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Streblid bat fly assemblage structure on Paraguayan *Noctilio leporinus* (Chiroptera: Noctilionidae): nestedness and species co-occurrence

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Abstract: Evaluation of proximate mechanisms (e.g. dispersal, immigration, competition, facilitation) that determine patterns of assemblage or community structure is an important step in the development of paradigms in ecology. Host–parasite systems are useful for such studies because host-parasite assemblages are easily defined units of study, each host individual harbours a sample from a community or assemblage, and many host species are common, providing replicate samples. I used ectoparasite assemblages from *Noctilio leporinus* collected from Paraguay to evaluate effects of host sex and body size on ectoparasite abundance and to determine if these assemblages exhibit a nested pattern of species co-occurrence. A total of 533 ectoparasites representing seven species and four families were collected from 28 hosts. Abundances of *Paradyschiria fusca* and *Noctiliostrebla aitkeni* responded positively to host body size. Host sex had no affect on ectoparasite abundances. Streblid bat fly assemblages from *Noctilio leporinus* were strongly and significantly nested. Abundances of all species of streblid were positively correlated with one another with Pearson product moment correlation coefficients between 0.424 and 0.646. Competition does not appear to affect community structure of streblids from Paraguayan *Noctilio leporinus*. Independent responses of species of streblid to host characteristics appear to mould assemblage structure in this system.

Key Words: community structure, competition, ectoparasite, facilitation, Streblidae

INTRODUCTION

Predicting community or assemblage composition from species pools is a prominent theme in community ecology (Keddy & Weiher 1999). Identification of mechanisms (e.g. dispersal, immigration, competition, facilitation) that structure communities and empirical patterns of community structure (e.g. chequerboards, Diamond 1975; nestedness, Patterson & Atmar 1986; anti-nestedness, Poulin & Guégan 2000) have been a focus of community ecology since Diamond's original treatise on assembly rules (Diamond 1975). The island paradigm for assembly of communities focuses on patterns of species co-occurrence that result from differential dispersal, immigration and competitive abilities of component taxa (Keddy & Weiher 1999). Studies based on the island paradigm use species occurrence lists and null models to test for possible patterns. One such pattern is nestedness, the extent to which taxa found in species-poor assemblages are proper subsets of those in species-rich assemblages (Patterson & Atmar 1986). Although nestedness is among the most frequently observed patterns of species co-occurrence (Wright *et al.* 1998), assignment of mechanisms to specific instances of nestedness often is tenuous (Higgins *et al.* 2006). Indeed, many mechanisms (e.g. dispersal, extinction, competition, niche breadth, environmental tolerance) may act in concert to produce patterns of species co-occurrence.

Host-ectoparasite assemblages are attractive systems to study community or assemblage composition because hosts are easily defined units of study, each host individual harbours a sample from a community, common host species provide replicate samples and host species differ in morphology, ecology and behaviour providing the necessary variation to analyse effects of host characteristics on ectoparasite assemblages. Host characteristics (e.g. body size, sex, population size, social/mating system, nesting/roosting ecology) likely affect ectoparasite population sizes, which in turn affect rates of ectoparasite speciation (VanderMeulen *et al.* 2001). Moreover, the same host characteristics

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may affect levels of ectoparasite dispersal, immigration or competition, which can influence patterns of species co-occurrence. Consequently, host characteristics are a good point of departure for investigation of mechanisms that may influence ectoparasite assemblage structure.

Streblidae are abundant and species-rich on many species of neotropical bat. Nonetheless, patterns of streblid co-occurrence were not studied until recently (Dick 2005). *Noctilio leporinus* has a sex-based social system that strongly influences rates of inter-host contact and subsequent opportunities for dispersal of ectoparasites (ter Hofstede & Fenton 2005, Whiteman & Parker 2004). In addition, *Noctilio leporinus* exhibits sexual size dimorphism with males being larger than females. Because host body size may affect ectoparasite abundances (Krasnov *et al.* 2005a, Morand *et al.* 2004, Soliman *et al.* 2001), sexual size dimorphism may confound attempts to evaluate effects of sex on ectoparasite assemblages. Therefore, sex and body size of *Noctilio leporinus* were used to investigate patterns of streblid abundance. In addition, patterns of streblid species co-occurrence were evaluated for nestedness. In conjunction, these analyses may elucidate which host characteristics, if any, affect ectoparasite assemblage structure and indicate the dominant mechanisms that influence patterns of species co-occurrence for bat flies.

