

# Intraspecific patterns of ectoparasite abundances on Paraguayan bats: effects of host sex and body size

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**Abstract:** Although levels of parasitism can vary greatly among individual bats of the same species, little is known about the characteristics of hosts that affect such variation. Bats were captured via mist nets from June 1995 to July 1997 from 28 localities throughout Paraguay. Over 17 500 ectoparasites were collected from 2909 bats; however, analyses of ectoparasite abundance were restricted to more abundant taxa of host and ectoparasite. We quantified the abundances of 29 taxa of ectoparasite on 19 species of bat host, as well as total abundance of ectoparasites regardless of taxonomic affiliation for 22 species of bat from Paraguay. The effects of host sex and host body size on these estimates of ectoparasite abundance were evaluated separately for each species of host. Ectoparasites did not respond consistently to host body size: ectoparasite abundance increased with host body size in 12 instances and decreased with host body size in 11 instances. Regardless of the existence or direction of effects of host body size on ectoparasite abundance, female hosts generally harboured more ectoparasites than did male hosts. Differences in host quality associated with the sex of bats, especially those related to behaviour, may be a more important determinant of ectoparasite abundance than are differences in size. Opportunities for host transfer are critical for species persistence of ectoparasites; consequently, ectoparasite populations on host individuals that form social groups or colonies should be larger, less prone to stochastic extinction, and have greater opportunity for speciation.

**Key Words:** Arthropoda, Chiroptera, ectoparasite abundance, host social system, host specificity, Macronyssidae, Paraguay, roosting ecology, Spinturnicidae, Streblidae

## INTRODUCTION

Abundance is a critical parameter in population- and community-level studies (McGill 2006), and potentially is responsive to a variety of ecological and evolutionary factors. In coevolved symbioses such as host–ectoparasite relationships, abundances of ectoparasites have important consequences for their hosts as well as for the ectoparasites themselves. Larger populations of ectoparasites are less likely to experience stochastic extinction (MacArthur & Wilson 1963) or inbreeding depression (Thornhill 1993), thereby enhancing species persistence. In contrast, high ectoparasite abundances potentially have multifarious negative effects on hosts. Ectoparasites can reduce long-term survival (Brown *et al.* 1995, Chapman & George 1991), reduce clutch or brood size (Mappes *et al.* 1994, Moss & Camin 1970), change

breeding behaviour (Emlen 1986, Møller 1991, Wimberger 1984), or increase the cost of reproduction in hosts (Møller 1993).

Ectoparasite abundances may be influenced by host characteristics such as home range, body size, sex, age, or social system (Altizer *et al.* 2003, Brown & Bomberger Brown 1986, Dick *et al.* 2003, Krasnov *et al.* 2005, Loye & Carroll 1991, Møller 1990, Moore & Wilson 2002, Morand *et al.* 2004, Patterson *et al.* 2007, Soliman *et al.* 2001, ter Hofstede & Fenton 2005, Tompkins & Clayton 1999, Whiteman & Parker 2004, Zelmer *et al.* 2004). The degree to which each factor determines ectoparasite abundance likely is specific to each host–parasite system. Understanding effects of host characteristics on ectoparasite abundance may provide insight into the selective forces that mould these complex symbiotic systems.

For ectoparasites of bats, body size and sex are host characteristics that likely influence ectoparasite

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abundances. A primary cause of positive relationships between species richness and body size is that larger habitats support more individuals, and as a result more species, than do smaller habitats (Rosenzweig 1995). If host body size is analogous to habitable area for ectoparasites, larger hosts should harbour more ectoparasites than do smaller hosts.

In general, males of mammalian species harbour more ectoparasites than do females (Moore & Wilson 2002). Explanations for this observation focus on sex-based differences in immunocompetence or home-range size (Krasnov *et al.* 2005 and sources therein, Morand *et al.* 2004). Males may have reduced immunocompetence compared with females because males exhibit higher androgen levels, which suppress immune function (Folstad & Karter 1992) and favours greater parasite abundances. Similarly, males typically have larger home-range sizes and disperse greater distances than do females, which influence exposure of hosts to ectoparasites (Morand *et al.* 2004, Zelmer *et al.* 2004). Because multiple mechanisms can produce similar patterns, determination of the relative contribution of each mechanism to parasite abundance is difficult. Bats provide an opportunity to decouple the effects of immunocompetence and home-range size/dispersal on parasite abundance. Bats are extremely unlikely to be exposed to new infestations of ectoparasites while in flight because no ectoparasites of bats are such accomplished flyers (Marshall 1982). For most parasites of bats, contact between hosts is required for host transfer (Marshall 1982). Outside of roosts, contact between bats that is sufficient for ectoparasites to achieve transfer is extremely unlikely. In addition, ectoparasites of bats are highly host specific (Dick 2007, Dick & Patterson 2007, ter Hofstede *et al.* 2004). Indeed, ectoparasites from species of bat that share large roosts (caves or buildings) rarely infest multiple host species (Dick & Patterson 2007, ter Hofstede *et al.* 2004). Consequently, if male bats harbour more ectoparasites than do females, immunocompetence is a more likely explanation than factors related to host vagility.

