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Bat fly species richness in Neotropical bats: correlations with host ecology and host brain

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Abstract Patterns of ectoparasite species richness in mammals have been investigated in various terrestrial mammalian taxa such as primates, ungulates and carnivores. Several ecological or life traits of hosts are expected to explain much of the variability in species richness of parasites. In the present comparative analysis we investigate some determinants of parasite richness in bats, a large and understudied group of flying mammals, and their obligate blood-sucking ectoparasite, streblid bat flies (Diptera). We investigate the effects of host body size, geographical range, group size and roosting ecology on the species richness of bat flies in tropical areas of Venezuela and Peru, where both host and parasite diversities are high. We use the data from a major sampling effort on 138 bat species from nine families. We also investigate potential correlation between bat fly species richness and brain size (corrected for body size) in these tropical bats. We expect a relationship if there is a potential energetic trade-off between costly large brains and parasite-mediated impacts. We show that body size and roosting in cavities are positively correlated with bat fly species richness. No effects of bat range size and group size were observed. Our results also suggest an association between body mass-independent brain size and bat fly species richness.

Key words Parasite species richness · Tropical bats · Roosting ecology · Group size · Body size

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Introduction

Several studies have tried to explain the observed patterns of parasite diversity in various host taxa at different geographical scales (Nunn et al. 2003; Krasnov et al. 2004; Ezenwa et al. 2006; see Poulin and Morand 2004). Parasite species richness (PSR) shows great variability among host species and the processes underlining this variability remain largely unexplored. Such heterogeneity may be related to life history or ecological traits, such as: body size, longevity, metabolism, density, distribution area, latitude distribution or behaviour (Morand and Poulin 1998; Morand and Harvey 2000; Clayton and Walther 2001; Arneberg 2002; Krasnov et al. 2004; Poulin and Morand 2004). PSR may also be subject to evolutionary history and other interactions with the physical or biotic environment (Krasnov et al. 1997). However, despite an increasing number of studies, the major determinants of PSR remain largely unexplored or unknown in most parasite groups (Morand 2000; Poulin and Morand 2004). Studies on mammals remain relatively few and these studies have focused on few host traits, and/or have restricted their investigation to some specific parasite groups, such as intestinal helminths or fleas (but see Nunn et al. 2003; Ezenwa et al. 2006 and Lindfors et al. 2007, for more various taxa of parasites).

Despite the high species diversity of bats, which represent about 20% of all mammalian species, and the high diversity of their parasites (Shimalov et al. 2002; Dick and Patterson 2006), studies on PSR of bats and the relationships between PSR and bat ecology are very limited and concern only a few bat species (Dick et al. 2003; Dick and Patterson 2006; ter Hofstede and Fenton 2005) or focus on the structure of roosts as a determinant of bat fly parasitism (Patterson et al. 2007).

In the present comparative study, we aim to identify the ecological traits of bats and their environments that may explain the species richness of their parasites, the streblid bat flies (Diptera: Streblidae). Bat flies are obligate and specialized ectoparasites of bats and are highly diversified in the tropics (Dick and Patterson 2006). They are viviparous dipterans living in the fur and on the wing membranes of their hosts where they feed on blood (ter Hofstede and Fenton 2005). Female bat flies deposit third-instar larvae on surfaces of the bat roosts where the larva immediately pupate. Newly emerging bat flies immediately seek a host for a blood meal.

PSR, representing all bat fly species found on a particular host species, has been chosen because it provides one estimate of the parasitic load (Poulin and Morand 2004; Bordes et al. 2007). PSR has been investigated in many previous comparative studies focusing on determinants of parasitism in various clades of mammals as well as fish and birds (Morand 2000). We have adopted the same metric to describe one aspect of host parasitic load even though other studies use additional measures (Patterson et al. 2007). Despite the fact that hosts suffer from multiple parasitic infestations in field conditions, most studies interested in host-parasite interactions have focused on a single parasite/single host system. They have adopted classic estimates of parasitic loads (prevalence, intensity, abundance) with the assumption that parasitic pressures always correlate with these metrics. However, low level parasitic infestations may also affect body condition (Irvine et al. 2006), a result which emphasizes the potential limits of predicting parasitic impacts by only evaluating the intensities of infestation for a given parasitic species. Moreover, there is now growing evidence that PSR may, by itself, impose strong selective pressure independently of intensity or prevalence. Recent empirical results have demonstrated that parasite communities can impact not only hosts' demography (Holmstad et al. 2005) or behaviour (Alzaga et al. 2008), but also promote adaptive responses at the genetic level (Wegner et al. 2003; Šimková et al. 2006). PSR seems to be a good estimate of both parasitic loads and parasitic pressures.