MATERIALS AND METHODS

Study organisms

Noctilio leporinus (Linnaeus) is a large piscivorous bat distributed throughout the Neotropics from eastern Mexico south to Argentina, including many Caribbean islands (Hood & Jones 1984, Willig *et al.* in press). *Noctilio leporinus* is found most commonly in tropical lowland habitats and forages over ponds, quiet streams, estuaries of major rivers and coastal lagoons (Hood & Jones 1984). It roosts in tree cavities or caves in small groups (i.e. harems) comprised of several adult females, one or two adult males and their offspring (Brooke 1997). Females maintain group residence for several years regardless of turnover in resident males, which retain group membership for one or two reproductive seasons (Brooke 1997). Several families of arthropod ectoparasite infest noctilionid bats including Streblidae, Macronyssidae, Chirodiscidae and Argasidae (Hood & Jones 1984, Moura *et al.* 2003). Three genera of streblid bat fly (*Noctiliostrebla*, *Paradyschiria* and *Xenotrichobius*) are restricted to species of *Noctilio*, with each host species harbouring distinct species from each genus (Dick 2005, Wenzel *et al.* 1966).

Field and laboratory methods

Bats and their ectoparasites were collected from July 1995 to June 1997 and from July to August in 1998 (Willig *et al.* 2000). All bats were collected using mist nets erected at ground level. All aspects of the protocol for mammal collection, specimen processing and preparation, and ectoparasite collection were designed to reduce the possibility of horizontal contamination (i.e. assignment of ectoparasites to the wrong host species). Research involving live animals followed guidelines approved by the American Society of Mammalogists (http://www.mammalsociety.org/committees/index.asp) for the capture, handling and care of mammals and was approved by the Animal Care and Use Committee of Texas Tech University. Details of biomes of Paraguay and mammal collection methods are available elsewhere (Willig *et al.* 2000).

Streblid identifications were confirmed via collaborations with personnel of the Field Museum of Natural History (C. Dick, R. Wenzel and M. Dean). All other taxa were identified by the author. Subsequently, identifications of macronyssid mites were reviewed by D. Gettinger. Mounted and fluid-preserved specimens will be deposited at the Field Museum of Natural History in Chicago, Illinois.

Analytical methods

Three host–parasite parameters were estimated separately for each of the seven ectoparasite species collected from *Noctilio leporinus* (Table 1). Prevalence is the per cent of inspected host individuals that were infested by a particular ectoparasite species (Bush *et al.* 1997, Margolis *et al.* 1982). Mean abundance is the mean number of ectoparasites per inspected host. Mean intensity is the mean number of ectoparasites per infested host. In addition, two indices of host specificity (SI and S_{td*}) were calculated. For each ectoparasite species, SI is the proportion of individuals that occurred on a particular host species (Gettinger & Ernest 1995); SI is calculated separately for each host–parasite association. The index S_{td*} combines phylogenetic and ecological information and calculates a single specificity value for each ectoparasite species within the context of the entire host assemblage (Poulin & Mouillot 2005). This work is part of a large collection of bats and their ectoparasites that included 2909 bats representing 44 species and five families of host (López-González 1998, 2005) that yielded 17 505 ectoparasites representing 104 species, 39 genera and 11 families (Presley 2004); calculations of specificity indices were based on this collection.

Host sex or body size may affect ectoparasite abundances (Krasnov *et al.* 2005b, Morand *et al.* 2004,

Table 1. Prevalence (per cent of hosts infested), mean abundance (mean number of individuals per inspected host), mean intensity (mean number of individuals per infested host) and two indices of host specificity (SI and S_{td*}) for ectoparasites of Paraguayan *Noctilio leporinus* ($n = 28$).