We focused on variation in the body size and sex of hosts as points of departure for understanding variation in ectoparasite abundance among individuals within host species. More specifically, we hypothesized that larger hosts should harbour more ectoparasites than do smaller hosts and that males should harbour more ectoparasites than females. These hypotheses may be powerfully tested in bats because their ectoparasites generally spend all or most of their lives on the body of the host. In contrast, the abundances of ectoparasites on other homeotherms may be influenced additionally by environmental characteristics of nests or burrows in which their ectoparasites often spend appreciable time or entire life history stages. Elsewhere, we address topics related to effects of host characteristics on ectoparasite diversity.

## MATERIALS AND METHODS

### Study area

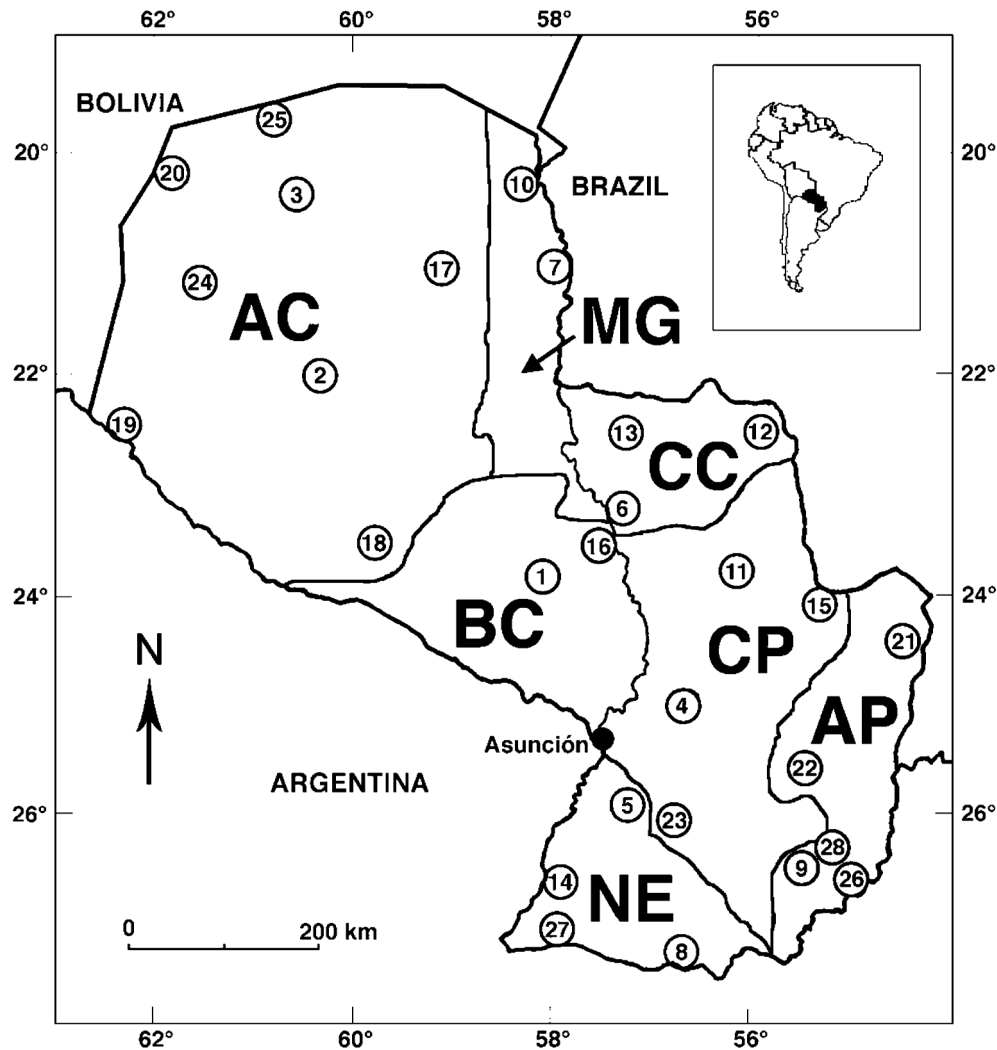
Paraguay is a small (406 752 km<sup>2</sup>) landlocked country, bisected by the Tropic of Capricorn (Figure 1). Climate is characterized by alternating hot, wet and cool, dry seasons. Western Paraguay is mostly hot and dry; however, edaphic features create distinct phytogeographic zones (Hayes 1995). Soils of the Alto Chaco facilitate water percolation and annual rainfall is low (~400 mm); therefore it is characterized by xerophytic thorn-scrub forest. In contrast, the Matogrosense and Bajo Chaco are inundated seasonally and support palm savannas and marshland. Eastern Paraguay is more humid and physiographically diverse. Ñeembucú is edaphically similar to Bajo Chaco and contains similar habitats that interdigitate with tall, humid forests similar to nearby environs of eastern Paraguay. Campos cerrados is a savanna-like formation characterized by a mosaic of xerophytic woodlands and grasslands over rolling terrain. The Central Paraguay region is diverse, including marshes along the eastern banks of the Río Paraguay, as well as low and tall humid forests in the hilly terrain to the east. Alto Paraná is separated from Central Paraguay by a series of low mountain ranges and is characterized by fast-flowing rivers and tall, humid forests. After the 1960s, most of eastern Paraguay experienced extensive deforestation (Keel *et al.* 1993, Ríos & Zardini 1989).

