Ecology of Ectoparasites from Tropical Bats

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ABSTRACT Incidence, prevalence, and density of ectoparasites are reported for 3 species of tropical bats, *Stenoderma rufum* Demarest, *Artibeus jamaicensis* Leach, *Monophyllus redmani* Leach, from the tabonuco forest of Puerto Rico. In addition, patterns of ectoparasite associations were examined with respect to several host characteristics including age and sex, as well as with respect to season. Levels of ectoparasite infestation differed because of host age, but not sex, with juveniles harboring higher numbers than adults. No ectoparasite attribute differed with season. Significantly different assemblages of parasites occurred on adult male, adult female, and juvenile *A. jamaicensis*. Moreover, *S. rufum*, *A. jamaicensis*, and *M. redmani* each have a significantly different ectoparasite assemblage.

KEY WORDS Puerto Rico, Luquillo Experimental Forest, arthropoda, mammals, parasitism, Neotropics

ALTHOUGH ECTOPARASITES LIVE and feed on external surfaces and provide no net benefit to their host, they usually do not cause host mortality. As a consequence, it is unclear for bats, as it is unclear for most mammals, whether or under what circumstances parasites have an appreciable effect on individual fitness of hosts or on emergent population level processes (Anderson 1982, Holmes 1982, May 1983). Moreover, little is understood concerning the manner in which differences in host characteristics affect population densities of ectoparasites or the composition of species assemblages (for example, species, age, sex) on individual hosts.

Many bat ectoparasites are highly host-specific because of the ecologically and geographically isolated nature of their hosts. All species show some degree of host limitation (Marshall 1982), but some groups appear to be more host-specific than others. Consequently, the potential exists to use host–parasite relationships as taxonomic characters in the same way that morphological characteristics are used in systematics (Hafner and Nadler 1988, Whitaker 1988, Hafner 1991).

Bat ectoparasites usually either spend their entire life on the body of the host, where they continually feed, or remain in the host's roost, where they feed during periods of host inactivity (Marshall 1981). Continuous feeders remaining with the host usually exhibit a small, flattened form and are capable of movement over the surface of the host, although most show a distinct preference for particular locations on the body. This locational specificity may reduce the possibility of being removed

or dislodged during grooming activities, the major source of mortality for most species of bat ectoparasites (Marshall 1982), or could represent a microhabitat that facilitates coexistence of multiple parasite species.

Over 687 species of arthropods have been recorded as parasites of bats, with members of all but 3 chiropteran families acting as hosts (Marshall 1982). Bats of the New World family Phyllostomidae harbor a diversity of ectoparasites, including over 250 species (Webb and Loomis 1977). Details concerning the interspecific relationships between phyllostomid bats and their ectoparasites are cursory, because few species of ectoparasites have been studied from an ecological perspective. Individual bats may be associated with complex communities of ectoparasites, comprising 7 or more species; nonetheless, 2–3 species are the most common numbers of coexisting ectoparasites on a single host individual. In general, the number of individuals per host is negatively correlated with size of the parasite, with highest infestations recorded for the smallest parasites (Marshall 1982).

The diversity of ectoparasites associated with an individual is related to many factors, including home range, behavior, size, and roost type of the host; these factors may also result in differences in ectoparasite associations among species, as well as between age or sex groups within a species. For example, if roosting behavior affects ectoparasite dispersal, then ectoparasites of colonial bats should have an even or random distribution whereas ectoparasites of solitary hosts should exhibit a clumped distribution.

In addition to the above factors, competition among ectoparasites may influence their diversity on a particular host (Wenzel and Tipton 1966). For

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competition to structure parasite communities on individual hosts (that is, produce patterns), it must be sufficiently intense to cause local extinction of species, it must be pervasive enough to affect most species of parasites, and it must be the predominant factor determining ectoparasite coexistence at the community level (Moulton and Pimm 1986, Willig and Moulton 1989). Current information concerning the life history of ectoparasites and their hosts is insufficient to begin to address these prerequisites.