Ectoparasite taxon	Prevalence (%)	Mean abundance (Mean ± SD)	Mean intensity (Mean ± SD)	SI	S_{td*}
Streblidae					
Noctiliostrebla aitkeni Wenzel	46.4	2.8 ± 4.89	6.08 ± 5.69	0.99	3.00
Noctiliostrebla dubia (Rudow)	25.0	0.6 ± 1.20	2.29 ± 1.38	1.00	0.00
Paradyschiria fusca Speiser	75.0	8.1 ± 10.84	10.9 ± 11.31	1.00	0.00
Macronyssidae					
Chiroptonyssus haematophagus (Fonseca)	10.7	0.6 ± 2.30	5.33 ± 5.77	0.00	2.05
Steatonyssus sp.	10.7	0.4 ± 1.25	3.33 ± 2.52	0.91	1.00
Argasidae					
Ornithodoros hasei (Schulze)	57.1	6.1 ± 10.78	10.75 ± 12.51	0.14	2.55
Chirodiscidae					
Parkosa tadarida McDaniel & Lawrence	7.1	1.1 ± 4.23	16 ± 2.83	0.03	2.15

Soliman *et al.* 2001, Whiteman & Parker 2004). A suite of analyses was designed to examine the effects of host sex and body size on abundance of each species of ectoparasite. Analyses were performed separately for each of the four most prevalent species of ectoparasite (i.e. *Noctiliostrebla aitkeni*, *Noctiliostrebla dubia*, *Paradyschiria fusca* and *Ornithodoros hasei*; Table 1) found on *Noctilio leporinus*. Because species of ectoparasite may be restricted to patagia or the trunk of the host, forearm length was used to estimate patagial area and mass was used to estimate host trunk area. However, mass and forearm length do not have a linear relationship with body surface area, which is the variable of interest in these analyses. In general, area should scale as $\text{mass}^{2/3}$ or length^2 (Emerson *et al.* 1994). In addition, ectoparasite abundances were log-transformed to enhance correspondence to assumptions of parametric tests (i.e. general linear models) and to linearize the relationships between surrogates of body size and estimates of ectoparasite abundance. Therefore, all analyses used $\text{mass}^{2/3}$ and $(\text{forearm length})^2$ to quantify linear relationships with log(ectoparasite abundance). 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 abundance.

In addition to environmental characteristics associated with the host, interactions among ectoparasite species may affect abundances of component taxa. To investigate potential pairwise interspecific interactions, Pearson product moment correlation coefficients and associated levels of significance were determined for each pairwise combination of the seven species of ectoparasite recorded from *Noctilio leporinus* in Paraguay. All analyses of covariance and correlations were conducted using the R programming environment (http://www.R-project.org).

To investigate potential interactions among species of streblid that may affect patterns of species co-occurrence, nestedness was estimated using presence–absence data for the three species of streblid that occurred on *Noctilio leporinus* in Paraguay. PN0, PN1 and PNc were used to measure nestedness. These metrics are standardized versions of N0 (Patterson & Atmar 1986), N1 (Cutler 1991), and Nc (Wright & Reeves 1992) and remove correlations between matrix size and magnitude of the index (Wright *et al.* 1998).

Several null models are used to evaluate statistical significance of nestedness indices (Gotelli 2000). These models differ in the constraints placed on the randomization procedure and, therefore, in their susceptibility to Type I and Type II errors. The RANDOM1 null model (Coleman *et al.* 1982, Patterson & Atmar 1986) was employed because it is not prone to Type I errors (Gotelli 2000) and has been used extensively in the literature. Significance of each index of nestedness (i.e. PNc, PN0 or PN1) was assessed by comparing its z-score to zero based on a standard normal distribution (Patterson & Atmar 1986, Wright & Reeves 1992). Each z-transformation was calculated using the means and standard deviations of randomized distributions of the index of nestedness based on 1000 iterations of RANDOM1 (Patterson & Atmar 1986, Wright *et al.* 1998). Simulations were performed with algorithms written in MATLAB version 6.0 for Windows.