### Field methods

Bats and their ectoparasites were surveyed from July 1995 to June 1997 and from July to August in 1998 at 28 sites (Figure 1) representing all major biomes in Paraguay (Willig *et al.* 2000). Generally, bats were collected using mist nets erected at ground level, although specimens also were obtained on occasion from roosts (e.g. buildings, culverts). Details of collection of bats are available elsewhere (Willig *et al.* 2000). Research involving live animals followed the guidelines for capture, handling, and care of mammals approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and was approved by the Animal Care and Use Committee of Texas Tech University. We followed the treatment of Simmons (2005) regarding bat nomenclature.

### Ectoparasite collection and identification

Captured bats were maintained in separate containers before being anaesthetized and brushed for ectoparasites. Time limitations associated with a great number of specimens, tissue collection, specimen preparation,



**Figure 1.** Map of 28 collection sites (circled numbers) for bats and their ectoparasites from Paraguay (modified from Willig *et al.* 2000). Alphabetic codes identify biomes: Matogrosense, MG; Alto Chaco, AC; Bajo Chaco, BC; Campos Cerrados, CC; Central Paraguayan, CP; Alto Paraná, AP; Neembucú, NE.

preparation of karyotypes, small-mammal trapping, netting of bats, and travel did not permit inspection of hosts under a microscope. Nonetheless, the entire surface of the host was inspected closely with particular attention to areas of the body (e.g. toes, ears, nose, axilla, patagia) typically preferred by specific parasite taxa. All aspects of the protocol for mammal collection (Presley 2004), mammal specimen processing, and ectoparasite collection, handling, and storage were designed (Sheeler-Gordon & Owen 1999) to reduce the likelihood of contamination (i.e. assignment of ectoparasites to the wrong host individual). Mammal specimens are deposited in the Museum of Texas Tech University and the Museo Nacional de Historia Natural del Paraguay.

Identifications of the Streblidae were confirmed via collaborations with personnel of the Field Museum of Natural History (M. Dean, C. Dick and R. Wenzel). Fleas were identified by R. Lewis (Iowa State University).

Polyctenidae were identified by D. Gettinger (University of Central Arkansas) and C. Dick. All other taxa were identified by the first author. Subsequently, identifications of the Macronyssidae and Spinturnicidae were reviewed by D. Gettinger. Voucher specimens of ectoparasites will be deposited at the Field Museum of Natural History. Complete species lists and host–ectoparasite relationships are available elsewhere (Presley 2004).

Three host–parasite parameters (prevalence, mean abundance and mean intensity) were estimated separately for each species of ectoparasite on each host species (Presley 2004, 2007). In addition, a specificity index (SI) was calculated for each host–ectoparasite association (Gettinger & Ernest 1995). For each ectoparasite species, SI is the proportion of individuals that occurred on a particular host species. Host–parasite associations with prevalence  $\geq 0.05$ , and with mean abundance  $\geq 1.0$  or SI  $\geq 0.90$ , were considered to be primary. Hosts

and parasites of these associations are referred to as primary hosts and primary ectoparasites, respectively. Most non-primary ectoparasite–host associations result from disturbance transfers or contamination during sampling (Dick 2007). Use of host–parasite parameters to define primary relationships established a non-arbitrary basis for determination of which host–ectoparasite relationships likely are ecologically meaningful and, therefore, suitable for analysis.

### Statistical analysis

We used host mass and forearm length as surrogates of body size and evaluated their effects on ectoparasite abundance. Because many species of ectoparasite are restricted to patagia or the trunk of the host, we estimated area for each portion of the host separately; patagial area was estimated by forearm length and host trunk area was estimated by mass. Forearm length and mass do not have a linear relationship with surface area, which is the attribute of interest. Area should scale as length<sup>2</sup> or mass<sup>2/3</sup> (Emerson *et al.* 1994); therefore, all analyses used (forearm length)<sup>2</sup> and mass<sup>2/3</sup> to quantify linear relationships between ectoparasite abundance and host body size. Because host attributes related to sex may affect ectoparasite infestation levels, we evaluated effects of host sex on ectoparasite abundance.