At least four major predictions can be proposed to explain the variability in bat fly richness in relation to their biology. First, and like other ectoparasites, reproductive success of bat flies may be largely dependant on the host environment, i.e. the roosts (Krasnov et al. 1997). The roosting ecology of bats is diverse and they use a variety of structures, including foliage, tree cavities, tents, termite nests, rocks, buildings, mines etc.. Some of these structures are abundant and ubiquitous while others are uncommon. In addition, the duration of roost utilization and the protection roosts afford to pupae may also affect species richness (Kunz and Lumdsen 2003). These factors suggest that roost site structure may affect bat fly parasitism as bat flies pupate in the wall of the roost itself (Ter Hofstede and Fenton 2005; Patterson et al. 2007). Pupal deposition on the wall of the host's roost seems rather hazardous for an ectoparasite as its reproductive success strongly depends on the host behaviour, such as bats returning to the same roost site (Patterson et al. 2007; Reckardt and Kerth 2006). Semi-permanent structures such as mines, tunnels, and bridges, but also caves, hollow trees and rock crevices, provide cavity roosts that are often used by many successive generations of bats (Kunz and Lumdsen 2003) as they offer better-protected environments from weather or predators than foliage or open roosts (Kunz 1982). We can also postulate that these enclosed roosting structures may offer better opportunities for transmission than "foliage" roosting structures (such as branches and/or leaves) for which fidelity is lower.

Secondly bats show significant variability in body size (from a few grams to up to 300 g), and if hosts can be considered as "islands" for parasites (Kuris 1980; Morand 2000), an increase in body size is likely to be associated with an increase in parasite species as larger hosts represent larger habitats and may then offer better opportunities for colonisation. This hypothesis may be especially valid for external parasites, compared to endoparasites which may be acquired through predator–prey relationships (Morand 2000). Thirdly, because bats can be social animals and bat flies are directly transmitted parasites, the increase in group size (as an approximation of sociality and density) is likely to favour an increase in transmission rates and in parasite diversity. Several studies have reported that an increase in PSR was effectively correlated to an increase in group size in some comparative studies (Arneberg 2002; Stanko et al. 2002; Nunn et al. 2003). Finally, geographical range is also seen as an important determinant of PSR, as an increase in host range may allow the host to encounter and accumulate a high number of parasites species (Lindfors et al. 2007).

These characteristics of the host's ecology and life traits may favour the accumulation of parasite species. This increased parasite pressure may, in turn, affect some host life history traits due to the negative effects of parasitism and to investment of host resources in defence mechanisms (Møller 1997; Agnew et al. 2000). If this investment in immune defence is costly, a trade off with other physiological tasks should be observed. For example, a recent study of

Møller et al. (2005) has shown that the relative mass of immune defence organs in birds covaries positively with the relative mass of the brain. This result supports the hypothesis that the evolution of an increase in investment in the immune system may negatively impact evolution of brain size.

Brain size in mammals generally scales with body size to the *x*th power with an exponent of 0.75 (Pagel and Harvey 1998). Some species have larger (or smaller) brains relative to their body mass and two functional hypotheses have been proposed to explain this variation. The "adaptive" brain size or ecological competence hypothesis is related to the particularities of the species ecology. The second, the social brain hypothesis, postulates a relation between brain size and social interactions (Dunbar 1998). Studies can be found which support both hypotheses and show that large brains are associated with ecologically relevant behaviours in mammals (Reader and Laland 2002) and also with sociality (Dunbar 1995; Shultz and Dunbar 2006). Large brains are costly to develop and maintain (Jones and MacLarnon 2004) and as a consequence trade offs should exist between brain size and other expensive tissues (for testes and brains in bats see Pitnick et al. 2005) or might be balanced against other physiological constraints such as seasonal changes in resources (Jacobs 1996).

Ectoparasites have been show to impose strong selective pressures on life history traits of birds (Fitze et al. 2004) and mammals (Kohkhlova et al. 2002; Neuhaus 2003) though investment in immune (Christe et al. 2000) and behavioural defences such as time spent grooming (Moore 2002), both of which may have energetic (Giorgi et al. 2001) and/or associated fitness costs (Richner and Tripet 1999; Hanssen et al. 2004). As resources are often limited, we can hypothesize that parasite pressure may impact brain size through a trade-off between costs of immune defence and energetic cost of brain maintenance. In contrast, Møller et al. (2005) suggest that there may be a positive correlation between brain size and immune defences.

