

Interspecific aggregation of ectoparasites on bats: importance of hosts as habitats supersedes interspecific interactions

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Patterns of aggregation of species or individuals may result from combinations of interspecific interactions such as competition, facilitation, or apparent facilitation, as well as from equivalent responses to environmental factors. Host–parasite systems are ideal for the investigation of mechanisms that structure assemblages. Interspecific aggregation is documented for multiple groups that are ectoparasitic on mammals and host-mediated apparent facilitation has been suggested to explain these aggregation patterns. To investigate the generality of this pattern and to determine likely structuring mechanisms, I analyzed species co-occurrence, correlations of abundances, and nestedness for ectoparasite assemblages from each of 11 species of Neotropical bat. Ectoparasite assemblages on four of 11 host species exhibited significant positive co-occurrence for the entire assemblage or for at least one pair of species in the assemblage; ectoparasites on two host species exhibited positive co-occurrence that approached significance. There was no evidence of negative co-occurrence. Nine species-pairs exhibited positive abundance correlations, including seven of the eight species-pairs that exhibited positive co-occurrence. No species-pair exhibited a negative correlation of abundances (i.e. density compensation). Ectoparasite assemblages from five of 11 host species exhibited nestedness, including all three assemblages that exhibited assemblage-wide positive co-occurrence. Multiple mechanisms associated with host characteristics may contribute to host aggregation in ectoparasite assemblages, including host body size, vagility, home range size, burrow or roost size and complexity, immunocompetence and social structure. In general, data in this study and elsewhere are not consistent with interspecific interactions among ectoparasites, including apparent facilitation, being primary structuring mechanisms of ectoparasite assemblages on mammalian hosts. Rather, host behavior and ecology are likely to affect the frequency of host–ectoparasite encounters and of conspecific host interactions that facilitate transfer of ectoparasites, thereby, molding patterns of ectoparasite co-occurrence, abundance and species composition on mammalian hosts. Combinations of characteristics that are primarily responsible for molding ectoparasite assemblage composition likely are host-taxon specific.

Patterns of species co-occurrence in space and identification of associated structuring mechanisms are major themes in large-scale ecological research (Weiher and Keddy 1999). In general, evaluations of species co-occurrence patterns focus on interspecific competitive interactions (Weins 1977, Connell 1983, Goldberg and Barton 1992, Denno et al. 1995) that result in patterns of negative species co-occurrence such as mutual exclusion (Diamond 1975) or density compensation (Stevens and Willig 2000). In contrast, little research has evaluated mechanisms for aggregation of species (i.e. positive species co-occurrence). Although the aggregation model of coexistence is well developed (Shorrocks et al. 1979, Shorrocks 1996), these approaches focus on how the intraspecific aggregation of individuals in a patchy environment can reduce competition among species to facilitate co-existence. In general, evaluations of assemblages document interspecific segregation and intraspecific aggregation, consistent with predictions of the aggregation model of coexistence. In contrast, positive interspecific aggregation among species that, a priori, are expected to compete is uncommon (but see Krasnov et al. 2006a, b, Presley 2007,

Tello et al. 2008). As a result, proximate mechanisms that explain positive interspecific aggregation are understood poorly. Facilitation and apparent facilitation (Levine 1976, Davidson 1980) are the only interspecific interactions for which expectations are consistent with positive interspecific aggregation. Alternatively, interspecific aggregation could result if multiple potentially competing species exhibit weak interspecific interactions, but strong equivalent responses to one or more environmental variables (i.e. environmental filtering).

Biotas in which species-poor communities are comprised of subsets of species that occur in increasingly more species-rich communities form nested subsets (Patterson and Atmar 1986). In general, nested structures are characterized by a predictable pattern of species loss among sites, with species absent from a particular site also being absent from all sites with fewer species. These patterns of species loss are thought to be associated with variation in species-specific characteristics (e.g. dispersal ability, habitat specialization, tolerance to abiotic conditions) that combine to determine the compositions of a suite of communities. Despite the commonness of nested patterns

(Ulrich and Gotelli 2007), assignment of specific mechanisms to explain nested structures has been rare. Recently, nested structures have been incorporated into metacommunity frameworks, and other metacommunity properties (e.g. co-occurrence, boundary clumping) of nested structures have been evaluated (Leibold and Mikkelsen 2002, Lewinsohn et al. 2006, Ulrich and Gotelli 2007, Presley et al. 2010); these new contexts for the evaluation and understanding of nested structures may help to more reliably couple nestedness with structuring mechanisms. A recent evaluation of the relationship between nestedness and patterns of species co-occurrence concluded that metacommunities that exhibit segregation (negative co-occurrence) may be nested or non-nested, depending on the biological processes that structure the metacommunity (Ulrich and Gotelli 2007); presumably, the same things are true for metacommunities that exhibit aggregation. Consequently, analysis of both co-occurrence and nestedness may better identify structuring mechanisms than either analysis in isolation.

Hosts and parasites as model systems

Host–parasite systems have many tractable qualities that make them useful model systems for studies of community structure: hosts are well-defined units, each host individual harbors a sample community, common host species provide replicate samples, and species-rich host taxa provide opportunities to determine if patterns are general or idiosyncratic. In addition, host species differ in morphology, ecology, and behavior providing the necessary variation to analyze effects of host characteristics on assemblages of parasites. Host characteristics (e.g. body size, sex, population size, social/mating system, nesting/roosting ecology) can affect ectoparasite population sizes or diversity, as well as dispersal, immigration, and specialization of ectoparasites (Morand et al. 2004, Krasnov et al. 2005a, 2006b, Patterson et al. 2007, 2008, Presley and Willig 2008). As a result, host–parasite systems are ideal for investigations of species co-occurrence and aggregation (Combes 2001).