Ectoparasite abundance was measured at two levels for each host individual. Total ectoparasite abundance (TEA) equalled the number of individuals of all ectoparasite species on a host individual. Specific ectoparasite abundance (SEA) equalled the number of individuals of a particular ectoparasite taxon. Estimates of TEA and SEA were log<sub>10</sub>-transformed to enhance correspondence to assumptions of parametric tests and to linearize relationships between surrogates of body size and estimates of ectoparasite abundance.

The response of TEA to host body size or sex was investigated separately for each common host species (i.e. bat species for which  $\geq 25$  host individuals were inspected for ectoparasites). To ensure that analyses of SEA were ecologically meaningful and based on reasonable sample sizes, analyses were conducted separately for each primary host–ectoparasite relationship in which the host species was common. A general linear model was used that included one factor (host sex) and two covariates (host forearm length and mass) to evaluate variation in ectoparasite abundances (i.e. TEA or SEA).

We were more concerned about the consequences of ignoring results that have biological implications than about potential type I errors. Therefore, we interpreted results based on exact P-values without application of the overly conservative and controversial (Hurlbert 2003, Moran 2003) Bonferroni sequential adjustment (Rice

1989), with the understanding that a few significant ( $P \leq 0.05$ ) results contributing to overall patterns may represent type I errors. Unless otherwise stated, analyses were conducted using the R programming environment (<http://www.R-project.org>).

## RESULTS

### Field collections and sexual size dimorphism in hosts

Over 17 500 ectoparasites representing 104 species and 11 families were collected from 2909 bats representing 44 species and five families (Presley 2004). Five families (Streblidae, Spinturnicidae, Macronyssidae, Chirodiscidae and Argasidae) accounted for 94.5% of all ectoparasites. Macronyssid mites were the most abundant and species-rich family of ectoparasite on Paraguayan bats, representing 23 species and 55% of all ectoparasites.

Fifteen of 22 host species exhibited sex-related size dimorphism (Table 1). Males were larger than females in six species (*Noctilio albiventris*, *Noctilio leporinus*, *Sturnira lilium*, *Molossus ater*, *Molossus currentium* and *Molossus molossus*) and females were larger than males in nine species (*Glossophaga soricina*, *Carollia perspicillata*, *Desmodus rotundus*, *Artibeus lituratus*, *Platyrrhinus lineatus*, *Pygoderma bilabiatum*, *Lasiurus ega*, *Myotis albescens* and *Myotis nigricans*).

### Total ectoparasite abundance

TEA evinced significant responses to host sex or body size in 11 of 22 host species (Table 1). Total ectoparasite abundance differed between sexes regardless of body size in four species. Ectoparasites were more abundant on females in three host species (*Artibeus fimbriatus*, *A. lituratus* and *S. lilium*) and were more abundant on males in one host species (*Eumops glaucinus*). In addition, TEA varied with size in eight species of bat, consistently increasing in two species (*N. albiventris* and *M. albescens*), consistently decreasing in two species (*S. lilium* and *Eumops patagonicus*), and exhibiting complex responses in four species (*P. bilabiatum*, *M. ater*, *M. molossus* and *Nyctinomops laticaudatus*).

### Specific ectoparasite abundance

Effects of host body size and sex on SEA were analysed for 41 primary host–ectoparasite associations involving 29 taxa of ectoparasite and 19 species of host (Table 2). Specific ectoparasite abundance differed between sexes regardless of body size in 12 associations involving 12 species of ectoparasite and six species of bat. Ectoparasites were more abundant on females than on males in 11 of these associations. In addition, SEA varied with body size

**Table 1.** Significance levels for ANCOVA quantifying the effects of host sex as well as host mass (MA) and forearm length (FA) on total ectoparasite abundance for each of 22 host species. Significant ( $P \leq 0.05$ ) results are bold. The larger sex is indicated for each species of bat that exhibited sexual size dimorphism in Paraguay. Slopes indicate the direction (positive or negative) of responses of ectoparasite abundance to host body size for male and female hosts.