RESULTS

In Paraguay, *Noctilio leporinus* averaged 19.7 ectoparasite individuals per host; 553 individuals representing seven species and four families of ectoparasite were collected from 28 *Noctilio leporinus* (Table 1). The ectoparasite assemblage on *Noctilio leporinus* in Paraguay was dominated by three species of monoxenous streblid (*Noctiliostrebla aitkeni*, *Noctiliostrebla dubia* and *Paradyschiria fusca*) and a tick (*Ornithodoros hasei*).

Host sex or body size did not affect abundances of *Noctiliostrebla dubia* or *O. hasei* (Table 2). Abundance of *Noctiliostrebla aitkeni* increased with host mass

Table 2. P-values for analyses of covariance determining the effects of host sex as well as host mass (MA) and forearm length (FA) on ectoparasite abundance for common ectoparasite species from Paraguayan *Noctilio leporinus*. Values in bold are significant (P < 0.05).

	Noctiliostrebla aitkeni	*Noctiliostrebla dubia*	*Paradyschiria fusca*	*Ornithodoros hasei*
Sex	0.181	0.480	0.766	0.944
MA	**0.049**	0.203	**0.009**	0.656
FA	0.076	0.985	0.821	0.577
Sex × MA	0.603	0.316	0.386	0.121
Sex × FA	0.492	0.979	0.512	0.167
MA × FA	0.348	0.692	0.832	**0.042**
Sex × FA × MA	0.261	0.301	**0.030**	0.223

(1 fly per 5 g; Table 2). Abundance of *Paradyschiria fusca* exhibited a significant three-way interaction; however, the interaction indicated a difference in the rate of increase in abundance and not a difference in the direction (i.e. positive or negative) of responses. More specifically, abundance increased with host mass and forearm length; however, abundance increased at a faster rate with mass and on females than it did with forearm length or on males (Figure 1).

Abundances of each species of streblid were positively correlated with abundances of each other species of streblid (Table 3). In addition, abundances of *O. hasei* were correlated negatively with abundances of *Noctiliostrebla dubia* and *P. fusca* (Table 3). Abundances of mite species exhibited no significant correlations with abundances of any species of ectoparasite (Table 3).

Streblid assemblages on *Noctilio leporinus* were strongly nested regardless of index of nestedness ($PNc = 83.8$, $P < 0.001$; $PN0 = 93.4$, $P < 0.001$; $PN1 = 54.3$, $P = 0.012$). If *Noctilio leporinus* harboured one species of streblid, it always was *P. fusca*. *Noctiliostrebla aitkeni* never occurred without *P. fusca* and occurred on 62% of all *Noctilio leporinus* with *P. fusca*. Moreover, 46% of *Noctilio leporinus* with *P. fusca* and *Noctiliostrebla aitkeni* also harboured *Noctiliostrebla dubia*. Instead of illustrating competitive exclusion, these flies co-existed frequently and occurred in greater abundances when sympatric (Table 3). For example, *P. fusca* had a mean intensity of 3.3 flies per bat on hosts without *Noctiliostrebla aitkeni*, but a mean intensity of 14.6 flies per bat on hosts with *Noctiliostrebla aitkeni*.

DISCUSSION

Ectoparasites are more abundant on *Noctilio leporinus* than on other species of neotropical bat, (Presley unpubl. data). This was especially true for streblids. Streblid abundances on phyllostomids ranged from 0.1 to 4 flies per bat, whereas abundances on *Noctilio leporinus* averaged 11.5 flies per bat (Table 1). Because bats are small and space on a host is limited, greater ectoparasite abundances increase the likelihood that interspecific and intraspecific competition may affect ectoparasite assemblage structure.