The two aims of this study are: (1) to explore the various potential ecological determinants of bat fly species richness in Neotropical bats; and (2) to test the potential impact of parasitism, estimated by bat fly species, on a bat life history trait, the residual variation in bat brain size.

Materials and methods

Host and parasite sampling

Data on bats and their bat flies came from two sources, the Smithsonia Venezuelan Project (1965–1967) and the Colección de Parasitología del Museo de Biologia de la Universidad Central de Venezuela (1964–1966; 1980–1998)

supplied by one of us (R. G.) from Venezuela (140 localities) and Peru (two localities) {see the Electronic supplementary material and references therein).

To prevent loss of ectoparasites during manipulation, bats were collected and kept in plastic bags. Bat flies were counted, fixed and preserved in 70° ethanol until identification.

A total of 24,831 individuals representing 138 species of bats from nine families were examined for bat fly species richness (Electronic supplementary material). Bat fly species richness, referred to here as PSR, represents the number of species of bat fly found on a given host species.

Data on host traits and host ecology

For the taxonomy of bats we followed Simmons (2005). The taxonomy and evolution of large *Artibeus* is still contentious as many *Artibeus*, which had been previously referred to as *Artibeus jamaicensis* on mainland South America, are actually *Artibeus planirostris* (Limm et al. 2004). In Venezuela the delimitation of these two species is particularly confusing. This is the reason why we listed *Artibeus jamaicensis* as *A. jamaicensis/planirostris* (see the Electronic supplementary material).

Data on host body mass, geographic range, host group size, brain size and associated body mass, and roosting ecology in Venezuela and Peru were obtained from various sources (see Electronic supplementary material).

Group size was classified from 1 to 4 for all species:

1. From one to ten individuals per colony.
2. From 11 to 100 individuals per colony.
3. From 100 to 990 individuals per colony.
4. More than 1,000 individuals per colony.

Roosting ecology of bats was classified into two categories: cavity roosting (CR), when individuals always, or preferentially, roost in structures that provide darkness like caves, cavern hollows and/or hollows or fallen trees; foliage roosting (FR), where individuals always, or preferentially, roost in structures more exposed to light such as under branches or leaves or in tents.

A similar approach was proposed by Ter Hosftede and Fenton (2005). We are aware that this classification allows for uncertainty in roosting ecology as some bat species may use both roost types. However, using both the field experience of one of us (R. G.) and Linares (1998) we are confident that it is reasonable to use this system for the species studied.

Information on bat brain size and associated mass for brain size was obtained for 68 bat species (see Electronic supplementary material).

We controlled for allometry of host traits (geographic range, host group size, brain size) with body mass by using

residuals obtained from linear regression analysis. Residuals of these traits were used for further comparative analysis using independent contrasts (see below).

Comparative analysis

To control for potential confounding effects, we used independent contrasts (Felsenstein 1985). Sources for the phylogeny were Jones et al. (2002) and Teeling et al. (2005). We used the CAIC 2.0 program (Purvis and Rambaut 1995) with the brunch option for continuous data and the crunch option for dichotomous data (roost type).

Body mass, brain mass and geographical range were log transformed.

PSR may be biased by sampling effort (i.e. the number of hosts examined) resulting in confounding variation of PSR (Morand 2000). We used the residuals of the regression analysis between the richness of bat fly species (log) against the number of hosts examined.

We performed the following analyses on the pooled bat species by separating them according to roost type, i.e. CR (caves and tree hollows) versus FR (tree branches, leaves and well-lighted sites). We first tested the influence of roost type on PSR of bat flies using the brunch option of CAIC. We secondly performed analyses on the two subsets of data.

Results

The final host-parasite dataset includes 138 bat species from nine families with 24,831 individual bats (ter Hofstede and Fenton 2005; Dick and Gettinger 2005 but see Patterson et al. 2007).

A total of 102 bat fly species were identified. All species belong to the Streblidae, a large group containing 33 genera and 231 species (Dick and Graciolli 2005). Of nine families, Phyllostomidae, Molossidae, Natalidae and Noctillionidae were highly infested whereas individuals of Thyropteridae and Vespertilionidae which were sampled harboured no bat flies. This result is consistent with previous findings (Dick and Gettinger 2005). In our data set, 96 species (69.5%) harboured one or more bat fly species, with a maximum of 31 bat fly species identified for *Carollia perspicillata*.