Host family									Sex ×	Larger	Slope		Sex-biased
Host species	Sample size	Sex	MA	FA	Sex × MA	Sex × FA	MA × FA	MA × FA	sex	sex	♂	♀	parasitism
<b>Noctilionidae</b>													
<i>Noctilio albiventris</i>	68	0.857	<b>0.040</b>	0.686	0.055	0.754	0.071	0.368	♂		+	+	
<i>Noctilio leporinus</i>	28	0.735	0.151	0.146	0.925	0.320	0.137	0.332	♂				
<b>Phyllostomidae</b>													
<i>Glossophaga soricina</i>	54	0.578	0.927	0.596	0.895	0.920	0.259	0.411	♀				
<i>Carollia perspicillata</i>	75	0.173	0.974	0.744	0.074	0.370	0.642	0.099	♀				
<i>Desmodus rotundus</i>	51	0.337	0.156	0.814	0.589	0.566	0.160	0.600	♀				
<i>Artibeus fimbriatus</i>	79	<b>0.032</b>	0.093	0.440	0.184	0.902	0.794	0.496					♀
<i>Artibeus jamaicensis</i>	42	0.928	0.780	0.962	0.871	0.198	0.850	0.738					
<i>Artibeus lituratus</i>	351	<b>&lt;0.001</b>	0.100	0.439	0.413	0.423	0.189	0.879	♀				♀
<i>Platyrrhinus lineatus</i>	90	0.061	0.337	0.747	0.517	0.884	0.593	0.806	♀				
<i>Pygoderma bilabiatum</i>	53	0.246	0.944	0.523	<b>0.007</b>	0.422	0.125	0.833	♀	+	-		
<i>Sturnira lilium</i>	404	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.015</b>	0.059	0.166	0.096	0.985	♂	-	-		♀
<b>Vespertilionidae</b>													
<i>Eptesicus furinalis</i>	69	0.595	0.654	0.902	0.230	0.412	0.895	0.522					
<i>Lasiurus ega</i>	72	0.972	0.100	0.458	0.184	0.761	0.190	0.775	♀				
<i>Myotis albescens</i>	87	0.289	<b>&lt;0.001</b>	0.606	0.079	0.366	0.350	0.999	♀	+	+		
<i>Myotis nigricans</i>	128	0.138	0.089	0.940	0.753	0.058	0.592	0.383	♀				
<b>Molossidae</b>													
<i>Eumops glaucinus</i>	56	<b>&lt;0.001</b>	0.088	0.206	0.102	0.195	0.672	0.446					♂
<i>Eumops patagonicus</i>	526	0.638	<b>0.001</b>	<b>0.021</b>	0.660	0.803	0.310	0.676			-	-	
<i>Molossops temminckii</i>	160	0.934	0.156	0.073	0.677	0.659	0.527	0.377					
<i>Molossus ater</i>	100	0.837	0.965	0.799	0.493	0.435	<b>0.016</b>	<b>0.011</b>	♂				
<i>Molossus currentium</i>	27	0.885	0.305	0.922	0.183	0.389	0.298	0.205	♂				
<i>Molossus molossus</i>	228	0.128	0.880	0.131	<b>0.007</b>	0.375	<b>0.007</b>	0.452	♂	+	-		
<i>Nyctinomops laticaudatus</i>	42	0.879	0.989	0.367	0.791	0.861	<b>0.035</b>	0.609					

in 19 associations involving 17 species of ectoparasite and 11 species of bat (Table 2), consistently increasing in seven associations, consistently decreasing in five associations, and exhibiting complex responses in seven associations.

**DISCUSSION**

**Host body size**

In contrast to the expectation that larger hosts support greater ectoparasite abundances than do smaller hosts, body size had no effect on ectoparasite abundances in more than half of the cases (for TEA in 14 of 22 host species and for SEA in 22 of 41 host–ectoparasite associations). Moreover, nearly half (for TEA in two of four host species and for SEA in five of 12 host–ectoparasite associations) of the significant and consistent responses of ectoparasite abundance to host body size were negative. Clearly, host body size does not mould ectoparasite abundances on bat species in a predictable or consistent fashion.

**Host sex**

In general, males of endothermic vertebrates (i.e. birds and mammals) have greater parasite densities than

do females because of sex-related differences in body size, immunocompetence, vagility, or home-range size (Krasnov *et al.* 2005). For these taxa, decreased carrying capacity related to smaller body sizes, increased androgen-related immune responses, and fewer parasite encounters due to lower levels of vagility or smaller home ranges work in concert to reduce parasite abundances on females compared to males (Krasnov *et al.* 2005, Morand *et al.* 2004). If ectoparasite abundance on bats responds to differences in body size, ectoparasites should be more abundant on the larger sex. However, ectoparasite abundances were greater on the smaller sex (i.e. negative response to host body size) as often as on the larger sex (i.e. positive response to host body size). Because the rate of exposure of bats to ectoparasites need not be related to vagility or home range size, expectations for effects of bat vagility or home range size on ectoparasite abundance are unclear. Nonetheless, increased immunocompetence of female bats was expected; therefore, males were expected to harbour more ectoparasites than were females. Contrary to these expectations, female hosts harboured more ectoparasites than did male hosts in 14 of 16 cases in which a consistent sex-biased pattern of ectoparasite abundance was documented (Tables 1 and 2). Consequently, sex-related immunocompetence

**Table 2.** Significance levels for ANCOVA quantifying the effects of host sex as well as host mass (MA) and forearm length (FA) on specific ectoparasite abundance for selected primary host-parasite associations. Significant (i.e.  $P \leq 0.05$ ) results are bold. The larger sex is indicated for each species of bat that exhibited sexual size dimorphism in Paraguay. Slope indicates the direction (positive, negative) of responses of ectoparasite abundance to host body size for male and female hosts. Absence of a sign indicates a non-significant response.