Effects of host characteristics

If larger hosts provide more area for ectoparasites, then host body size should positively affect ectoparasite abundance. Indeed, host mass evinced significant, positive responses in abundance in the two most prevalent and abundant species of streblid (*Noctiliostrebla aitkeni* and *P. fusca*). Nevertheless, host sociality complicates simple interpretation of analyses of host body size if bats roost in groups (e.g. harems) that provide regular, frequent and prolonged opportunities for ectoparasites to switch hosts. Because space on a host is limited and hosts are ephemeral, location of new hosts for dispersal of offspring is paramount to individual ectoparasite fitness and to species persistence. If among-host differences in the frequency, regularity or duration of host transfer opportunities are related to host characteristics (e.g. sex, age, reproductive status or harem size) that are detectable to ectoparasites, abilities should evolve for ectoparasites to detect proximate cues indicative of potential transfer opportunities conferred by a host. For example, if host body size reflects aspects of host social status such as length of harem membership or harem size to which ectoparasites may respond, it will be difficult to disentangle effects of host body size on ectoparasite abundance from effects of host sociality.

If strong interspecific competition exists, it seems unlikely that all species would respond similarly to differences in host body size; rather, density compensation is expected. More specifically, if a competitively dominant species responds positively to body size, the increase in abundance of the dominant species would prevent subordinate species from responding similarly, which may explain why the most prevalent and abundant species responded positively to host body size but other species did not. In addition to host characteristics affecting ectoparasite abundances, similar responses by ectoparasites to host characters may explain patterns of

Table 3. Pearson product moment correlations for abundances of each species of ectoparasite recorded from *Noctilio leporinus* in Paraguay. * P < 0.05, ** P < 0.01, *** P < 0.001

	Noctiliostrebla dubia	*Paradyschiria fusca*	*Chiroptonyssus haematophagus*	*Steatonyssus* sp.	*Ornithodoros hasei*	*Parkosa tadarida*
Noctiliostrebla aitkeni	0.424*	0.633***	0.298	−0.170	−0.267	−0.214
Noctiliostrebla dubia	—	0.646***	−0.015	−0.172	−0.434*	−0.148
Paradyschiria fusca	—	—	0.170	0.079	−0.495**	−0.339
Chiroptonyssus haematophagus	—	—	—	−0.101	−0.136	−0.087
Steatonyssus sp.	—	—	—	—	−0.169	−0.089
Ornithodoros hasei	—	—	—	—	—	0.279