Descriptions of bat–ectoparasite associations in Puerto Rico are based on serendipitous collections from 1 or a few host specimens, <10 individuals for most bat species (see Gannon and Willig 1994b). Few published data address the ecology of these arthropods or interactions with their hosts. We examine both population and community characteristics of ectoparasites, focusing on incidence, prevalence, density, and species composition. More specifically, we address questions concerning the effects of host age and sex, as well as seasonal variation, on the distribution of ectoparasites. Differences among age or sex groups of a particular host species, as well as differences among host taxa constitute habitat variation for exploitation by ectoparasites. The effects of these sources of variation are evaluated for ectoparasites found on 3 common bat hosts in the tabonuco forest of Puerto Rico.

Materials and Methods

Study Area. Puerto Rico is the smallest and easternmost island of the Greater Antilles. The Luquillo Experimental Forest is coincident with the Caribbean National Forest (18° 10' N; 65° 30' W) and occurs in the northeastern corner of the island, within the Luquillo Mountains. Increasing elevation in the Luquillo Mountains is accompanied by changes in climate, soil, and vegetation structure and composition. As a result, distinct life zones occur within the bounds of the Luquillo Experimental Forest (Ewel and Whitmore 1973, Brown et al. 1983). The tabonuco forest is classified as a subtropical wet forest in the Holdridge system (Ewel and Whitmore 1973). It is the largest life zone and is located on lower mountain slopes below 600 m. Average rainfall exceeds 2,000 mm annually.

Host Description. Compared with mainland areas or other islands of similar size and habitat diversity, Puerto Rico harbors few mammal species, and population numbers are generally low. Bats compose the major portion of the Puerto Rican mammal fauna in terms of species richness and density (Willig and Bauman 1984). Within the tabonuco forest, 3 species of bats dominate. Two of these species, *Stenoderma rufum* Demarest and *Artibeus jamaicensis* Leach, are frugivores; the 3rd, *Monophyllus redmani* Leach, is a nectarivore.

Stenoderma rufum, the red fig-eating bat, has been reported only at a few localities on Puerto

Rico and the nearby islands of St. John and St. Thomas (Genoways and Baker 1972). Nonetheless, recent work indicates a broad distribution throughout Puerto Rico. Until recently, it was thought to be extinct and was known only from fossil records. As a result, it is a poorly known species and is rare in scientific collections. Only the population in the Luquillo Experimental Forest has been sampled and studied to any extent during the past 25 yr. It is currently designated as a "sensitive" species by the Forest Service (U.S. Department of Agriculture). The status of other populations on Puerto Rico or the Virgin Islands is unknown. Recent studies have examined various aspects of its population biology and ecology, including foraging and home range (Gannon 1991, Gannon and Willig 1994a), reproduction (Gannon and Willig 1992), and diet (Willig and Bauman 1984, Gannon and Willig 1994a), and suggest that *S. rufum* consumes a variety of fruits, exhibits asynchronous bimodal polyestry, roosts in canopy foliage, and has a relatively small home range (mean = 2.5 ha) to which it exhibits site tenacity for at least several months.

Artibeus jamaicensis, the Jamaican fruit bat, has a wide geographic distribution in tropical and subtropical America. It is a much studied species and is known to consume a variety of fruits, as well as some flowers and insects. Although extensive work has examined aspects of the ecology of several mainland populations (for example, Morrison 1975, 1978 a–c, 1979; Handley et al. 1991), little work has focused on island populations in general or on Puerto Rican populations specifically. Previous research from the Luquillo Experiment Station indicates that it comprises ≈60% of the bat fauna (Willig and Bauman 1984) and exhibits aseasonal polyestry (Willig and Bauman 1984, Gannon and Willig 1992).

Monophyllus redmani, the Greater Antillean long-tongued bat, feeds primarily on flower nectar. It has a distributional range restricted to the Greater Antilles and several islands of the Bahamas (Homan and Jones 1975). Little is known of its ecology other than anecdotal observations. It is widely distributed on Puerto Rico and is common in the Luquillo Experiment Forest (Willig and Bauman 1984).