Bat fly species richness was strongly correlated with the number of bats of each species sampled ($P < 0.001$).

Determinants of PSR

The statistical analysis was performed using independent contrasts.

We first conducted a multiple linear regression for all bats. Body mass was the only determinant positively correlated

with residuals of PSR ($n = 97$, $r = 0.28$, $P = 0.005$; Fig. 1a). No significant relationships were observed between PSR and bat geographic range or between PSR and host group size (Table 1).

Second, we compared PSR according to bat roost type. We found a significant effect of roost site, with higher PSR for cavity-roosting bats than for foliage-roosting bats. For 11 evolutionarily independent transitions from foliage to cavity roosting, nine were associated with an increase in bat fly species richness (mean value of 0.57), whereas only two were associated with a decrease in bat fly species richness (mean value of -0.30) (sign test two-sided, $P < 0.05$).
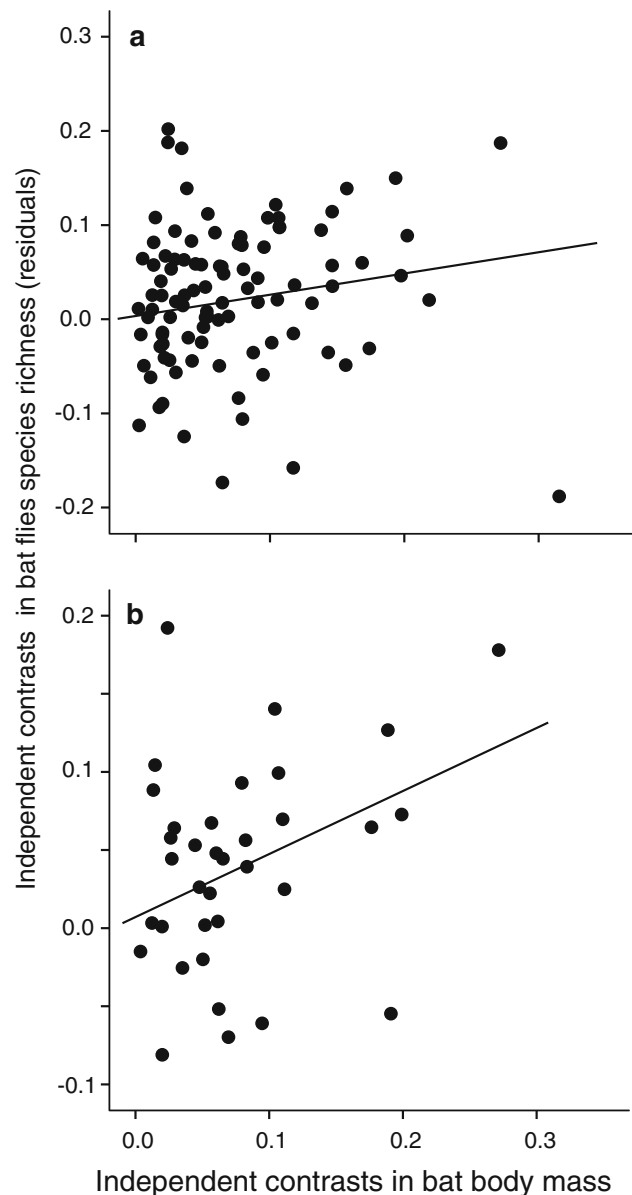

Fig. 1 Relationships between species richness of bat flies and bat body mass using independent contrasts for **a** all bat species (slope = 0.24; $r^2 = 0.08$, $P = 0.005$); **b** foliage-roosting bats (slope = 0.44, $r^2 = 0.32$, $P = 0.0003$)

Table 1 Results of a multiple linear regression on independent contrasts explaining bat flies species richness of neotropical bats

Roost type	Explanatory variables	Statistics
All types	Body mass	Partial $P = 0.01$
	Group size	Partial $P = 0.28$
	Geographic range	Partial $P = 0.98$
		$n = 97$, $r = 0.30$, $P = 0.028$
		$F_{3,97} = 3.169$
Cavity	Body mass	Partial $P = 0.40$
	Group size	Partial $P = 0.78$
	Geographic range	Partial $P = 0.49$
		$n = 64$, $r = 0.16$, $P = 0.65$
		$F_{3,64} = 0.549$
Foliage	Body mass	Partial $P = 0.0056$
	Group size	Partial $P = 0.072$
	Geographic range	Partial $P = 0.26$
		$n = 35$, $r = .62$, $P = 0.0011$
		$F_{3,35} = 6.689$

We found no effect of body mass, range and group size on PSR of cavity-roosting bats ($n = 64$, all $P > 0.05$; Table 1). There was a significant influence of body mass on PSR of foliage-roosting bats ($n = 35$, $r = 0.57$, $P = 0.0003$; Table 1, Fig. 1b).

