individuals over the course of their lifetime. For example, both chewing and sucking lice are very limited in dispersal capability, cannot survive long off-host, and are permanent ectoparasites, completing all stages of the life cycle on-host (Hafner et al. 2003). As a result, lice rely on host-to-host contact for dispersal, unlike more vagile parasites such as bat flies. Indeed, small rodent species are known to be less intensely parasitized by lice than larger species (Marshall 1981 and references therein). So while roost permanence and fidelity (faithfully and regularly returning to a specific roost site) are crucial for bat flies to complete their life cycle, the importance of host body size would be lessened if parasites were able, via dispersal, to easily utilize a number of different host individuals. Although not yet tested, one might predict stronger host body size correlations with parasitism by the other family of bat flies, Nycteribiidae, all of whose members are flightless.

Other studies have failed to identify relationships between host size and parasitism by bat flies. These variables were inconsistently related in a study of Paraguayan bats (Presley and Willig 2008), and host size, sex, and reproductive stage failed to account for the size or structure of component bat fly communities on *Noctilio* bats in Brazil (Moura et al. 2003). Sexual size dimorphism of hosts does not explain the levels of parasitism by bat flies and other ectoparasites in Paraguay or Brazil (Presley and Willig 2008; Patterson et al. 2008). However, sex differences in body size (0–20%) pale alongside the 19-fold difference in size within the Venezuelan species (Table 3 of the Appendix). This study's large sample sizes may be responsible for its documenting small but significant effects of body size.

Correlations of host body size with mean number of fly species were especially consistent and strong. Larger bats tend to host larger assemblages of parasites. Although few studies have assayed parasite richness at the individual level, as we did, Guégan et al. (1992) examined monogenean gill ectoparasites on African freshwater fishes and found that host body size and ecology explained 85% of variation in species richness—as in our study, host distribution and diversity were unimportant. Similarly, Krasnov et al. (1997) found that host body size, but not

the number of its habitats or the size of its geographic range, was correlated with the richness of rodent flea assemblages. Poulin (1995) documented correlations between parasite richness and host body size in gastrointestinal communities of fish, birds, and mammals.

New World bat flies vary greatly in overall morphology, including features that reflect how they move and adhere to a bat's body. Lateral versus dorsoventral compression of the thorax, the presence of ctenidia functioning as hold-fast organs in fur, and greatly elongated legs for scrambling over the host are a few of the more conspicuous differences (Dick and Patterson 2006). Bat flies also show distinct microhabitat preferences for furred or membranous substrates of the host (ter Hofstede et al. 2004). Because host grooming is thought to be a major cause of fly mortality (Marshall 1982) and given that bats cannot groom all regions of their bodies with equal effectiveness, larger bats should afford fly parasites greater opportunity and area for safe space. Randomization analyses suggest that the abundances of fly species inhabiting fur and membrane are independent, but that species cohabiting furred regions are negatively associated (Tello et al. 2008). Experimental evidence points to a similar phenomenon where the presence of membrane-loving flies on host bats precluded the colonization of conspecific flies, whereas the presence of fur flies did not preclude the colonization of wing-loving flies (Dick and Dick 2006). Together, these results are indicative of competition for host microhabitats, which could drive the evolution of divergent ecomorphologies of bat flies, thereby increasing species richness. Although more detailed studies regarding the evolution of bat fly ecomorphology are necessary, these factors may in part explain the strong and positive relationship observed between host body size and the number of fly species they support.

This study also used proxies for abundance and distribution—sample size and number of collecting localities, respectively. Conceivably, their lack of correlation with parasitism could reflect an inappropriate proxy rather than a lacking biological association. Yet our measures of commonness, distribution, and local abundance accord with subjective estimations of these variables derived from years

of monitoring neotropical bat assemblages. Local abundance even reflects the tendency for cave-dwelling species to be dense but localized (restricted to caves) and foliage-roosters to be sparser and widespread. Although more elaborate measures for each are possible (e.g., estimating distribution by the area of the minimum convex polygon that includes collecting localities), there remains the problem of gauging the attributes of a species that have shaped its coevolutionary associations. Most of these bat species range widely outside Venezuela (Gardner 2008), as do their fly parasites, and their ecological and physiological interactions over this broader area almost certainly contribute to their dynamics in Venezuela.