Field Collections. Bats were collected during the dry (March) and rainy (June–August) seasons of 1988 and 1989. Specimens were captured in mist nets at various localities near El Verde Field Station in the tabonuco forest. Upon capture, each bat was held in a separate cloth bag until inspected for ectoparasites. All examinations were performed on live specimens within 20 min of capture. Wing and tail membranes, pelage, ears, and face were examined thoroughly for the presence of arthropods. All visible ectoparasites were removed and placed in vials containing 70% ethyl alcohol, using a separate vial for each bat. Species, age, and sex were recorded for each host before its release. The number of individuals of each category (adult

Table 1. Associations of *P. iheringi* with *S. rufum* in the tabonuco forest of Puerto Rico (seasons combined)

Parameter	Host characteristics[a]	FE	ME	IE	TE
Incidence	% hosts infested	22.1	26.3	18.9	34.7
	% adult males infested	38.1	33.3	28.6	52.4
	% adult females infested	8.6	11.4	2.9	14.3
	% juveniles infested	25.6	35.9	28.2	43.6
Prevalence	All hosts	0.46 + 1.09	0.70 ± 1.52	0.34 ± 0.83	1.48 ± 3.20
(mean ± SD)	Adult males	0.76 ± 1.45	0.76 ± 1.41	0.43 ± 0.81	1.95 ± 3.19
	Adult females	0.09 + 0.28	0.14 ± 0.43	0.03 + 0.17	0.23 ± 0.65
	Juveniles	0.64 ± 1.27	1.15 ± 2.01	0.56 + 1.10	2.39 ± 4.16
Density (mean ±	All hosts	2.06 + 1.45	2.64 ± 1.93	1.78 ± 1.06	4.28 ± 4.22
SD)	Adult males	2.00 ± 1.77	2.29 ± 1.60	1.50 ± 0.84	3.73 ± 3.61
	Adult females	1.00 ± 0.00	1.25 ± 0.50	1.00 ± 0.00	1.60 ± 0.89
	Juveniles	2.50 ± 1.27	3.21 ± 2.16	2.00 ± 1.18	5.41 ± 4.84

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total.

[a] Host sample size: 95 (21 adult males, 35 adult females, 39 juveniles).

male, adult female, and immature [nymphs and larvae]) of each ectoparasite species was recorded for each bat host. Host voucher specimens were deposited in the mammal collection of The Museum, Texas Tech University, Lubbock, and the mammal collection of The Carnegie Museum of Natural History, Pittsburgh, PA. Ectoparasite voucher specimens were deposited at the Wilbur R. Enns Entomology Museum, Unversity of Missouri, Columbia.

For each of the 3 common bat hosts, several host–ectoparasite parameters were estimated, including incidence (the percentage of infested bats), prevalence (mean number of ectoparasites per bat), and density (mean number of ectoparasites per infested bat).

Statistical Procedures. For each host species, pure model I 2-way analysis of variance (ANOVA) was used to evaluate whether differences in ectoparasite prevalence occurred because of host age–sex (adult males, adult females, juveniles), season (rainy or dry) of capture, or their interaction (Sokal and Rohlf 1981). Age–sex was used as a single factor because sample sizes of juveniles of each sex for all hosts were small. Powerful a priori tests were performed to compare prevalence of adult males with that of adult females and prevalence of adults with that of juveniles, regardless of sex. Ectoparasites were analyzed with respect to 4 groups:

Table 2. Significance levels from a series of 2-way ANOVAs that evaluated the effects of host age–sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) on the prevalence of *P. iheringi* on *S. rufum*

Factor	df	FE	ME	IE	TE
Season	1	0.54	0.34	0.29	0.35
Age–sex	2	0.12	0.04*	0.07	0.04*
Season by age–sex	2	0.37	0.44	0.44	0.36

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total. * Indicates significance ($P \leq 0.05$).

adult males, adult females, immatures (nymphs and larvae), and total (all ectoparasites combined).

Similarly, interspecific and seasonal comparisons of ectoparasitic prevalence were performed with a pure model I 2-way ANOVA. A posteriori Tukey multiple comparison for unequal sample sizes (Zar 1984) was used to evaluate pair-wise differences between host species. Season and the season-by-species interaction data in the more powerful ANOVAs were nonsignificant, hence data on seasons were combined in subsequent a posteriori comparisons of bat species.

For host-specific comparisons, the observed density function of parasites was compared with a random density function (generated by the Poisson distribution) using a goodness-of-fit test (Sokal and Rohlf 1981). When the goodness-of-fit test is significant, hyperdispersion of parasites among host individuals is indicated by a CD > 1, whereas hypodispersion is suggested when CD < 1.