Parasite pressure and host brain

We first performed our analysis across all bat species. We obtained 44 independent contrasts. We found a positive allometric relationship between brain size and body size ($n = 44$, $r = 0.97$, $P < 0.0001$). We used the residuals of this relationship. No correlations were found between residuals of brain size and residuals of PSR ($P = 0.56$).

We performed a second analysis according to the roosting ecology and obtained seven independent contrasts associated with change in roost type. We found a positive relationship between residuals in PSR and residuals in brain mass ($n = 7$, $r = 0.75$, $P = 0.03$; Fig. 2). These results should be treated with caution due to the low number of contrasts.

Discussion

In accordance to our predictions, we show that host ecology (roosting site) and body size are related to species richness of bat flies. Moreover, our results suggest that brain size is correlated with PSR.

Bat flies are highly diversified in Neotropical bats and their species richness is highly correlated to host sample
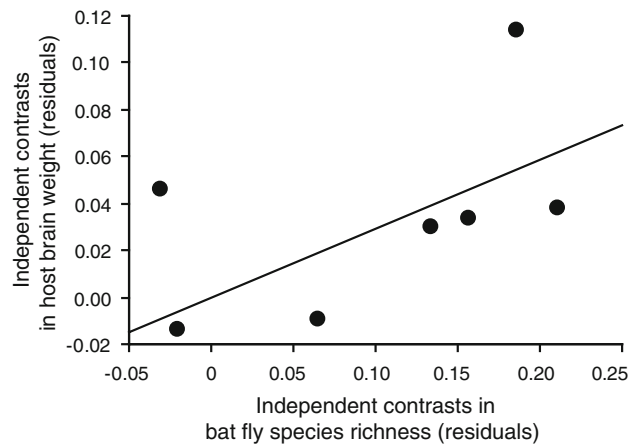
Fig. 2 Effect of foliage versus cavity roost site on the relationship between species richness of bat flies and brain weight of bats using independent contrasts (residuals shown, based on seven independent transitions; slope = 0.30, $r^2 = 0.56$, $P = 0.03$)

size, which is a classic pattern found in parasitic surveys (Poulin and Morand 2004; Guégan et al. 2004). Bat flies are considered to be highly host specific (Dick and Patterson 2006). Concerning data on bat fly species richness, we are acutely aware that, in such a highly specific system, considering all bat fly species found on a given host may seem spurious as some records can be the result of cross contamination (sampling accidents) or accidental (transitory), so they only represent a tiny fraction of the total bat flies infesting bats (Wenzel 1976; Dick and Gettinger 2005). However, bats have often been found to be infested by several bat fly species in field studies, especially when considering larger samples (Wenzel 1976; Dick and Gettinger 2005), even after taking great care to avoid cross contamination (Dick and Gettinger 2005). Moreover, previous studies have already explored determinants of ectoparasite diversity in host-parasite system in which the specificity of parasites is high [see for example Clayton and Walther (2001) for neotropical birds and their associated lice]. We assume, all things been equal, that these potential confounding factors are the same for all the species in this study and that the great heterogeneity in the number of bat fly species (i.e. bat fly species richness) found on a given host may then be better explored when increasing the number of sampled hosts.

Determinants of bat fly species richness

Our results show significant effects of host body size and roosting behaviour on PSR, leading to the more global conclusion that ectoparasite loads may result from the interplay between life history traits, ecology and behaviour.