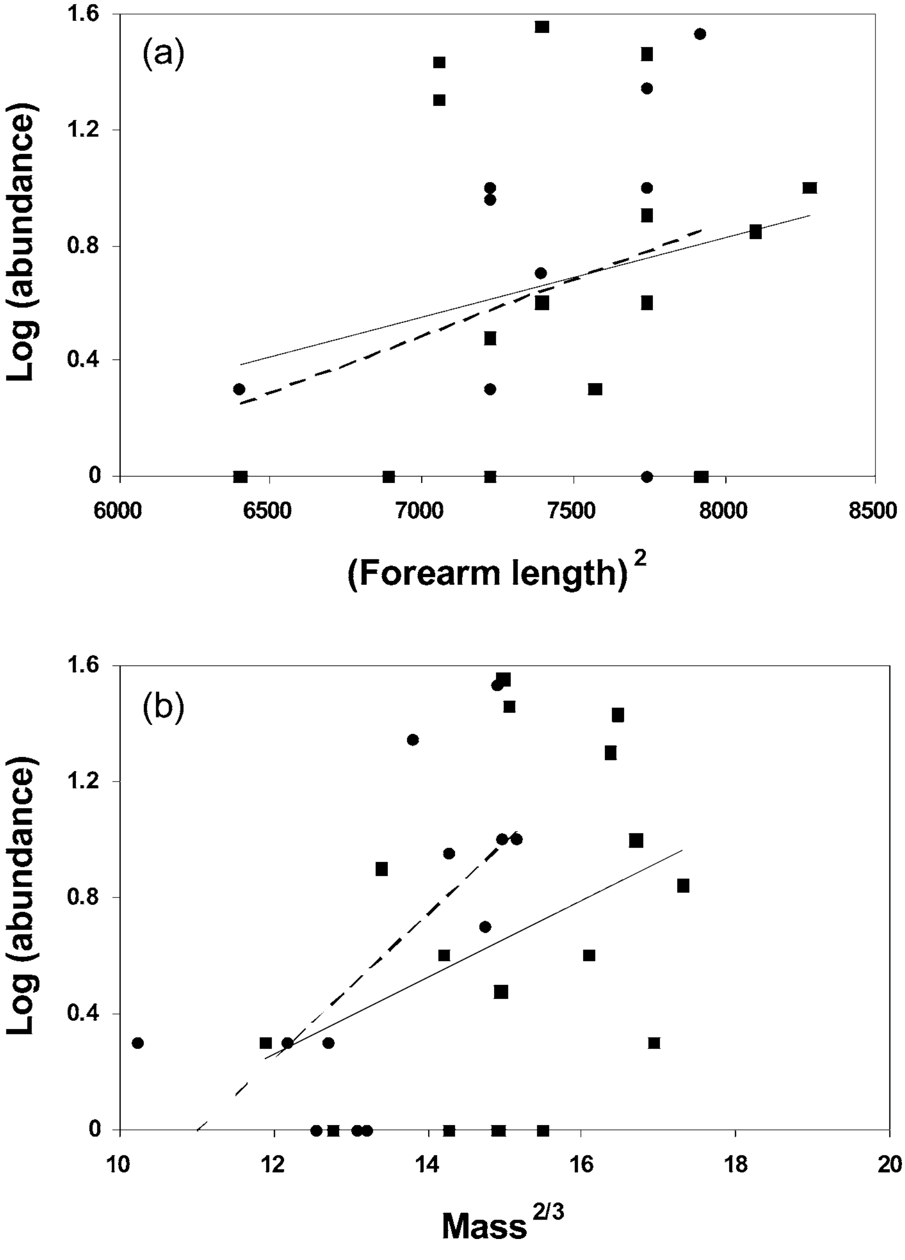

Figure 1. Scatter plots with best-fit lines derived from linear regression for log(abundance) of *Paradyschiria fusca* as a function of host (forearm length)^2 (a) and host mass$^{2/3}$ (b) for female and male hosts, separately. Data and best-fit lines from female hosts are indicated with circles and dashed lines. Data and best-fit lines from male hosts are indicated with squares and solid lines.

species co-occurrence and positive correlations between abundances.

Niche partitioning and interspecific competition

Because space on a host is limited, for species of streblid to co-exist on a single host species requires some degree of niche partitioning. There are three broad niches (i.e. in the fur, on the fur, or on the patagia) for bat flies based on microhabitat distribution on hosts (Dick 2005). Ectoparasites adapted to each niche have a distinctive suite of adaptations (i.e. ecomorphology) to facilitate movement on and attachment to the host (Dick 2005, ter Hofstede *et al.* 2004). In general, interspecific competition among ectoparasites of bats is thought to be weak (Marshall 1982) and recent experiments show that intraspecific competition likely is stronger than interspecific competition of flies from different ecomorphological groups (Dick & Dick 2006). Considering the high degree of specialization required for ectoparasites of bats, priority effects may be sufficient to explain patterns of competitive exclusion among families, genera and species of ectoparasitic insects.

Phyllostomids have long, thick fur and provide suitable habitat for each ecomorphological group of bat fly. Indeed, common species of phyllostomid bat (e.g. *Artibeus fimbriatus*, *A. jamaicensis* and *Sturnira lilium*) from Paraguay each harbour a single species from each ecomorphological group. In contrast, noctilionids have short, sparse fur and do not provide suitable habitat for species that live in or on the fur. In addition, observations (Carl Dick, pers. comm.) of streblids on *Noctilio* spp. collected from Paraguay, Peru, Honduras and Venezuela indicate that all species of streblid usually occur on patagia and not the trunk. Therefore, less species-rich assemblages of streblids could be expected on *Noctilio* spp. due to a reduction in available niches. Contrary to expectations, *Noctilio leporinus* harbours three species of streblid that have the same ecomorphology (i.e. for living on patagia). In addition, these species are common, abundant, exhibit positive associations, a strong pattern of nestedness and their abundances are correlated positively.