Comparisons of ectoparasite community composition were achieved using G tests (Sokal and Rohlf 1981) in 2 different circumstances. In the 1st, the effect of host age–sex on ectoparasite community composition was determined for *A. jamaicensis*. In the 2nd, comparison of ectoparasite community composition focused on interspecific differences among the 3 common hosts (*A. jamaicensis*, *S. rufum*, and *M. redmani*) regardless of the age or sex of the hosts. In both circumstances, a sum of squares simultaneous test procedure performed as an a posteriori test to evaluate factors affecting significance in the G test (Pimentel and Smith 1986).

Results

Ectoparasite Variation within Host Species. Seven species of ectoparasites were collected from 5 species of bats. These primarily include spinturnicid wing mites, *Periglischrus iheringi* Oudemans, speleaeorhynchid ear mites, *Spelaeorhynchus praecursor* (Neumann), argasid ticks, *Ornithodoros* sp.,

Table 3. Associations of ectoparasites with *A. jamaicensis* in the tabonuco forest of Puerto Rico (seasons combined)

Parameter Host characteristics[a]	*P. iheringi*				*M. aranea*		
	FE	ME	IE	TE	FE	ME	TE
Incidence							
% hosts infested	50.0	50.0	54.2	69.1	23.4	19.1	35.1
% adult males infested	47.6	40.0	43.3	60.0	23.3	10.0	33.3
% adult females infested	30.5	36.1	47.2	58.3	19.4	19.4	30.5
% juveniles infested	78.6	78.6	75.0	92.9	28.6	28.6	42.9
Prevalence (mean ± SD)							
All hosts	2.26 ± 3.69	1.30 ± 1.99	1.40 ± 1.79	4.96 ± 6.10	0.31 ± 0.69	0.25 ± 0.56	0.55 ± 0.55
Adult males	1.67 ± 2.82	0.60 ± 0.93	1.10 ± 1.75	3.37 ± 4.97	0.23 ± 0.43	0.10 ± 0.31	0.33 ± 0.48
Adult females	0.92 ± 2.64	0.83 ± 1.42	1.00 ± 1.55	2.75 ± 4.31	0.28 ± 0.74	0.19 ± 0.40	0.47 ± 0.88
Juveniles	4.61 ± 4.55	2.64 ± 2.71	2.25 ± 1.90	9.50 ± 6.85	0.43 ± 0.84	0.46 ± 0.84	0.89 ± 1.50
Density (mean ± SD)							
All hosts	4.51 ± 4.13	2.60 ± 2.13	2.59 ± 1.69	7.17 ± 6.16	1.32 ± 0.84	1.28 ± 0.58	1.58 ± 1.20
Adult males	3.57 ± 3.23	1.50 ± 0.91	2.54 ± 1.85	5.61 ± 5.37	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00
Adult females	3.00 ± 4.20	2.31 ± 1.49	2.12 ± 1.65	4.71 ± 4.77	1.43 ± 1.13	1.00 ± 0.00	1.55 ± 0.94
Juveniles	5.86 ± 4.35	2.63 ± 2.63	1.58 ± 1.58	6.55 ± 6.55	0.93 ± 0.93	0.74 ± 0.74	1.68 ± 1.68

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total.

[a] Host sample size: 94 (30 adult males, 36 adult females, 29 juveniles).

and streblid bat flies, *Megistopoda aranea* (Coquillett), *Nycterophilia parnelli* Wenzel, *Aspidoptera phyllostomatus* (Perty), *Trichobius intermedius* Peterson & Hurka. Only 1 ectoparasite, *P. iheringi*, occurred on all host species. All ectoparasites occurred on at least 2 bat species, except for *M. aranea*, *N. parnelli*, and *Ornithodoros* sp., which were host-specific.

Stenoderma rufum. Although various authors (Tamsitt and Fox 1970a, b; Tamsitt and Valdivieso 1970; Gannon and Willig 1994b) have reported a number of ectoparasites of the red fig-eating bat from the tabonuco forest, only 1 species, *P. iheringi*, a spinturnicid mite, was found on this host during this study (Table 1). Thirty-three of 95 captured bats harbored this ectoparasite. Variation in level of prevalence of *P. iheringi* is related to the age–sex of the host (Table 2). Juvenile bats harbored a significantly higher number of wing mites than did adult males or females (a priori test, $F = 5.664$; df $= 1$, 89; $0.025 > P > 0.01$). This is largely because of the significantly greater number of male *P. iheringi* present on juvenile bats (a priori test, $F = 5.342$; df $= 1$, 89; $0.025 > P > 0.01$). Levels of prevalence of female as well as immature *P. iheringi* did not differ among age–sex groups of bats. Finally, no differences in prevalence due to season existed for any ectoparasite groups. The lack of a significant interaction between main treatment effects indicates that the effect of age–sex is independent of season.