Our results suggest that parasitism is more strongly affected by proximate factors than by species-wide attributes. Attributes of the host (as a habitat for flies), its social groupings (indicating the dispersion of these resources),

and its roost microhabitat all show correlations with parasite loads. On the other hand, bat commonness and ubiquity were not correlated with bat fly parasitism. Perhaps the striking diversity of bat social systems (which were not tracked in this survey) modulates the well-known influences of host density and cohesion on parasite transmission (Krasnov et al. 2002; Whiteman and Parker 2004).

**Acknowledgements** We owe special debts of gratitude to Charles O. Handley, Jr. and Rupert L. Wenzel, both now deceased, for their remarkable taxonomic expertise and great efforts to sort, identify, and describe the mammals and streblids of the SVP. We are grateful to Scott Lidgard for insightful discussions of analyses, Matt Dean and Jamie Bender for their help in developing a database of the SVP records, and the National Science Foundation (DBI-0545051 and DEB-0640330/1) and Stephanie Ware for the support to complete their development.

## Appendix

**Table 3** Ecological attributes and measures of parasitism for 53 well-sampled bat species in Venezuela

	Samples	Localities	Local abundance	Body mass	Roosting habits <sub>a</sub>	Prevalence <sup>b</sup>	Mean intensity	SD intensity	Maximum intensity	Mean fly species
Emballonuridae										
<i>Peropteryx macrotis</i>	18	9	2	5.6	5	0.095	2.17	1.58	5	1
Phyllostomidae										
<i>Anoura caudifer</i>	52	19	2.74	10.5	4.83	0.517	2.02	1.86	13	1.19
<i>Anoura geoffroyi</i>	113	27	4.18	12.7	4	0.673	2.09	1.81	12	1.4
<i>Anoura latidens</i>	49	11	4.45	14.6	4	0.445	2.24	2.18	12	1.2
<i>Artibeus amplus</i>	28	11	2.54	60	1	0.627	2.12	1.77	8	1.5
<i>Artibeus lituratus</i>	140	43	3.26	74.8	1.33	0.150	1.39	0.71	6	1.01
<i>Artibeus obscurus</i>	40	10	4	37	1	0.112	1.73	1.14	6	1.13
<i>Artibeus planirostris</i> <sup>c</sup>	499	106	4.71	59.3	2	0.406	1.56	1.03	9	1.33
<i>Carollia brevicauda</i>	212	29	7.31	14.2	4	0.408	1.40	0.86	8	1.25
<i>Carollia perspicillata</i>	1057	107	9.88	17.7	3.91	0.274	1.98	1.97	34	1.4
<i>Chiroderma villosum</i>	16	8	2	25.4	1.66	0.017	2.47	3.52	16	1.19
<i>Chrotopterus auritus</i>	25	9	2.78	77	4.8	0.757	4.19	4.17	18	1.48
<i>Dermanura glauca</i>	76	20	3.8	12.7	1	0.177	1.33	0.55	3	1.07
<i>Desmodus rotundus</i>	533	87	6.13	36	4.5	0.717	5.94	6.46	63	1.54
<i>Diaemus youngi</i>	12	9	1.33	37.5	5	0.722	7.64	7.82	32	1.83
<i>Enchisthenes hartii</i>	39	9	4.33	15.8	1	0.331	1.72	1.12	5	1
<i>Glossophaga longirostris</i>	119	33	3.61	12.8	4.52	0.148	1.53	0.89	6	1.11
<i>Glossophaga soricina</i>	231	55	4.2	8.7	4.66	0.288	1.46	1.07	11	1.35
<i>Leptonycteris curasoae</i>	261	11	23.73	25.6	5.3	0.364	15.63	17.65	100	1.71
<i>Lionycteris spurrelli</i>	95	14	6.79	9	1	0.564	1.82	1.35	9	1.23
<i>Lonchophylla robusta</i>	26	6	4.33	14	6	1	3.38	3.12	17	1.5
<i>Lonchorhina aurita</i>	40	16	2.5	14.5	5.66	0.361	3.11	3.45	17	1.4
<i>Lonchorhina orinocensis</i>	177	9	19.67	8.8	5	0.764	2.14	1.62	12	1.27
<i>Lophostoma brasiliense</i>	33	9	3.67	12	2.66	0.569	4.04	6	29	1.55
<i>Lophostoma sylvicolum</i>	26	8	3.25	27.9	3	0.619	2.26	2.09	12	1.65
<i>Macrophyllum macrophyllum</i>	27	10	2.7	9	5	0.540	3.15	3.56	20	1.52
<i>Micronycteris minuta</i>	30	15	2	8.5	4	0.478	3	3.19	16	1.27
<i>Phylloderma stenops</i>	22	12	1.83	52	1	0.786	8.08	6.05	18	1.18