A positive association between body size and bat fly species richness is expected when hosts are considered as

"islands" for parasites, with larger hosts providing a great variety of niches for ectoparasites. This positive correlation has been previously found in comparative studies for some groups of vertebrates (see Poulin and Morand 2004) but not for others [Clayton and Walther (2001) for birds and lice; Krasnov et al. (2004) for rodents and fleas; Nunn et al. (2003) for primates and overall parasites]. Two recent studies found a positive correlation between body size and parasite diversity in ungulates (Ezenwa et al. 2006) and fissiped carnivores (Lindfors et al. 2007), which suggests that we can expect the relation between PSR and body size to largely depend on the taxa studied. We also found that body size is a good predictor of PSR in foliage-roosting bats, but not in cavity roosters. This observation suggests that when the conditions of transmission are expected to be difficult (i.e. reduced temporal utilisation) only larger hosts can accumulate more ectoparasites.

This is one hypothesis to explain our observations, and we note that a number of other traits such as longevity, for example, scale with body size. Longevity is thought to scale allometrically with body size in bats, but the lack of data for most species prevented an analysis of longevity and PSR (Speakman 2005). Host longevity was shown to correlate with PSR in mammals (Morand and Harvey 2000; Wilkinson and South 2002). We found information on longevity for only 11 species of our dataset.

We found that cavity-roosting bats have higher PSR than foliage-roosting bats. Our results are in agreement with the observation that cavity roosts provide more hospitable environments for bat fly larva. This result agrees with previous studies (Ter Hosftede et al. 2005; Patterson et al. 2007) which have also demonstrated positive correlations between parasitic loads and protected and permanent roosts in Neotropical bats. Temporary roosts and roost switching may thus be a strategies that reduces parasitic loads. As switching of roost sites is frequent in some bat species (Kunz and Lumsden 2003), we can postulate that the short duration of their occupation could have evolved as a behavioural strategy to minimize parasitism rates. This prediction has found some empirical support as roost switching was recently demonstrated to prevent massive ectoparasite infestations (see Reckardt and Kerth 2006 for a bat fly and Bartonicka and Gaisler 2007 for a bat bug).

We found no significant effect of group size on PSR, which is in agreement with non-conclusive results in other studies (Nunn et al. 2003; Ezenwa et al. 2006). Our results may suggest that group size per se is not a determinant of parasite diversity and that sociality should be defined in a more complex way in order to better understand the factors that really affect contact rates, transmission and diversity of parasites (Altizer 2003). We can imagine that an increase in social contact may be associated with an increase in allogrooming between bats, a behavioural defence which may lead to reduce bat fly diversity (Moore 2002). Our results also suggest that other parasitic parameters, such as prevalence and intensity, should be examined when exploring these patterns.

We found no correlation between range size and bat fly species richness and our analysis thus differs from other studies on terrestrial mammals (Krasnov et al. 2004; Lindfors et al. 2007). This pattern was, however, not verified in birds and lice in the tropics (Clayton and Walther 2001).

Host brain size and parasite richness

Our results suggest an association between brain size and bat fly species richness. However, this correlation is positive and was not expected from an energetic trade-off perspective. This positive relationship is evidenced through the changes in roost ecology, although the number of independent contrasts, from foliage roosting to cavity roosting, is low. This relationship could be spurious, as we only show an increase in brain size related to changes in roosting ecology, which is also associated with an increase in PSR. In this case, the increase in brain size associated with roosting ecology would support the adaptive brain size hypothesis linked to some ecological competence associated with cavity roosting. The social brain hypothesis cannot be refuted, as roosting in cavities may also be associated with adapted social behaviours. Taking into account all these potential covariations, it remains hazardous to postulate a direct link between parasite pressure (PSR) and brain weight. Our results and those of Møller et al. (2005), which established a positive correlation between brain weight and the weight of immune organs of birds, indicate the need for future investigations on the causal interactions between brain, immunity and parasites.

To summarize, our results demonstrate that roost site has a strong influence on PSR. Identifying potential host traits that may limit parasite infestations should be the aim of future studies.

References

Agnew P, Koella JC, Michalakis Y (2000) Host life history responses to parasitism. Microbes Infect 2:891–896

Altizer S, Nunn C, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JRC (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. Annu Rev Ecol Syst 34:517–547

Arneberg P (2002) Host population density and body mass as determinants of species richness in parasites communities: comparative

analyses of directly transmitted nematodes of mammals. Ecography 25:88–94

Alzaga V, Vicente J, Villanua D, Acevedo P, Casas F, Gortazar C (2008) Body condition and parasite intensity correlates with escape capacity in Iberian hares. Behav Ecol Sociobiol 62:769–775

Bartonicka T, Gaisler J (2007) Seasonnal dynamics in the numbers of parasitic bugs (Heteroptera, Cimicidae): a possible cause of roost switching in bats (Chiroptera, Vespertilionidae). Parasitol Res 100:1323–1330