Artibeus jamaicensis. Eighty-two of 94 Jamaican fruit bats harbored ectoparasites representing 5 different species (Table 3): 2 mites (*P. iheringi* and *S. praecursor*) and 3 streblid bat flies (*M. aranea*, *A. phyllostomatus*, and *T. intermedius*). Differences in the level of prevalence of *P. iheringi* occurred (Table 4) among age–sex categories of the host. Juvenile bats harbored a significantly higher

number of adult male ectoparasites than did adult bats, regardless of sex (a priori test, $F = 39.98$; df $= 1$, 88; $P < 0.001$). When all age groups of *P. iheringi* (adult males, adult females, and immatures) were combined, a similar overall trend was evident (a priori test, $F = 41.63$; df $= 1$, 88; $P < 0.001$). No difference in prevalence could be attributed to seasonal variation for any group of *P. iheringi*, and all interactions were nonsignificant, indicating that the effects of age–sex are independent of season. No significant differences (Table 4) in prevalence of any of the other ectoparasites (*M. aranea*, *A. phyllostomatus*, *T. intermedius*, or *S. praecursor*) were detected as a consequence of host age–sex, season, or their interaction. Overall prevalence of ectoparasites, regardless of species, varied significantly with regard to age–sex of host, but not to season; juvenile bats consistently harbored more parasites than did adults (a priori test, $F = 22.57$; df $= 1$, 88; $P < 0.001$).

Monophyllus redmani. Twelve of 21 adult *M. redmani* were infested with ectoparasites representing 4 species: *P. iheringi*, *N. parnelli*, *T. intermedius*, and *S. praecursor* (Table 5). *M. redmani* harbored few individuals of *P. iheringi*. The dominant ectoparasite on this nectarivorous bat was *T. intermedius*, with an incidence of 42.9% (density per bat = 0.76). Moreover, *N. parnelli* was found on no other bat species from the Luquillo Experiment Forest. As in the case of *A. jamaicensis*, only females of *S. praecursor* were collected from *M. redmani*. Because of small sample sizes, juvenile bats (*n* = 2) and females from the rainy season (*n* = 0) were eliminated from analyses. As a consequence, host categories were restricted to 3 groups of adults (males from the rainy season, males from the dry season, females from the dry season). Regardless of ectoparasite category (Table 6), no dif-

Table 3. Extended

A. phyllostomatus			T. intermedius			S. prae-cursor	Total
FE	ME	TE	FE	ME	TE	TE	
14.9	13.8	21.3	10.6	2.1	11.7	11.7	87.2
6.7	10.0	16.7	10.0	3.3	13.3	10.0	80.0
16.7	13.9	22.2	8.3	0.0	13.3	10.0	80.0
14.3	21.4	25.0	14.3	3.6	14.3	7.1	96.4
0.17 ± 0.43	0.20 ± 0.57	0.37 ± 0.82	0.12 + 0.36	0.02 ± 0.15	0.14 ± 0.43	0.30 ± 1.00	6.32 ± 6.40
0.40 ± 0.55	0.10 ± 0.40	0.30 ± 0.75	0.10 ± 0.31	0.03 ± 0.18	0.13 ± 0.13	0.23 ± 0.77	4.37 ± 5.14
0.17 ± 0.38	0.17 ± 0.45	0.33 ± 0.72	0.08 ± 0.28	0.00 ± 0.00	0.08 ± 0.28	0.36 ± 0.90	4.00 ± 4.54
0.14 ± 0.36	0.36 ± 0.73	0.50 ± 1.00	0.18 ± 0.48	0.04 ± 0.19	0.21 ± 0.63	0.29 ± 1.33	11.39 ± 6.92
1.14 ± 0.36	1.46 ± 0.52	1.75 ± 0.85	1.10 ± 0.32	1.00 ± 0.00	1.18 ± 0.60	2.55 ± 1.75	7.24 ± 6.34
1.50 ± 0.58	1.50 ± 0.71	1.80 ± 0.84	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	2.33 ± 1.16	5.46 ± 5.21
1.00 ± 0.00	1.20 ± 0.45	1.50 ± 0.76	1.00 ± 0.00	0.00 ± 0.00	0.76 ± 0.76	0.98 ± 0.98	4.57 ± 4.57
0.00 ± 0.00	0.52 ± 0.52	1.00 ± 1.00	0.50 ± 0.50	0.00 ± 0.00	1.00 ± 1.00	4.24 ± 4.24	6.67 ± 6.67