**Table 3** (continued)

	Samples	Localities	Local abundance	Body mass	Roosting habits <sub>a</sub>	Prevalence <sup>b</sup>	Mean intensity	SD intensity	Maximum intensity	Mean fly species
<i>Phyllostomus discolor</i>	306	33	9.27	36.7	4	0.956	4.87	5.14	35	2.08
<i>Phyllostomus elongatus</i>	90	20	4.5	37.3	3.66	0.669	3.08	3.78	34	1.89
<i>Phyllostomus hastatus</i>	222	42	5.28	95	2.6	0.486	3.07	3.09	22	1.6
<i>Platyrrhinus aurarius</i>	29	3	9.67	34.2	1	0.468	1.53	1.1	6	1.48
<i>Platyrrhinus helleri</i>	60	18	3.33	12.8	1	0.075	1.11	0.36	3	1.07
<i>Platyrrhinus umbratus</i>	69	9	7.67	24.5	1	0.320	1.79	2.82	26	1.19
<i>Rhinophylla pumilio</i>	19	5	3.8	11.3	3	0.333	1.35	0.81	4	1.05
<i>Sturnira erythromos</i>	26	6	4.33	17.4	1	0.108	1.36	0.56	3	1.08
<i>Sturnira lilium</i>	671	67	10.01	21.7	3	0.391	1.85	1.61	24	1.24
<i>Sturnira ludovici</i>	147	19	7.74	24.2	1	0.478	1.70	1.34	9	1.2
<i>Sturnira tildae</i>	104	11	9.45	28	1	0.491	1.92	1.29	6	1.37
<i>Tonatia saurophila</i>	11	7	1.57	29.7	3	0.579	4.93	5.08	16	1.27
<i>Trachops cirrhosus</i>	101	24	4.21	36.5	3.9	0.373	2.62	2.49	15	1.37
<i>Trinycteris nicefori</i>	21	7	3	8.6	3	0.117	1.58	0.86	4	1.24
<i>Uroderma bilobatum</i>	73	31	2.35	19.1	1	0.142	1.24	0.54	4	1.01
<i>Uroderma magnirostrum</i>	13	6	2.17	20.4	1	0.025	1	0	1	1
<i>Vampyressa pusilla</i>	24	5	4.8	8.8	3	0.209	1.33	0.7	4	1
Mormoopidae										
<i>Mormoops megalophylla</i>	42	7	6	16	6	0.616	3.99	3.78	21	1.81
<i>Pteronotus davyi</i>	98	5	19.6	9.4	6	0.507	10.95	19.74	135	1.55
<i>Pteronotus gymnonotus</i>	31	4	7.75	13.3	5.66	0.620	1.58	0.95	4	1.23
<i>Pteronotus parnellii</i>	284	17	16.71	15	5.66	0.764	4.99	7.03	57	1.68
Noctilionidae										
<i>Noctilio albiventris</i>	196	17	11.53	31	3	0.437	4.70	5.77	46	1.38
<i>Noctilio leporinus</i>	61	17	3.59	70	4.9	0.750	7.78	8.6	45	1.75
Natalidae										
<i>Natalus tumidirostris</i>	83	8	10.37	6.2	6	0.486	3.06	2.85	15	1.23
Molossidae										
<i>Molossus rufus</i>	28	6	4.67	32	3.33	0.049	1.24	0.51	3	1.04

Local abundance calculated as the mean number of samples per locality; body mass is given in grams. Prevalence (infested proportion of sampled individuals), mean intensity (numbers of flies per infested bat), SD and maximum intensity, and mean fly infrapopulations per infested bat are given for each species

<sup>a</sup>Sources and methods for roosting habit determinations in Patterson et al. (2007): 1—leaves and foliage; 2—branches and bark; 3—tree roots, hollows, logs, and holes; 4—rocks and buildings; 5—culverts and tunnels; 6—mines and caves. Tabulated figures are a weighted average of typical roosts

<sup>b</sup>From Patterson et al. (2007)

<sup>c</sup>Reported by Handley (1976) under *Artibeus jamaicensis*. We follow Lim et al. (2004) in calling all Venezuelan forms *A. planirostris*

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