Fifty-four species of bat are known from Paraguay (López-González 2005), representing six families and a diverse suite of foraging guilds. Frugivorous phyllostomids dominate bat assemblages of eastern Paraguay, which is humid, physiographically diverse, and dominated by tall, humid forests that produce fruits and flowers on which many species of phyllostomid rely. In contrast, insectivorous molossids dominate assemblages in the flooded and xeric environs of western Paraguay (Willig et al. 2000, López-González 2004). Flooded areas are adjacent to the Paraguay River, inundated seasonally or permanently, and support palm savannas or marshlands, whereas western Paraguay is dominated by low xerophytic thorn–scrub vegetation because annual rainfall is low (~400 mm) and soils facilitate percolation of water. Vespertilionids occur throughout the country, but never are the predominant taxon of bat (Stevens et al. 2007, Presley et al. 2009).

Two families of batfly (Streblidae and Nycteribiidae) and one family of bat bug (Polyctenidae) infest Neotropical bats. In Paraguay, most batflies and bugs are associated with three families of host: Phyllostomidae, Vespertilionidae, and Molossidae (Presley 2004, Dick and Gettinger 2005, Presley

and Willig 2008). Species of streblid predominantly infest phyllostomid or noctilionid bats; however, a few species (e.g. *Trichobius jubatus*) primarily are associated with molossids. Nycteribiids are restricted to vespertilionids, and Paraguayan polyctenids occur only on molossids (Marshall 1982, Presley 2004). Streblids and polyctenids are highly host-specific (Presley 2004, Dick and Gettinger 2005, Dick 2007, Dick and Patterson 2007), and usually are associated with a single primary host species (i.e. monoxenous). In contrast, nycteribiids in Paraguay commonly occur on multiple host species of the same genus (i.e. oligoxenous; Gracioli et al. 2006).

Insects ectoparasitic on bats spend their entire lives on the bodies or in the roosts of their hosts (Marshall 1982). Bat flies have three larval instars that develop within the adult female and pupae are deposited in the roost. Batbugs are viviparous with three nymphal instars and adults that always reside on the host. Adult flies survive <30 h without a blood meal. Streblids may be found anywhere on a host, whereas nycteribiids are found only on pelage. Polyctenids are documented only from the host body (never from the roost), incapable of locomotion when not within host fur (Marshall 1971, 1982), require blood meals every few hours, inhabit only colonial hosts that roost in cavities, and require direct body contact between hosts to transfer from one host to another. Host grooming is a major cause of mortality in ectoparasitic insects on bats (Fritz 1983). If hosts are ineffective at grooming due to poor health or deformities, ectoparasite populations can increase quickly. Nonetheless, high ectoparasite densities on bats are not thought to cause poor host health, but are considered to be consequences of it (Marshall 1982). Because host grooming poses a significant risk of mortality for batflies and bugs, spaces on a host where they are relatively safe from grooming are important and may limit their abundance or richness on bats. Based on microhabitat distribution on hosts, there are three distinct niche spaces (i.e. on the fur, in the fur, and on the patagia) for bat flies and bugs (Dick 2005): fur runners move across the surface of pelage, fur swimmers move within the pelage, and wing crawlers live on patagia. Species that occupy each of these niche spaces have distinctive adaptations that facilitate movement on and attachment to the host in those locations. In Paraguay, streblids occupy each of these niches, nycteribiids occur only on the fur, and polyctenids occur only in the fur.

Recent work on ectoparasitic insects on bats (Presley 2007, Tello et al. 2008) and fleas on rodents (Krasnov et al. 2006a) documented interspecific aggregation of parasites on individual hosts. Previous studies of ectoparasites of bats focused on ectoparasite assemblages from a single host species (*Noctilio leporinus*, Presley 2007; *Carollia perspicillata*, Tello et al. 2008). Batflies and bugs are highly adapted to life on their hosts (Marshall 1982, Kim 1985a, b) and have distinct niche spaces on their hosts. Moreover, interspecific competition and antagonistic interactions are thought to be weak among these taxa (Marshall 1982), though tests of these hypotheses generally are lacking. If competition structures these assemblages, species should exhibit segregation and non-nested structures. If adaptation to microhabitats on hosts structure these assemblage and interspecific interactions are unimportant, species should exhibit random co-occurrence patterns and non-nested structures. If host characteristics (e.g. body

size, sex, population size, social/mating system, nesting/roosting ecology) determine the quality of each host as an ectoparasite habitat, species should exhibit aggregation on high quality hosts and nested structures with species-rich assemblages on high quality hosts and species-poor assemblages on low quality hosts. In this study, I analyzed patterns of species co-occurrence, nestedness, and correlations of species abundances for ectoparasites from 11 host species that represent four families and employ a diversity of roosting systems (solitary, harem, maternity colony, colonial) to determine (1) if general patterns of assemblage structure (aggregation or segregation) exist for ectoparasitic assemblages on Neotropical bats, (2) if there is a relationship between patterns of co-occurrence and nested structures for ectoparasite assemblages, and (3) which of the proposed mechanisms are most consistent with those general patterns.

Material and methods

Field and laboratory methods

Bats and their ectoparasites were collected from July 1995 to June 1997 and from July to September in 1998. Bats were collected using mist nets erected at ground level, with collections occasionally supplemented by bats taken from roosts in buildings or hollow trees. The protocol for mammal collection, host processing, and ectoparasite collection were designed to minimize the likelihood of contamination (i.e. assignment of ectoparasites to the wrong host individual). Research involving live animals conformed to guidelines of the American Society of Mammalogists (Gannon et al. 2007) and was approved by the Animal Care and Use Committee of Texas Tech Univ. Details concerning collection methods of bats and their ectoparasites are available elsewhere (Willig et al. 2000, Presley 2004, Presley and Willig 2008).