ferences in prevalence occurred among any host group of adults.

Ectoparasite spatial distributions are affected by differences among age–sex groups. Ectoparasites of *A. jamaicensis* (x^2 = 6.48, df = 4, $P > 0.05$) and *M. redmani* (x^2 = 1.15, df = 1, $P > 0.05$) each exhibited a random spatial distribution of among individuals, but ectoparasites of *S. rufum* (x^2 = 6.84, df = 1, $P < 0.01$) had a nonrandom distribution in which individuals were hyperdispersed (CD = 6.84).

Seasonal and Interspecific Comparisons. Only 2 species of ectoparasites (*P. iheringi* and *T. intermedius*) occurred on all 3 common bat species. Seasonal and interspecific host comparison of infestation by *P. iheringi*, *T. intermedius*, and all ectoparasites combined, yielded the same results based upon ANOVA. Consistent host-specific differences in ectoparasite infestation exist regardless of season (Table 7). Nonetheless, a posteriori contrasts revealed differences in the response of the ectoparasites to host species. For *T. intermedius*, prevalence levels were the same on *S. rufum* and *A. jamaicensis* (q = 2.56; df = 2, 206; $P > 0.05$), but levels on each of these bat species were less than those on *M. redmani* (*S. rufum*: q = 7.91; df = 2, 206; $P < 0.001$, *A. jamaicensis*: q = 9.70, df = 2, 206; $P > 0.001$). Results of a posteriori comparisons of prevalence by *P. iheringi* or all ectoparasites combined were the same: prevalence levels on *S. rufum* and *M. redmani* were indistinguishable (*P. iheringi*: q = 1.68, df = 2, 206; $P > 0.05$; for all ectoparasites combined: q = 0.12, df = 2, 206; $P > 0.05$) and prevalence on each of them differed from that on *A. jamaicensis* (*S. rufum*: q = 5.76; df = 2, 206; $P < 0.01$; *M. redmani*: q = 9.74, df = 2, 206; $P < 0.001$).

Community Comparisons. Samples were sufficiently large to evaluate if differences in the ectoparasite community are evidenced by age–sex categories of *A. jamaicensis*. Differences among the 3 age–sex groups (adult males, adult females,

and juveniles) were significant (G test, G = 16.64, df = 8, $P < 0.03$). Although the less powerful a posteriori comparisons failed to detect a significant difference between any age–sex groups, the difference between adult females and juveniles approached significance (G test, G = 15.42, df = 8, $P < 0.052$) and most likely contributed to intergroup variation. Moreover, differential incidence of *T. intermedius* among these groups (G test, G = 17.30, df = 8, $P < 0.05$) was a significant contribution to the community-wide effect.

Other Host Taxa. Two other bat species were captured during this study. In both cases, the sample size of hosts was too low for any type of statistical comparisons. Six specimens of *Erophylla sezekorni* (Gundlach) were captured, 4 of which were infested with 2 types of ectoparasites. Individual bats harbored from 1 to 23 *P. iheringi* (incidence = 10.25), all of which were female. Three bats were infested with a tick, *Ornithodoros* sp. One host was heavily parasitized with 41 ticks, most occurring on the dorsal pelage. The other 2 individuals harbored 2 or 3 ticks. Three specimens of *Eptesicus fuscus* (Beauvois) were captured, all of which were infested at moderate levels by *P. iheringi* (density per bat = 7.0).