Host family									Slope		Sex-biased parasitism	
Host species (sample size)	Ectoparasite species	Sex	MA	FA	Sex × MA	Sex × FA	MA × FA	Sex × MA × FA	Larger sex	♂		♀
<b>Noctilionidae</b>												
<i>Noctilio albiventris</i> (68)									♂			
	<i>Noctilio strebla maai</i>	<b>0.018</b>	0.053	<b>0.010</b>	0.184	0.084	0.203	0.067		+	+	♀
	<i>Paradyschiria parvula</i>	<b>0.005</b>	< <b>0.001</b>	0.482	<b>0.031</b>	0.090	0.153	0.924		+	+	♀
	<i>Ornithodoros hasei</i>	<b>0.007</b>	0.698	<b>0.010</b>	<b>0.024</b>	0.138	0.601	<b>0.048</b>		-	+	
<i>Noctilio leporinus</i> (28)									♂			
	<i>Noctilio strebla aitkeni</i>	0.325	0.100	0.184	0.683	0.339	0.559	0.362				
	<i>Paradyschiria fusca</i>	0.982	<b>0.016</b>	0.540	0.323	0.332	0.818	0.052		+	+	
	<i>Ornithodoros hasei</i>	0.927	0.787	0.381	0.101	0.096	0.094	0.309				
<b>Phyllostomidae</b>												
<i>Carollia perspicillata</i> (75)									♀			
	<i>Trichobius joblingi</i>	0.088	0.902	0.626	0.173	0.421	0.914	0.975				
<i>Desmodus rotundus</i> (51)												
	<i>Strebla weidmanni</i>	0.603	0.300	0.503	0.242	0.694	0.157	0.514				
	<i>Trichobius parasiticus</i>	0.663	0.139	0.677	0.431	0.686	0.205	0.868				
	<i>Radfordiella desmodi</i>	0.836	0.584	0.868	0.742	0.184	0.231	0.807				
<i>Artibeus fimbriatus</i> (79)												
	<i>Periglischrus iheringi</i>	0.523	0.709	0.603	0.242	0.896	0.388	0.422				
	<i>Macronyssoides kochi</i>	0.063	0.083	0.457	0.919	0.219	0.948	0.846				
<i>Artibeus jamaicensis</i> (42)												
	<i>Periglischrus iheringi</i>	0.720	0.699	0.486	0.329	0.112	0.664	0.477				
	<i>Macronyssoides kochi</i>	0.139	0.260	0.447	0.204	0.654	0.724	0.880				
<i>Artibeus lituratus</i> (351)									♀			
	<i>Paratrachobius longicrus</i>	<b>0.046</b>	< <b>0.001</b>	0.121	0.678	0.258	0.158	0.633		+	+	♀
	<i>Periglischrus iheringi</i>	< <b>0.001</b>	< <b>0.001</b>	0.153	0.314	0.950	0.612	0.983		-	-	♀
<i>Platyrrhinus lineatus</i> (90)									♀			
	<i>Periglischrus iheringi</i>	0.895	<b>0.018</b>	0.679	0.583	0.510	0.508	0.930		-	-	
	<i>Macronyssoides conciliatus</i>	< <b>0.001</b>	0.697	0.981	0.903	0.828	0.665	0.807				♀
<i>Sturnira lilium</i> (404)									♂			
	<i>Aspidoptera falcata</i>	<b>0.006</b>	<b>0.009</b>	0.501	0.080	0.234	0.100	0.234		-	-	♀
	<i>Megistopoda proxima</i>	<b>0.017</b>	0.306	0.536	0.335	0.955	0.614	0.056				♀
	<i>Periglischrus ojasti</i>	< <b>0.001</b>	< <b>0.001</b>	0.205	0.062	0.528	<b>0.014</b>	0.848		-	-	♀
	<i>Parichoronyssus euthyesternum</i>	< <b>0.001</b>	<b>0.001</b>	< <b>0.001</b>	0.126	0.292	0.687	0.638		+	+	♀
<b>Vespertilionidae</b>												
<i>Eptesicus furlinalis</i> (69)												
	<i>Spinturnix surinamensis</i>	0.767	<b>0.008</b>	< <b>0.001</b>	0.529	0.280	<b>0.001</b>	0.688		-	-	
	<i>Steatonyssus joaquimi</i>	0.938	0.412	0.328	0.112	0.750	0.183	0.163				
<i>Lasiurus ega</i> (72)									♀			
	<i>Steatonyssus furmani</i>	0.966	0.135	0.422	0.251	0.764	0.218	0.780				
<i>Myotis albescens</i> (87)									♀			
	<i>Macronyssus crosbyi</i>	0.244	< <b>0.001</b>	<b>0.022</b>	0.834	0.424	0.922	0.553		+	+	
	<i>Steatonyssus joaquimi</i>	0.761	0.909	<b>0.026</b>	0.424	0.713	0.532	0.570		+	+	
<i>Myotis nigricans</i> (128)									♀			
	<i>Macronyssus crosbyi</i>	< <b>0.001</b>	0.137	0.260	0.474	0.104	0.731	0.535				♀
	<i>Steatonyssus joaquimi</i>	<b>0.003</b>	0.983	0.819	0.914	0.349	0.628	0.293				♂
<b>Molossidae</b>												
<i>Eumops glaucinus</i> (56)												
	<i>Hesperoctenes unknown sp.</i>	< <b>0.001</b>	<b>0.006</b>	0.788	<b>0.010</b>	0.896	< <b>0.001</b>	<b>0.035</b>		0 <sup>a</sup>	+ <sup>a</sup>	♀
	<i>Chirotonyssus haematophagus</i>	0.174	0.237	0.758	0.987	0.099	0.206	0.509				
<i>Eumops patagonicus</i> (526)												
	<i>Hesperoctenes longiceps</i>	<b>0.001</b>	0.615	0.264	0.350	0.216	0.168	0.180				♀
	<i>Chirotonyssus haematophagus</i>	<b>0.017</b>	< <b>0.001</b>	<b>0.006</b>	0.610	0.934	0.093	0.673		-	-	♀
<i>Molossops temminckii</i> (160)												
	<i>Hesperoctenes parvulus</i>	0.436	0.623	<b>0.038</b>	0.893	0.488	0.516	0.655		-	-	
	<i>Chirotonyssus venezolanus</i>	0.137	0.402	0.603	0.817	0.457	0.665	0.182				
<i>Molossus ater</i> (100)									♂			
	<i>Chirotonyssus robustipes</i>	0.919	0.079	0.777	0.150	0.233	0.754	0.096				
<i>Molossus currentium</i> (27)									♂			
	<i>Chirotonyssus haematophagus</i>	0.547	0.134	0.789	0.173	0.380	0.673	0.242				
<i>Molossus molossus</i> (228)									♂			
	<i>Chirotonyssus haematophagus</i>	<b>0.041</b>	0.511	<b>0.019</b>	< <b>0.001</b>	0.606	0.219	0.446		+	-	
	<i>Parkosa maxima</i>	0.411	<b>0.005</b>	0.780	0.543	<b>0.042</b>	0.811	0.159		-	-	
	<i>Parkosa tadarida</i>	0.730	<b>0.006</b>	0.837	0.087	0.163	0.060	0.220		+	+	
<i>Nyctinomops laticaudatus</i> (42)												
	<i>Chirotonyssus venezolanus</i>	0.831	0.720	0.470	0.438	0.109	0.213	0.503				