Streblid identifications were confirmed via collaborations with personnel of the Field Museum of Natural History (M. Dean, C. Dick and R. Wenzel). Polyctenid identifications were performed by D. Gettinger (Univ. of Central Arkansas) and C. Dick. Nycteribiids were identified by the author. Voucher specimens were deposited at the Field Museum of Natural History in Chicago, IL. Complete lists of host-ectoparasite associations are available elsewhere (Presley 2004).

Analytical approach

To numerically describe primary host–parasite associations, three parameters (prevalence, mean abundance, and mean intensity) were estimated separately for each species of ectoparasite on each host species and two indices of host specificity (SI and Std*) were calculated (Table 1). Prevalence is the percent of inspected host individuals infested by a particular ectoparasite species, mean abundance is the mean number of ectoparasites per inspected host, and mean intensity is the mean number of ectoparasites per infested host (Bush et al. 1997, Margolis et al. 1982). SI is the proportion of individuals of an ectoparasite species that occur on a particular host species, is calculated separately for each host–parasite association, and sum to 1.00 for each species of parasite for an entire host assemblage. The index

Std* combines phylogenetic and ecological information to calculate a single specificity value for each ectoparasite species within the context of the entire host assemblage. Std* measures ‘the average taxonomic distinctness of all host species used by a parasite species’ (Poulin and Mouillot 2005). Monoxenous parasites have an Std* of 0; oligoxenous parasites occur on multiple species of the same genus and have an Std* of 1.0; and parasites that are less specific have higher values. This research is based on data that were part of a collection of bats and ectoparasites that included 2909 bats representing 44 species (López-González 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. Bat–parasite associations with a prevalence ≥ 0.05 , and with a mean abundance ≥ 1.0 or a SI ≥ 0.90 , were considered to be primary. The vast majority of non-primary host–ectoparasite associations result from disturbance transfers or contamination during sampling (Dick 2007). All analyses were restricted to primary associations. Definition of primary relationships based on host–parasite parameters established a non-arbitrary basis for determination of which relationships likely were ecologically meaningful and, therefore, suitable for analysis.

Three analytical approaches were used to evaluate patterns of ectoparasite aggregation. First, patterns of species co-occurrence were evaluated using presence–absence data. Second, correlations of species abundances were conducted to evaluate interspecific aggregation or segregation of individuals. Third, nestedness was analyzed for each ectoparasite assemblage to determine the relationship between species co-occurrence and nestedness (Ulrich and Gotelli 2007). Analyses were conducted separately for ectoparasite assemblages from each of 11 host species, including six phyllostomids, two molossids, two noctilionids, and one vespertilionid (Table 1). To be selected for analysis, a host species had to be the primary host for ≥ 2 species of batfly or bug and have ectoparasites collected from ≥ 25 host individuals. All analyses were conducted with an α -level of 0.05.

Co-occurrence

A null model approach was used to evaluate patterns of ectoparasite species co-occurrence in a presence–absence matrix in which each row represented a species of ectoparasite and each column represented a host individual. All aspects related to null model analyses of co-occurrence were conducted using EcoSim 7.0 (Gotelli and Entsminger 2001). Of the metrics that are available to measure co-occurrence in presence–absence matrices, I used the C-score (Stone and Roberts 1990). The C-score measures the average number of checkerboard units between all possible pairs of species. If used with an appropriate null model, the C-score is less prone to type I and type II errors and is less sensitive to noise in the data than are other metrics (Gotelli 2000). Moreover, calculation of the C-score is more easily understood and its interpretation less problematic than the V-ratio, the only other metric with good type I and type II error properties. If species co-occur more often than expected by chance, the C-score should be significantly less than expected by chance (i.e. a low checkerboard score).

Table 1. Prevalence (percent 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 Std*) for streblids, nycteribiids, and polyctenids from 11 species of bat from Paraguay. SD = standard deviation; n = number of hosts inspected for ectoparasites; empty = number of hosts devoid of batflies and bugs. Data for *Noctilio leporinus* are published elsewhere (Presley 2007).