Discussion

Some species of ectoparasites showed specificity for particular host taxa. Streblids (*A. phyllostomatus* and *M. aranea*) occurred only on *A. jamaicensis*, whereas *T. intermedius* occurred on both *A. jamaicensis* and *M. redmani*. Streblids are obligate bat parasites whose distributions are, at least partially, related to ecological factors that are associated with colonial cave-dwelling species; few have been found on bats restricted to forest habitats (Webb and Loomis 1977). The absence of streblids from *S. rufum* is consistent with the idea that it is a solitary, foliage-roosting bat. *N. parnelli*, also a streblid bat fly, was found only on *M. redmani*, and

Table 4. Significance levels from a series of 2-way ANOVAs that evaluated the effects of host age–sex (adult males, adult females, and juveniles) and season of collection (rainy and dry) on the prevalence of *A. jamaicensis* infested with each of 5 different ectoparasites

Factor	df	P. theringi			M. aranea			A. phyllostomatus			T. intermedius			S. praecursor		Total
		FE	ME	IE	FE	ME	TE	FE	ME	TE	FE	ME	TE	TE		
Season	1	0.42	0.32	0.71	0.91	0.29	0.62	0.33	0.17	0.16	0.80	0.30	0.58	0.13		0.50
Age–sex	2	0.002*	0.001*	0.03*	0.55	0.13	0.20	0.75	0.37	0.75	0.42	0.78	0.45	0.99		0.001*
Season by age–sex	2	0.81	0.72	0.92	0.76	0.49	0.70	0.81	0.53	0.89	0.75	0.78	0.89	0.94		0.81

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total. * Indicates significance ($P \le 0.05$).

Table 5. Associations of ectoparasites with *M. redmani* in the tabonuco forest of Puerto Rico (seasons combined)

Parameter Host characteristics[a]	P. theringi			N. parnelli			A. phyllostomatus			T. intermedius			S. praecursor	Total
	FE	ME	IE	FE	ME	TE	FE	ME	TE	FE	ME	TE	TE	
Incidence														
% hosts infested	4.7	4.7	9.5	4.7	9.5	14.3	28.6	9.5	14.3	28.6	42.9	14.3	14.3	57.1
% adult males infested	5.6	5.6	5.6	11.1	16.7	33.3	33.3	16.7	33.3	16.7	22.2	50.0	50.0	61.1
% adult females infested	0.0	0.0	25.0	0.0	0.0	25.0	0.0	0.0	0.0	25.0	25.0	0.0	0.0	50.0
Prevalence (mean ± SD)														
All hosts	0.05 ± 0.22	0.05 ± 0.22	0.10 ± 0.30	0.05 ± 0.22	0.10 ± 0.30	0.19 ± 0.51	0.43 ± 0.81	0.14 ± 0.36	0.14 ± 0.36	0.33 ± 0.58	0.76 ± 1.14	0.29 ± 0.75	0.29 ± 0.75	1.38 ± 1.50
Adult males	0.06 ± 0.24	0.06 ± 0.24	0.06 ± 0.24	0.06 ± 0.24	0.12 ± 0.33	0.18 ± 0.53	0.53 ± 0.87	0.18 ± 0.39	0.18 ± 0.39	0.29 ± 0.47	0.84 ± 1.19	0.35 ± 0.86	0.35 ± 0.86	1.53 ± 1.59
Adult females	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.50	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.50 ± 0.10	0.50 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.75 ± 0.96
Density (mean ± SD)														
All hosts	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.33 ± 0.58	1.50 ± 0.84	1.00 ± 0.00	1.00 ± 0.00	1.17 ± 0.41	1.78 ± 1.09	2.00 ± 1.00	2.00 ± 1.00	2.42 ± 1.17
Adult males	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.50 ± 0.71	1.50 ± 0.84	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.75 ± 1.17	2.00 ± 1.00	2.00 ± 1.00	2.60 ± 1.17
Adult females	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.50 ± 0.71

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total.
[a] Host sample size: 21 (17 adult males, 4 adult females).