Bordes F, Blumstein DT, Morand S (2007) Rodent sociality and parasite diversity. Biol Lett 3:692–694

Clayton DH, Walther BA (2001) Influence of host ecology and morphology on the diversity of Neotropical bird lice. Oikos 94:455–467

Christe P, Arlettaz R, Vogel P (2000) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). Ecol Lett 3:207–212

Dick CW, Gannon MR, Little WE, Patrick M (2003) Ectoparasites associations of bats from Central Pennsylvania. J Med Entomol 40:813–819

Dick CW, Gettinger D (2005) A faunal survey of streblid flies (Diptera: Streblidae) associated with bats in Paraguay. J Parasitol 91:1015–1024

Dick CW, Graciolli G. (2006) Checklist of world Steblidae (Diptera:Hippoboscidae) found at http://www.fieldmuseum.org/aa/files/cdick/streblidae_checklist_eoct.06.pdf

Dick CW, Patterson BD (2006) Bat flies: obligate ectoparasites of bats. In: Morand S, Krasnov BR, Poulin R (eds) Micromammals and macroparasites, from evolutionary ecology to management. Springer, Tokyo, pp 179–191

Dunbar RIM (1995) Neocortex size and group size in primates: a test of the hypothesis. J Hum Evol 28:282–287

Dunbar RIM (1998) The social brain hypothesis. Evol Anthropol 6:178–190

Ezenwa V, Price SA, Altizer S, Vitone ND, Cook C (2006) Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. Oikos 115:526–537

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Fitze PS, Tschirren B, Richner H (2004) Life history and fitness consequences of ectoparasites. J Anim Ecol 73:216–226

Giorgi MS, Arlettaz R, Christe P, Vogel P (2001) The energetic grooming costs imposed by a parasitic mite (*Spinturix myoti*) upon its bat host (*Myotis myotis*). Proc R Soc Lond B 268:2071–2075

Guégan JF, Morand S, Poulin R (2004) Are there general laws in parasite community ecology? The emergence of spatial parasitology and epidemiology. In: Thomas F, Guégan JF, Renaud F (eds) Parasitism and ecosystems. Oxford University Press, Oxford, pp 22–42

Hanssen SA, Hasselquist D, Folstad I, Erikstad KE (2004) Costs of immunity: immune responsiveness reduces survival in a vertebrate. Proc R Soc Lond B 271:925–930

Holmstad PR, Hudson PJ, Skorping A (2005) The influence of a parasite community of a host population: a longitudinal study on willow ptarmigan and their parasites. Oikos 111:377–391

Irvine JT, Corbishley H, Pilkington JG, Albon SD (2006) Low levels of parasitic worms burdens may reduce body condition in free ranging red deer (*Cervus elaphus*). Parasitology 133:465–475

Jacobs LC (1996) The economy of winter: phenotypic plasticity in behavior and brain structure. Biol Bull 191:92–100

Jones KE, Purvis A, MacLarnon A, Bininda-Emonds ORP, Simmons NB (2002) A phylogenic supertree of the bats (Mammalia: Chiroptera). Biol Rev 77:223–259

Jones KE, Mac Larnon AM (2004) Affording large brains: testing hypotheses of mammalian brain evolution in bats. Am Nat 164:20–31

Kohkhlova IS, Krasnov BR, Kam M, Burdelova NI, Degen AA (2002) Energy costs of parasitism by the flea *Xenopsylla ramenis* on the desert gerbil *Gerbillus dasyurus*. J Zool 256:349–354

Krasnov B, Shenbrot GI, Khokhlova I, Degen AA (2004) Flea species richness and parameters of host body, host geography and host "milieu". J Anim Ecol 73:1121–1128

Krasnov B, Shenbrot GI, Medvedev SG, Vatschenok VS, Khokhlova I (1997) Host-habitat relation as an important determinant of spatial distribution of fleas assemblages (Siphonaptera) on rodents in the Negev desert. Parasitology 114:159–173

Kunz TH (1982) Roosting ecology. In: Kunz TH (ed) Ecology of bats. Plenum Press, New York, pp 1–55

Kunz TH, Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago London, pp 3–89

Kuris AM, Blaustein AR, Alio JJ (1980) Hosts as islands. Am Nat 116:570–586

Lim BK, Engstrom MD, Lee TEJ, Patton JC, Bickam JW (2004) Molecular differentiation of large species of fruit eating bats (*Artibeus*) and phylogenic relationships based on the cytochrome b gene. Acta Chiropterol 6:1–12