Host species (n, empty) Ectoparasite species	Prevalence (%)	Mean abundance (mean ± SD)	Mean intensity (mean ± SD)	SI	Std*
<i>Noctilio albiventris</i> (68, 6)					
<i>Noctiliostrebla maai</i>	66.2	3.1 ± 3.60	4.7 ± 3.47	1.00	0.00
<i>Paradyschiria parvula</i>	89.7	6.4 ± 8.07	7.1 ± 8.21	1.00	0.00
<i>Xenotrichobius noctilionis</i>	8.8	0.1 ± 0.29	1.0 ± 0.00	1.00	0.00
<i>Noctilio leporinus</i> (28, 7)					
<i>Noctiliostrebla aitkeni</i>	46.4	2.8 ± 4.89	6.9 ± 5.69	0.99	3.00
<i>Noctiliostrebla dubia</i>	25.0	0.6 ± 1.20	2.3 ± 1.38	1.00	0.00
<i>Paradyschiria fusca</i>	75.0	8.1 ± 10.84	10.9 ± 11.31	1.00	0.00
<i>Glossophaga soricina</i> (54, 42)					
<i>Strebla guajiro</i>	5.6	0.1 ± 0.45	1.7 ± 1.15	0.16	2.00
<i>Trichobius dugesii</i>	9.3	0.2 ± 0.49	1.6 ± 0.55	1.00	0.00
<i>Trichobius uniformis</i>	11.1	0.2 ± 0.45	1.3 ± 0.52	1.00	0.00
<i>Carollia perspicillata</i> (75, 34)					
<i>Strebla guajiro</i>	22.7	0.3 ± 0.70	1.5 ± 0.72	0.81	2.00
<i>Trichobius joblingi</i>	44.0	0.9 ± 1.30	1.9 ± 1.32	0.96	2.00
<i>Desmodus rotundus</i> (51, 35)					
<i>Strebla weidemanni</i>	23.5	1.5 ± 3.91	6.3 ± 5.99	1.00	0.00
<i>Trichobius parasiticus</i>	31.4	4.3 ± 9.13	13.7 ± 11.86	1.00	0.00
<i>Artibeus fimbriatus</i> (79, 28)					
<i>Aspidoptera phyllostomatis</i>	19.0	0.2 ± 0.58	1.3 ± 0.70	0.66	1.00
<i>Megistopoda aranea</i>	53.2	0.8 ± 0.90	1.5 ± 0.71	0.58	1.02
<i>Metelasmus pseudoapterus</i>	19.0	0.2 ± 0.47	1.1 ± 0.35	0.81	1.00
<i>Artibeus jamaicensis</i> (42, 22)					
<i>Aspidoptera phyllostomatis</i>	14.3	0.2 ± .051	1.3 ± 0.52	0.28	1.00
<i>Megistopoda aranea</i>	38.1	0.9 ± 1.70	2.4 ± 2.00	0.36	1.02
<i>Sturnira lilium</i> (404, 160)					
<i>Aspidoptera falcata</i>	30.0	0.6 ± 1.22	1.9 ± 1.56	0.99	2.00
<i>Megistopoda proxima</i>	48.3	0.9 ± 1.27	1.8 ± 1.27	0.98	2.00
<i>Metelasmus wenzeli</i>	1.0	0.0 ± 0.13	1.3 ± 0.50	1.00	0.00
<i>Myotis nigricans</i> (128, 109)					
<i>Basilispeiseri</i>	7.0	0.1 ± 0.66	2.0 ± 1.66	0.82	1.00
<i>Basilis carteri</i>	7.8	0.2 ± 0.88	2.8 ± 1.69	0.45	1.09
<i>Molossus molossus</i> (228, 158)					
<i>Trichobius jubatus</i>	7.5	0.1 ± 0.38	1.2 ± 0.75	0.26	1.56
<i>Hesperoctenes fumarius</i>	26.8	0.5 ± 1.14	2.0 ± 1.43	0.74	1.00
<i>Molossus rufus</i> (100, 73)					
<i>Trichobius jubatus</i>	17.0	0.3 ± 0.74	1.6 ± 1.06	0.34	1.56
<i>Hesperoctenes fumarius</i>	13.0	0.4 ± 1.49	3.2 ± 3.00	0.25	1.00

A suite of row and column constraints are available that can be imposed on the randomization procedure to produce null matrices for comparison to empirical data. Null models that employ randomly generated matrices that have no structure whatsoever are prone to type I errors. Forcing row totals (i.e. number of occurrences for each species) to equal observed values ameliorates this problem (Gotelli 2000). Moreover, abundance and incidence are species-level characteristics, with few species being abundant and widely dispersed and many species being less common and occurring less frequently. As a result, maintaining fixed row totals improves the biological realism of randomizations that evaluate patterns of co-occurrence. Column totals (i.e. ectoparasite richness on host individuals) may be subjected to various constraint rules without necessarily compromising the performance of the null model (depending on matrix size). An a priori null assumption is that individuals of a particular host species should represent equivalent habitats that provide the same fundamental resources and environment for

their primary ectoparasites; therefore, each host individual of the same species should be capable of supporting the same assemblage of ectoparasites. Any deviations from this assumption would be evidence for particular host characteristics that are important to ectoparasite assemblage structure. Of the available column constraint options, equiprobable columns best represents the sampling universe of host-parasite systems (i.e. that all hosts represent habitats of equal quality or likelihood of colonization). Moreover, this null model has desirable type I and II error properties for the C-score metric (Gotelli 2000). For these reasons, null models with fixed row totals and equiprobable columns were employed in all analyses of co-occurrence.

Inclusion of 'empty' sites can be important in null model analyses; hosts without parasites represent such empty sites and empty observations are common for ectoparasites of bats. Bats that are free of ectoparasites may reflect a lack of suitability of the host or non-colonization by chance. Based on the extensive literature on Neotropical bat ectoparasites,

there is no reason to expect that any particular individual is an unsuitable host for primary ectoparasites associated with that host species. This is particularly true for common species of host that harbor multiple species of ectoparasitic insect. Consequently, it is more likely that bats without ectoparasites are not colonized by chance or because of some individual-level attribute than it is that they represent unsuitable habitat *per se*. Importantly, empty hosts represent empirical observations that inform patterns of ectoparasite occurrence on host individuals; therefore, empty sites were included in randomizations so that construction of null communities was consistent with biological understanding of bats and their ectoparasites.