Nestedness

Traditional explanations for patterns of nestedness that use colonization- or extinction-based mechanisms may not apply to patterns of nestedness and positive associations of streblids on *Noctilio leporinus*. Differential extinction probabilities may lead to a sequential loss of species that produces nested subsets. However, because hosts are born without ectoparasites and because hosts are ephemeral habitats, nestedness in ectoparasite assemblages is more likely to arise as a result of differences in colonization opportunities coupled with priority effects rather than because of differential susceptibility to extinction. In addition, because *Noctilio leporinus* is a social species, colonization events and rescue effects associated with parasite transfer from harem mates may overwhelm effects of host body size per se (i.e. area). Alternatively, host body size may affect harem membership; consequently, apparent responses of ectoparasite abundance to host body size (Table 2) may indicate effects of host group size and associated colonization opportunities and not host body size, per se.

Nestedness has been documented in many host–parasite systems (Krasnov *et al.* 2005a, Norton *et al.* 2004, Zelmer *et al.* 2004). Host immunocompetence (Krasnov *et al.* 2005a) or host dispersal abilities (Zelmer *et al.* 2004) are postulated explanations for patterns of nestedness, coexistence or abundance in parasites. Because colonization opportunities do not exist when bats are in flight, host dispersal ability and home-range size likely have little effect on exposure of bats to ectoparasites. In contrast, type of roost, number of roosts and social system employed are more likely to affect the ability of an ectoparasite to colonize bats than are factors of host vagility. Because *Noctilio leporinus* lives in harems, harem membership is dynamic, and several harems may exist in the same structure (e.g. cave), it is unclear how host attributes could produce nested subsets (or any other non-random assemblage structure). However, responses of ectoparasites to host cues could explain nested streblid assemblages. If species of streblid similarly evaluate the potential for transfer opportunities on hosts (as described above), and if interspecific competition is weak, positive correlations between ectoparasite abundances would result. If species abundances are correlated positively, positive co-occurrence of species and nested assemblages would result.

Combinations of co-occurrence and abundance correlations

Nine combinations of types of species co-occurrence and correlations of species abundances that represent unique assemblage structures are possible. To date, a list of potential mechanisms to explain each type of ectoparasite assemblage structure (i.e. combination of species abundance and co-occurrence patterns) has not been published; therefore, a list of mechanisms that may produce each type of ectoparasite assemblage structure is presented in Table 4. Streblids on Paraguayan *Noctilio leporinus* exhibit positive co-occurrence, and their abundances are positively correlated (Table 3). Because the three species of streblid on Paraguayan *Noctilio leporinus* have the same ecomorphology, mutual

Table 4. All possible combinations of species co-occurrence and correlations of species abundances and possible mechanisms that could explain each unique response combination for assemblages of ectoparasites.

Pattern of co-occurrence	Correlation of abundances	Possible mechanisms
random	none	No interspecific competition or facilitation, species do not respond to host characteristics or respond to different ones
random	negative	Potential weak competitive interactions, no facilitation, species do not respond to host characteristics or respond to different ones
random	positive	No interspecific competition, possible facilitation or species respond to the same host characteristics
negative	none	Strong interspecific competition leading to mutual exclusion, would only occur if ectoparasite species maintain low abundances and prevalences
negative	negative	Strong interspecific competition leading to mutual exclusion, or strong responses to different host characteristics
negative	positive	Unlikely to occur in nature
positive	none	No interspecific competition, possible weak facilitation or species respond to some but not all of the same host characteristics
positive	negative	Weak interspecific competition with density compensation but not mutual exclusion, species respond to the same host characteristics
positive	positive	No interspecific competition, possible facilitation or species respond to the same host characteristics