<sup>a</sup>Direction of slopes in this analysis were contingent on metrics of body size (significant 3-way interaction), SEA did not respond to FA in either sex (i.e. slopes were not significantly different than zero), SEA responded positively to MA in females (positive slope) but not to MA in males (slope  $\approx 0$ ).

did not mould patterns of ectoparasite abundance on hosts in this system. That females harboured more ectoparasites than males in spite of the presence of one (immunocompetence) or two (immunocompetence and body size in situations where male hosts were larger than female hosts) mechanisms that favoured male-biased parasitism, suggests the presence of strong mechanisms that favour females as hosts of ectoparasites.

### Interactions between host body size and sex

Although differences in ectoparasite abundance often exist between male and female hosts, ectoparasite abundances generally respond to variation in host body size in the same direction within each sex (Tables 1 and 2). In 10 cases, ectoparasite abundance increased with body size in both sexes, and in 10 cases ectoparasite abundance decreased with body size in both sexes. Ectoparasite abundance varied with host body size differently in females and males in five cases. The direction (positive or negative) of the relationship between ectoparasite abundance and host body size did not depend on host phylogeny or breeding system. Host behaviours (e.g. inter-individual grooming, social system) as well as characteristics (e.g. age, sex) of the host that are associated with body size may influence ectoparasite behaviour such that ectoparasite abundance appears to respond to body size. For example, grooming skills may improve with age, leading to greater ectoparasite mortality, which could present as a negative response to host body size. Alternatively, if ectoparasite abundances are affected by sex-related differences in host ecology, amount of exposure to ectoparasites of each sex may diverge as hosts mature. More specifically, females of many species of Neotropical bat form harems or maternity colonies, whereas most of the males of these species are solitary. In such scenarios, exposure to parasites for female hosts may increase (or stay the same) with age, whereas exposure to parasites for male hosts may decrease, which may appear as positive or negative responses, respectively, to host body size.