In each analysis, the observed C-score was compared to a distribution of C-scores from 10 000 randomly generated null matrices produced using the criteria outlined above. In order to detect interspecific segregation as well as interspecific aggregation, analyses were conducted as two-tailed tests. Results were considered significant if the probability of obtaining a random C-score \leq the observed C-score was ≤ 0.025 , indicating interspecific aggregation or if the probability of obtaining a random C-score \geq the observed C-score was ≤ 0.025 , indicating interspecific segregation. p-values were calculated based on the null distribution created by the 10 000 randomly generated matrices. These null distributions are not normal, which requires separate p-values for each tail of the distribution: one that is associated with aggregation and one that is associated with segregation (Gotelli and Entsminger 2001). Randomly generated C-scores that are equal to observed values are included in the calculation of each p-value. As a result, the sum of p-values for a single analysis typically is > 1.0 , depending on the number of 'ties'. To make values of C-score comparable, the standardized effect size (SES) was calculated using the mean and standard deviation of the C-score values from the 10 000 null matrices. In general, SES values < -2 or > 2 represent significant results, depending on how closely the distribution of null values approximates a normal distribution. Because patterns of co-occurrence may manifest among all species in an assemblage or be restricted to pairs of species, for each host that harbored more than two primary species of ectoparasite analyses were conducted for the entire ectoparasite assemblage as well as for each pair of species.

Correlations of abundances

Interspecific interactions or responses to environmental variables or host characteristics may not be sufficiently strong to manifest in analyses of presence–absence data, but may instead be reflected by changes in species abundances. To determine if ectoparasite species abundances were correlated, Pearson product moment correlation coefficients and associated levels of significance were determined for each pair-wise combination of ectoparasite species for each host-species. Because correlations of abundance may be monotonic but not linear, Spearman rank correlations also were conducted. Results for correlations were consistent regardless of analytical approach; therefore, only results for Pearson product moment correlations are presented. As in co-occurrence analyses, empty hosts were included in all correlations of abundances. Correlations were conducted using the R programming environment (R Development Core Team 2009).

Nestedness

Nestedness is a model of species distributions that may be consistent with positive species co-occurrence (Almeida-Neto et al. 2007, Leibold and Mikkelsen 2002); however, this relationship may be dependent on shape of the underlying species abundance distribution of the metacommunity (Ulrich and Gotelli 2007). Nestedness was evaluated for each ectoparasite assemblage to determine if this model of metacommunity structure is consistent with positive species co-occurrence among bat ectoparasites. Nestedness was estimated using presence–absence data of batflies and bugs from each host individual. As recommended by Ulrich and Gotelli (2009), the discrepancy index (D) was used to measure nestedness (Brualdi and Sanderson 1999). This index was standardized (PD) to remove correlations between matrix size and magnitude of the index such that a value of 100 represents perfect nestedness. Nonetheless, such transformations do not affect the power of null model analyses associated with matrix size (i.e. statistical power for small matrices remains low).

Null models that evaluate statistical significance of nestedness indices differ in the constraints placed on the randomization procedure, which affect their susceptibility to type I and type II errors (Gotelli 2000, Ulrich and Gotelli 2009). A null model that fixes species richness to equal empirical values of sites and that fixes the number of species occurrences to equal empirical values of species is recommended for analyses of nestedness (Ulrich and Gotelli 2009). However, this fixed–fixed null model is not applicable to cases where few matrix re-arrangements are possible with these constraints. Because few species (\leq three) of batfly/bug parasitize each species of bat, host by species matrices were small and have few arrangements that meet the constraints of a fixed–fixed null model, resulting in low statistical power. To address this situation, I used a fixed–proportional null model, which is similar to the recommended fixed–fixed model. The fixed–proportional model constrains species richness on hosts to equal empirical values, but assigns occurrences of ectoparasite species at random based on proportional occurrences of each species. Significance of PD was assessed by comparing its z-score to zero based on a standard normal distribution (Ulrich and Gotelli 2009). Transformations of PD were calculated using the means and standard deviations of randomized distributions of the index of nestedness based on 1000 iterations of the fixed–proportional null model. Simulations were performed with algorithms written in MATLAB ver. 7.8.0.347.

Considerable debate surrounds the use of methods to maintain type I experiment-wise error rates at predetermined α -levels for suites of analyses (Hurlbert and Lombardi 2003, Moran 2003, Roback and Askins 2005). Methods (e.g. Bonferroni sequential adjustment) that attempt to maintaining experiment-wise error rate at an a priori level are conservative and application of such methods always inflate type II error rates (i.e. failure to reject a null hypothesis that is false) in order to reduce type I error rates. Indeed, for large suites of analyses, it is likely that such adjustments result in type II error rates that are greater than type I error rates would have been in the absence of any adjustment. Consequently, for exploratory analyses such as those conducted herein,

as opposed to confirmatory analyses, corrections for multiple tests are not recommended (Roback and Askins 2005). I was more concerned about the consequences of ignoring results with ecological implications than about the potential for individual type I errors, which generally are a minor concern for most ecological studies (Hurlbert and Lombardi 2003). As such, I present exact p-values for all analyses and interpreted results without any correction for multiple tests.

Results

Nineteen species of streblid, two species of polyctenid, and one species of nycteribiid infested the 11 host species that harbored \geq two primary species of ectoparasitic insect (Table 1). Fourteen of the streblid species were monoxenous, and three species were oligoxenous on *Artibeus* spp. Polyctenids and nycteribiids were less host-specific than were streblids, with none restricted to a single species of host. Prevalence of ectoparasitic insects ranged from 1–90% (mean = 28.2%), mean abundances ranged from 0–8 insects per bat (mean = 1.3), and mean intensity ranged from 1–14 insects (mean = 3.2). In general, noctilionids were most heavily infested, phyllostomids exhibited intermediate levels of infestation, and infestations on vespertilionids and molossids were least intense. Empty hosts comprised 9–85% (mean = 52.7%) of host individuals (Table 1).