Linares OJ (1998) Mamiferos de Venezuela. Sociedad de Conservationista Audubon de Venezuela, Caracas, p 691

Lindenfors PL, Nunn CL, Jones KE, Cunningham AA, Sechrest W, Gittleman JL (2007) Parasites species richness in carnivores: effects of host body mass, latitude geographical range and population density. Global Ecol Biogr 1:1–14

Møller AP (1997) Parasites and the evolution of life history. In: Clayton D, Moore J (eds) Host-parasite evolution: general principles and avian models. Oxford University Press, Oxford, pp 105–127

Møller AP, Erritzoe J, Garamszegi Z (2005) Covariation between brain size and immunity in birds: implications for brain size evolution. J Evol Biol 18:223–237

Morand S, Poulin R (1998) Density, body mass and parasite species richness of terrestrial mammals. Evol Ecol 12:717–727

Morand S (2000) Wormy world: comparative tests of theoritical hypotheses on parasite species richness. In: Poulin R, Morand S, Skorping A (eds) Evolutionary biology of hosts–parasite relationships: theory meets reality. Elsiever, Amsterdam, pp 63–79

Morand S, Harvey P (2000) Mammalian metabolism, longevity and parasites species richness. Proc R Soc Lond B 267:1999–2003

Neuhaus P (2003) Parasite removal and its impact on litter size and body condition in Columbian ground squirrels (*Spermophilus columbianus*). Proc R Soc Lond B 270:213–215

Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasites species richness in primates. Am Nat 162:597–614

Pagel MD, Harvey PH (1998) The taxon-level problem in the evolution of mammalian brain size: facts and artefacts. Am Nat 132:344–359

Patterson BD, Dick CW, Dittmar K (2007) Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). J Trop Ecol 23:177–189

Pitnick S, Jones KE, Wilkinson G (2006) Mating systems and brain size in bats. Proc R Soc Lond B 273:719–724

Poulin R, Morand R (2004) The parasite biodiversity. Smithsonian Institution Press, Washington

Purvis A, Rambaut A (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. C A Bios 11:247–251

Reader S, Laland KN (2002) Social intelligence, innovation and enhanced brain size in primates. Proc Natl Acad Sci 99:4436–4441

Reckardt K, Kerth G (2006).The reproductive success of the parasitic bat fly *Basilia nana* (Diptera: Nycteribiidae) is affected by the low roost fidelity of its host, the Bechstein's bat (*Myotis bechsteinii*). Parasite Res 98:237–243

Richner H, Tripet F (1999) Ectoparasitism and the trade off between current and future reproduction. Oikos 86:535–538

Speakman JR (2005) Correlations between physiology and lifespan: two widely ignored problems with comparative studies. Aging Cells 4:167–175

Shimalov VV, Demyanchik MG, Demyanchik VT (2002) A study of the helminh fauna of the bats (Mammalia, Chiroptera: Vespertillionidae) in Belarus. Parasite Res 88:1011

Shultz S, Dunbar RIM (2006) Both social and ecological factors predict ungulate brain size. Proc R Soc Lond B 273:207–215

Šimková A, Ottová E, Morand S (2006) MHC variability, life traits and parasite diversity of European cyprinid fish. Evol Ecol 20:465–467

Simmons NB (2005) Chiroptera.In: Wilson DE, Reeder DAM (eds) Mammal species of the World: a taxonomic and geographic reference, vol 1. Smithsonian Institution Press, Washington DC, pp 312–529

Stanko M, Miklisova D, Goüy de Bellocq J, Morand S (2002) Mammal density and patterns of ectoparasites species richness and abundance. Oecologia 131:289–295

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307:580–584

ter Hofstede HN, Fenton MB (2005) Relationships between roosts prefernce, ectoparasites density ang grooming behaviour of Neotropical bats. J Zool 266:333–340

Wilkinson GS, South J (2002) Life history, ecology and longevity in bats. Aging Cells 1:124–131

Wegner KM, Reusch TBH, Kalbe M (2003) Multiple parasites are driving major histocompatibility complex in the wild. J Evol Biol 16:224–232

Wenzel RL (1976) The streblid batflies of Venezuela (Diptera: Streblidae). Brigham Young University Science Bulletin. Biol Ser 20:1–177