### Alternative mechanisms and future directions

Empirical patterns generally failed to corroborate theoretical expectations related to sex-based differences in immunocompetence or to host body size. Consequently, alternative sex-specific differences must cause female hosts to harbour more ectoparasites than male hosts. Parasites are more abundant on the larger sex of many orders of mammal including the Perissodactyla, Rodentia, Artiodactyla, Carnivora and Sirenia and have similar abundances on each sex regardless of sexual size dimorphism in the Lagomorpha, Artiodactyla, Marsupialia, Primates and Insectivora (Moore & Wilson

2002 and sources therein). Few instances of negative relationships between ectoparasite abundances and host body size are reported for the Chiroptera, Rodentia and Lagomorpha (Moore & Wilson 2002), with mechanisms that produce these patterns being understood poorly or not at all.

Because the data from this study were derived from mist-net captures during a large-scale mammal survey, information on roost type, group size, number of roosts, or home range size for bats associated with the data is scant. Nonetheless, sufficient ecological information exists for Neotropical bats to develop plausible hypotheses to direct future research regarding the determinants of ectoparasite abundance on bats. We suggest that considerations of host sociality and intraspecific interactions represent promising lines of inquiry.

Successful species (i.e. those that are common and widespread), whether free-living or parasitic, avail themselves of abundant and reliable resources. Therefore, hosts that are large-bodied, long-lived, maintain large populations, and have frequent intraspecific contact are ideal. Bats are relatively small and ephemeral habitats (compared with forests, prairies or oceans). Moreover, ectoparasites of bats rarely or never leave the body of their host, and are unlikely to survive more than 2 d without feeding. Consequently, the reliability of a host as a resource and the opportunities it affords for the infestation of new hosts are paramount to ectoparasite persistence. Within a host species, individuals may not provide equal transfer opportunities for ectoparasites. If differences exist among host individuals with respect to the frequency, regularity, or duration of host transfer opportunities, and if these differences are related to other host characteristics, abilities should evolve for ectoparasites to detect proximate cues indicative of the potential for transfer afforded by a host. Because bats exhibit sex-based social systems that affect host transfer opportunities, a potential proximate cue influencing host selection for ectoparasites of Neotropical bats may be host sex.

Mechanisms that structure ectoparasite assemblages of bats and non-volant mammals may be distinct because of fundamental differences in their ecology. First, in response to unique aspects of bat ecology (flight, high vagility), ectoparasites of bats leave the host less frequently than do those of non-volant mammals, which in part has resulted in a greater host specificity of ectoparasites of bats than ectoparasites of other mammals (Wenzel & Tipton 1966). Second, many generations of ectoparasite may infest a single bat because the average life span of most bat species is several years (Barclay & Harder 2003), whereas the average life span of most rodent species of similar size to bats is only a few months. Third, because the bodies of non-volant hosts are in constant contact with substrate (soil, plants, burrows), where ectoparasites may be encountered while traversing home

ranges, the likelihood of new infestations of ectoparasites may vary positively with area traversed by non-volant hosts (Zelmer *et al.* 2004). This is unlikely to be true for bats and their ectoparasites because the medium through which bats fly is not a refuge for ectoparasites, whereas the medium through which non-volant mammals move can be a refuge for ectoparasites. Rather, amount of exposure to ectoparasites more likely is related to number of roosts or sizes of social groups with which individuals are associated. Fourth, many species of Neotropical bat change roosts every few days and the number of possible roost locations for bats that are solitary or form small groups is large (Kunz & Lumsden 2003 and sources therein). Consequently, ectoparasites that remain in the roost have a high risk of starvation; as such, ectoparasites of bats rarely or never leave the host body (Marshall 1982, Radovsky 1966, Rudnick 1960). In contrast, many species of ectoparasite of birds and non-volant mammals shelter in burrows, nests, or nesting material, or have non-ectoparasitic developmental stages. Considering the relatively short life spans and dense populations of many small-mammal species, it is reasonable to conclude that abandoned nests or burrows are frequently re-inhabited by another suitable host of the same or similar species.

The combination of long life spans and flight may create strong selective forces that restrict distributions of ectoparasites of bats to host bodies and roost locations with high likelihoods for host transfer. Consequently, social interactions among hosts likely are the prime vehicle for host transfer. Harems, which consist of several adult females, one adult male and their offspring, and maternity colonies are common social systems among Neotropical bats. The majority of males for such species are solitary. Therefore, females of many Neotropical bat species likely experience greater intraspecific contact than do males. In addition, adult females are the conduit to future hosts (i.e. offspring), which could strengthen preferences for infestation of females over males. If host transfer opportunities mould patterns of ectoparasite abundance on bats, sex-based differences in intraspecific contact related to social systems may explain why females of many Paraguayan bat species harbour significantly more ectoparasites than do males.

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