Ectoparasite assemblages on four of 11 host species exhibited significant positive co-occurrence for the entire assemblage or for at least one pair of species in the assemblage (Table 2). Positive co-occurrence approached significance for ectoparasites on two additional hosts. All six host species for which positive co-occurrence was significant or approached significance were phyllostomids or noctilionids. Each assemblage that comprised three species of primary batflies exhibited positive co-occurrence for at least one pair-wise comparison. There was no evidence of negative co-occurrence; only five of 26 SES values were positive (indicating segregation), none were >1 , and associated p-values all were >0.47 . Nine species-pairs exhibited positive abundance correlations, including seven of the eight species-pairs that exhibited positive co-occurrence (Table 2). No species-pair exhibited a negative correlation of abundances. Five of 11 host species exhibited nestedness, including all four species that exhibited assemblage-wide positive co-occurrence. Bat flies on *Desmodus rotundus* were perfectly nested (PD = 100); however, because of the conservative nature of the fixed-proportional null model when applied to such a small matrix, the null distribution created by randomizations was insufficient to return a significant result (Table 2).

Discussion

Ten species-pairs of ectoparasites exhibited positive co-occurrence or positively correlated abundances, 11 species-pairs exhibited random patterns of co-occurrence and abundance, and no negative associations were detected at the assemblage-level or for any species-pair. Therefore, antagonistic interactions (e.g. interspecific or intraspecific competition) likely are not significant mechanisms that mold these

assemblages. Facilitation, apparent facilitation, or responses to host characteristics could produce aggregations of species or individuals. In general, mechanisms by which direct facilitation could occur among species of ectoparasite have not been identified. The presence or abundance of one species could negatively affect the immunocompetence of the host, thereby facilitating infestation by another species; however, this mechanism has been treated as host-mediated apparent facilitation (Krasnov et al. 2005b, c, 2006a). Alternatively, if interspecific interactions are weak, assemblages of ectoparasites may be structured based on similar responses to the same host characteristics by multiple species. Indeed, the null model used to analyze species co-occurrence included the assumption that all hosts represent equivalent habitats; the rejection of this null hypothesis by analyses of four of 11 host species indicates that this assumption often is not true.

Evidence for apparent facilitation lacking

Apparent facilitation via immunodepression of host defenses has been used to explain positively correlated flea abundances on rodent hosts (Krasnov et al. 2005b, c, 2006a). For immunocompetence to be considered a viable explanation for patterns of co-occurrence and aggregation, three things are required. First, intraspecific or interspecific variation in immunocompetence must exist among hosts. Second, observations must be consistent with expectation based on variation in immunocompetence. Third, predictions based on immunocompetence must be distinct from those of other mechanisms or analyses must account for possible effects related to alternate explanations.

Immunocompetence is important to the survival of all mammal species; therefore, general patterns of parasite abundance should be consistent with predictions based on the assumptions that immunocompetence is a primary factor affecting parasite co-occurrence. Within species of mammal, random variation in immunocompetence among individuals likely exists; however, typically, evaluation of individual immunocompetence and pairing that information with ectoparasite infestation levels is not performed. Nonetheless, systematic differences in immunocompetence of mammals that permit testing of predictions exist. Androgens suppress immune function and occur at higher levels in males than in females (Folstad and Karter 1992); therefore, if immunocompetence determines ectoparasite abundance on individuals, males should support greater parasite abundances than females. For mammals, parasites typically are more abundant on the larger sex (Perissodactyla, Rodentia, Artiodactyla, Carnivora and Sirenia) or have similar abundances on each sex (Lagomorpha, Artiodactyla, Marsupialia, Primata and Insectivora) regardless of sexual size dimorphism (Moore and Wilson 2002). Males do not generally maintain higher levels of infestation than females (Moore and Wilson 2002, Patterson et al. 2008, Presley and Willig 2008); the hypothesis that androgenic hormone-related immunodepression is a primary factor affecting parasite abundances of mammals is not supported by the preponderance of data.

Another argument for apparent facilitation via immunodepression is that it is more costly for a host to maintain multiple means of defense, and that associated increased immunological requirements may compromise efficacy of all

Table 2. Results for analyses of co-occurrence, species abundance correlations, and nestedness for batfly and bug assemblages from each of 11 host species. As appropriate, analyses were conducted for entire assemblages or for each pair of species from an assemblage. Significant results ($p \leq 0.025$ for each direction for analyses of co-occurrence; $p \leq 0.050$ for correlations of abundance and analyses of nestedness) are bold and indicate species aggregation (positive co-occurrence or positive correlation). Abbreviations are: SES, standardized effect size; r, Pearson product moment correlation coefficient; PD, standardized nestedness discrepancy metric.