exclusion (i.e. negative co-occurrence) or density compensation (i.e. negatively correlated abundances) should manifest if interspecific competition structures streblid assemblages. That neither of these things is true indicates that interspecific competition does not demonstratively affect structure of these assemblages. Nonetheless, competition may act to exclude other species of streblid from parasitizing *Noctilio leporinus* in Paraguay. There is evidence of competitive exclusion by streblids in Venezuela (Dick 2005); four species of streblid occur on *Noctilio leporinus* but only one of two species-pairs (*Noctiliostrebla aitkeni* and *P. fusca* or *Noctiliostrebla traubi* and *P. lineata.*) occurs on a single host individual. No member of a species pair ever occurs with a member of the other species pair. In addition, each species pair exhibits positive co-occurrence and positively correlated abundances. However, *Noctilio leporinus* has a disjunct geographic distribution in Venezuela, with one pair of ectoparasite species occurring on northern bats and the other occurring on southern bats. Therefore, it is possible that these sets of species evolved in isolation and represent an evolutionary effect and not competitive exclusion. Nonetheless, the distance between northern and southern populations of *Noctilio leporinus* is relatively short compared to the dispersal ability of this species; *Noctilio leporinus* has been recorded from 28 islands in the Bahamas, Greater Antilles and Lesser Antilles (Willig *et al.* in press). Therefore, it is likely that individual *Noctilio leporinus* traverse the apparent gap in the geographic distribution, which would provide congeneric species of ectoparasite opportunities to co-occur. Nevertheless, a strict pattern of exclusion is observed. Consequently, these two pairs of species may have evolved in isolation, but competitive exclusion operates to maintain the observed pattern of exclusion and co-occurrence.

Although the species of streblid that parasitize *Noctilio leporinus* are different in Paraguay and Venezuela (Dick 2005), similar patterns of co-occurrence and correlations of abundances were reported for each country. However, this pattern is an exception rather than the rule for streblids on neotropical bats. Of 61 pairs of streblid species that occur on the same species of bat host (Dick 2005), only four species-pairs exhibited positive co-occurrence and facilitation (i.e. positive correlation of abundances). In general, patterns of co-occurrence were random (39 pairs of ectoparasites) or positive (19), and correlations were non-significant (30) or negative (25), indicating that competition may have little effect in determining streblid assemblage structure. In a meta-analysis of 96 published data sets of free-living organisms (e.g. birds, mammals, fish, reptiles, ants, plants), fewer species combinations than expected to occur by chance were observed (i.e. negative species co-occurrence), indicating competition may commonly result in competitive exclusion and may be important in structuring communities (Gotelli & McCabe 2002). In this admittedly preliminary and cursory comparison, distinct differences in patterns observed in free-living and parasitic life forms may indicate that the degree to which competition moulds patterns of community structure may be contingent on the autecology of the organisms.

Facilitation through immunosuppression of host defences has been suggested as an explanation for positively correlated flea abundances (Krasnov *et al.* 2005a). Considering the high mean abundances of streblids on *Noctilio leporinus*, immunosuppression via cumulative ectoparasite load may apply to this system. Alternatively, each species of streblid may respond similarly and independently to particular characteristics of the host (e.g. proximate cues that indicate potential for host transfer opportunities) and no interspecific interaction is required to explain observed patterns.

Conclusions

Nestedness and anti-nestedness represent ends of a continuum of non-random assemblage structure (Poulin & Guégan 2000) from species coexistence (nested subsets) to competitive exclusion of species (anti-nested subsets). Increased specialization represented by distinct ecomorphologies may facilitate species coexistence and positive correlation of abundances in streblid assemblages. However, the fact that three species of streblid with the same ecomorphology are sympatric on *Noctilio leporinus* and exhibit positive associations raises the question of the importance of distinct ecomorphologies in facilitating coexistence: do ecomorphologies represent niche partitioning and reduction of interspecific competition that enhances species coexistence? Or are ecomorphologies adaptations that simply enhance survivorship and avoidance of host defences with little effect on interspecific competition or coexistence of species of ectoparasite? Parasites are highly specialized through obligate co-evolutionary relationships with their hosts; therefore, competition among parasite species may be negligible because adaptation to the host environment is the dominant mechanism that structures these assemblages.

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LITERATURE CITED

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