Host species	Pair-wise comparisons*	Batfly richness	Co-occurrence analyses			Correlations		Nestedness	
			SES	Aggregation p-value	Segregation p-value	r	p-value	PD	p-value
<i>Artibeus fimbriatus</i>	3		-1.82	0.029	0.972			27.68	0.050
	comparison 1		-0.63	0.375	0.811	0.101	0.377		
	comparison 2		-2.08	0.032	0.994	0.320	0.004		
<i>Artibeus jamaicensis</i>	3		-1.14	0.192	0.928	0.108	0.343		
	comparison 1	2	0.18	0.751	0.591	0.003	0.986	17.46	0.424
	comparison 2	2	-0.86	0.278	0.870	0.167	0.152	26.40	0.182
<i>Desmodus rotundus</i>	2		-3.52	<0.001	1.000	0.891	<0.001	100.00**	0.127
<i>Glossophaga soricina</i>	3		-0.49	0.315	0.701			-36.89	0.9796
	comparison 1		0.56	1.000	0.750	-0.071	0.610		
	comparison 2		-2.82	0.028	0.999	0.216	0.116		
<i>Molossus molossus</i>	3		0.86	1.000	0.541	-0.107	0.441		
	comparison 1	2	-1.93	0.051	0.986	0.119	0.072	32.32	0.124
	comparison 2	2	-0.65	0.391	0.848	0.048	0.634	-4.55	0.526
<i>Myotis nigricans</i>	2		0.93	1.000	0.473	-0.069	0.437	-16.32	0.910
<i>Noctilio albiventris</i>	3		-1.12	0.120	0.880			84.92	<0.001
	comparison 1		-3.39	<0.001	1.000	0.316	0.009		
	comparison 2		-0.05	0.676	0.666	0.085	0.490		
<i>Noctilio leporinus</i>	3		0.52	0.889	0.494	0.099	0.424		
	comparison 1		-3.31	<0.001	1.000			84.36	0.002
	comparison 2		-1.96	0.024	0.999	0.424	0.025		
<i>Sturnira lilium</i>	3		-2.23	0.006	1.000	0.633	<0.001		
	comparison 1		-1.59	0.095	1.000	0.646	<0.001		
	comparison 2		-3.17	<0.001	1.000			26.39	0.003
<i>Sturnira lilium</i>	3		-2.81	0.001	0.999	0.147	0.003		
	comparison 1		-0.89	0.347	0.921	0.105	0.035		
	comparison 2		-2.09	0.050	1.000	0.157	0.002		

*For host species with three primary species of batfly, comparison 1 = comparison of 1st and 2nd species listed in Table 1 for the respective host species; comparison 2 = comparison 1st and 3rd species listed in Table 1 for the respective host species; comparison 3 = comparison of 2nd and 3rd species listed in Table 1 for the respective host species.

**Batflies on *Desmodus rotundus* were perfectly nested; however, the fixed-proportional null model is relatively conservative and the associated null space created for this analysis lacked sufficient power to detect nestedness even for a perfectly nested structure.

host defense mechanisms, thereby benefiting all parasitic species. In lieu of focusing on the diversity of attacks a host may experience to infer effects of immunocompetence on parasite presence or abundance, one could consider the similarities among species of parasite based on phylogeny. Salivary anti-clotting, anti-platelet, and vasodilatory substances likely are more similar among closely related taxa than among more distantly related taxa. As a result, one would expect closely related ectoparasitic species to exhibit similar success against host defenses on the same host species and for more distantly related taxa to exhibit less similar levels of success (i.e. random associations of success) against the same host species. For ectoparasitic insects on bats, positive co-occurrence or abundance correlations were equally likely to occur between species belonging to the same subfamily (four of 11 instances) as they were between species belonging to different families or subfamilies (four of 10 instances). Similarly, rodent species infested with few species of fleas are infested with few species of ticks or mites, whereas species infested with many flea species are infested with many species of ticks and mites (Krasnov et al. 2005c). There is no apparent relationship between phylogeny and ability to infest a particular host. Observations do not support an argument for apparent facilitation and do not eliminate alternative hypotheses from consideration. As suggested by Krasnov

et al. (2006a), heterogeneity among hosts in body size, home range, vagility, or behavior may make some individuals or species of host better habitats than others. Indeed, investigation of host body size (Moore and Wilson 2002, Krasnov et al. 2006b), sex (Krasnov et al. 2005a, Patterson et al. 2008, Presley and Willig 2008), sociality (Patterson et al. 2007), and burrow system (Krasnov et al. 2006b) indicate that factors associated with the host aside from immunocompetence likely structure ectoparasite assemblages on mammals.

Importance of the host as a habitat

In addition to immunocompetence, for many taxa of mammals, additional sex-related traits that may explain aggregations of species or individuals of ectoparasites exist. More specifically, males generally are larger, disperse greater distances, and maintain larger home range sizes than females. Each of these characteristics may contribute to an observation that males harbor more parasites than do females (Krasnov et al. 2005b). Larger hosts provide more area for parasites, which may lead to increased abundances as well as increased parasite diversity if size differences are sufficient to allow for more finely divided niche spaces. Hosts that are more mobile or that maintain larger home ranges have greater

chances of encountering parasites. Each of these causes may be sufficient to explain patterns of parasite aggregation on males; however, for most host taxa it is difficult to decouple effects of body size, vagility, home range, and immunocompetence. Bats offer such an opportunity. In Neotropical bats, females are the larger sex as often as males (Presley and Willig 2008). In addition, bats are not exposed to ectoparasites while in flight, which de-couples sex from effects related to host vagility or home range size. If ectoparasite abundance is determined by immunocompetence, male bats would harbor more ectoparasites than females. Alternatively, if host size affects ectoparasite abundance, larger bats would harbor more parasites regardless of host sex. In general, neither is true (Patterson et al. 2008, Presley and Willig 2008). For half of the bat species examined in Paraguay, females harbored more parasites regardless of the existence or direction of sexual-size dimorphism (Table 2 of Presley and Willig 2008); for the other host species, there was no difference in ectoparasite abundance between sexes. Similarly, streblids on Venezuelan bats that exhibited sex-biased parasitism were more likely to be biased towards infestations on female bats than on male bats (Patterson et al. 2008). Of the remaining available alternative explanations, parasite encounter rates related to host social system appears to be a likely mechanism to explain parasite abundances on bats.

Most species of Neotropical bat, including all of those studied here, form harems (in the case of phyllostomids or noctilionids) or maternity colonies (in the case of vespertilionids or molossid). Indeed, each of the species that exhibited positive co-occurrence or positive abundance correlations (Table 2) of ectoparasite species form harems. Harems consist of one adult male, several adult females, and their offspring, whereas maternity colonies are devoid of males. In each social system, the majority of males are solitary. Consequently, males encounter conspecifics less often than do females, which may manifest as a phenomenon similar to an encounter filter (Combes 1991). This explanation is consistent with patterns of aggregation and abundance of ectoparasites on bat hosts (Kunz 1976, Presley 2007, Patterson et al. 2008, Presley and Willig 2008, Tello et al. 2008). In another example, infestation rates of batflies on males of a temperate bat (*Corynorhinus townsendii*) increase when males shift from the solitary behavior of summer to colonial behavior during winter (Kunz 1976), supporting the idea that contact with conspecifics is of primary importance in structuring ectoparasite assemblages on bat hosts. Because hosts are small and represent transient habitats, opportunity to infest new hosts is paramount for species persistence. Because female hosts are in contact with other suitable hosts more often than males, they may experience higher colonization rates. Moreover, if intraspecific differences exist among hosts with respect to the frequency, regularity, or duration of host transfer opportunities that are related to a host characteristic, such as sex, abilities should evolve for ectoparasites to detect proximate cues indicative of the potential for transfer afforded by a host. Such responses associated with host sex may be reinforced because females are the conduit to future generations of hosts. As a result, no interspecific interaction among ectoparasites is required to explain patterns of ectoparasite abundance, ectoparasite co-occurrence, or aggregations of ectoparasites on hosts.

It may be that some hosts simply represent better habitats than others (Krasnov et al. 2006b), in part because of the transfer opportunities they present, and that the aggregation of individuals or species of ectoparasite occurs because multiple ectoparasite species exhibit equivalent responses to the same host characteristic(s). Because bat ectoparasites are highly host-specific (Dick 2007, Dick and Patterson 2007), can not survive without a host for more than a few hours (Marshall 1982), and can only colonize a host in the roost, aspects of host transfer opportunity (i.e. frequency, regularity and duration) associated with individual hosts may mold patterns of ectoparasite abundance and aggregation. This mechanism may be extended to other systems for which explanations related to apparent facilitation have been explored (Krasnov et al. 2005b, c, 2006a), where later investigations (Krasnov et al. 2006b) have found positive relationships between aggregation of ectoparasites and burrow depth.

A consideration of competition

Competition may manifest as competitive exclusion, density compensation, or priority effects. Herein and elsewhere (Presley 2007, Tello et al. 2008) patterns of species co-occurrence and abundance correlations were in opposition to expectations if competitive exclusion or density compensation were important in structuring assemblages of ectoparasites on bats. Nonetheless, it is possible for species that already have primary relationships with a host to prevent other species that could inhabit that host from establishing populations, evincing priority effects (Paine 1977). For priority effects to be a functional mechanism preventing batflies from establishing populations on new host species, streblids introduced to non-primary hosts that are free of parasites should survive and reproduce on those hosts. In contrast, if adaptations to living on a primary host species prevent establishment of new host-parasite relationships, ectoparasites introduced to non-primary hosts would fail to persist on those hosts. In experiments (Overall 1980) that introduced streblids to non-primary hosts, streblids died of starvation or from host grooming within hours. It is likely that two primary factors represent obstacles to formation of new host relationships for streblids: (1) lack of appropriate adaptations designed to facilitate survival on the new host species and (2) extant specializations for life on primary hosts that typically are maladaptive in other environments.

Nestedness and aggregation

Each ectoparasite assemblage that exhibited positive assemblage-wide co-occurrence was nested. Similarly, nestedness and positive co-occurrence have been documented for fleas on rodents (Krasnov et al. 2005a). The relationship between nestedness and co-occurrence depends on the biological processes that determine species incidence (row totals) or richness of sites (column totals). For random matrices generated from equiprobable row and column distributions, nestedness and co-occurrence exhibited a positive relationship (Ulrich and Gotelli 2007). In contrast, random matrices generated from a log-normal species abundance distribution exhibited a negative relationship between nestedness and co-occurrence. That results for ectoparasites of bats (Table 2) and rodents

(Krasnov et al. 2005a) are consistent with those generated by equiprobable null models suggests that species abundance distributions of these assemblages is better represented by a flat species abundance distribution than by a log-normal distribution.

Conclusions

Multiple mechanisms associated with host characteristics may contribute to aggregation in ectoparasite assemblages, including host body size, vagility, home range size, burrow or roost system size and complexity, immunocompetence and social structure. In general, interspecific interactions among ectoparasites, including apparent facilitation, do not explain aggregation of ectoparasites on mammalian hosts. Parasites typically are co-evolved with their host taxon or exhibit a high degree of specialization that permits them to persist in a hostile host environment (Kim 1985a, Poulin 1997, Combes 2001). For obligate parasites, adaptation to the host as a habitat is the dominant mechanism of selection (Kim 1985b). Consequently, it is unsurprising that interspecific interactions among parasites would not supersede the importance of the host environment in determining patterns of species co-occurrence, aggregation, and composition for ectoparasites. For bats, aspects of host behavior and ecology that affect the likelihood of host–ectoparasite encounters and the frequency that a host interacts with conspecifics to facilitate transfer of ectoparasites likely mold patterns of ectoparasite co-occurrence, abundance, and composition. Because host groups differ in ecology, demography, morphology, phylogeny and behavior, the set of factors that most strongly molds ectoparasite assemblages likely is specific for each host taxon.

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