Table 6. Significance levels from a series of 1-way ANOVAs that evaluated the effectes of host age–sex (adult males, adult females, and juveniles) on the prevalence of *M. redmani* infested with 4 different ectoparasites

Factor	df	P. theringi				N. parnelli			T. intermedius			S. prae-cursor	Total
		FE	MF	IE	TE	FE	ME	TE	FE	ME	TE	TE	
Host age–sex	2	0.66	0.66	0.30	0.97	0.66	0.40	0.23	0.52	0.47	0.80	0.74	0.67

Ectoparasites were analyzed with respect to 4 groups: FE, adult females; ME, adult males; IE, immatures (larvae and nymphs); and TE, total. * Indicates significance ($P \leq 0.05$).

only during the rainy season. The scarcity of *S. praecursor* was not unusual. It is a rare species, the males of which are currently unknown (Fain et al. 1967, Webb and Loomis 1977). Females have highly specialized features that do not facilitate adaptation to new hosts (Webb and Loomis 1977), thus accounting for its low numbers and limited host range on Puerto Rico. The absence of male *S. praecursor* suggests either that males are free-living or that this species is parthenogenetic.

Prevalence levels of some ectoparasites differed with the age of their frugivorous hosts, with juvenile bats supporting higher numbers than did adults. Although no ectoparasite numbers were affected by variation in season, numbers of *P. theringi* differed with host age. Moreover, this occurred in both *A. jamaicensis* and *S. rufum*. It is possible, though unlikely, that juvenile bats represent inherently superior habitat that can support elevated ectoparasite population levels. However, if no major difference in host quality associated with age is assumed, 2 points of speculation remain. Either juvenile bats are more likely to acquire ectoparasites or adults are more adept at displacing them.

Age-specific host behaviors that might contribute to the differences in levels of ectoparasite infestation are known to occur in bats. Age groups, at least for *S. rufum*, differ in home range size and foraging patterns (Gannon 1991, Gannon and Willig 1994a). By traveling longer distances and occupying larger home ranges than do adults, juveniles may increase the likelihood of encountering additional ectoparasites. If so, other species of ectoparasites might increase as well, but this is not the case for *S. rufum* or for either of the other 2 species, *A. jamaicensis* and *M. redmani*. A more

Table 7. Significance levels from a series of 2-way ANOVAs that evaluated whether prevalence of ectoparasites differed among 3 host taxa (*A. jamaicensis*, *S. rufum*, and *M. redmani*) or between seasons (rainy and dry season)

Factor	df	T. inter-medius	P. iheringi	All ecto-parasites combined
Species	2	0.001*	0.001*	0.001*
Season	1	0.78	0.97	0.60
Species by season	2	0.80	0.86	0.99

* Indicates significance ($P \leq 0.05$).

probable explanation is that adults are more adept at grooming and dislodging mites than are juveniles. *P. iheringi* is wingless and slow-moving; it prefers exposed wing and tail membranes and may have a higher probability of being dislodged while a host is grooming than would other ectoparasites, such as bat flies.

Within the tabonuco forest, *P. iheringi* was the most widespread bat ectoparasite, occurring on all of the phyllostomid bats. Although its incidence on most host species was low, *P. iheringi* was the dominant ectoparasite on *A. jamaicensis* (incidence = 69.1%, density per bat = 4.96) and *S. rufum* (incidence = 34.7%, density per bat = 1.48). Although little is known of its ecology, its widespread distribution and numbers indicate a relatively well-developed means of dispersal.

Spatial distribution of ectoparasites was affected by differences among age–sex groups. These differences are related to behavioral attributes of each species. Ectoparasites of *A. jamaicensis* and *M. redmani* were distributed randomly among individuals, whereas ectoparasites of *S. rufum* were nonrandom and occurred in a hyperdispersed pattern. *A. jamaicensis* and *S. rufum*, although both dominant frugivores, exhibit different diet preferences, foraging patterns, and roosting patterns in the tabonuco forest (Gannon 1991, Gannon and Willig 1994a). These behavioral characteristics may either facilitate the spread of ectoparasites from host to host, as in the case of species that roost colonially (*A. jamaicensis* and *M. redmani*), or serve as a barrier to ectoparasite transmission, as in the case of species that roost in a solitary fashion (*S. rufum*). Others have demonstrated that ectoparasites of bats occupying long-established roosts are known to exhibit higher species richness and larger numbers (Wenzel and Tipton 1966). The apparent lack of fidelity to specific roosting sites by *S. rufum* (Gannon 1991, Gannon and Willig 1994a) may preclude infestation by ectoparasites that spend part of their life cycle off the host in the roost area, such as argasids (for example, *Ornithodoros* sp.) or streblids, which, although widespread among phyllostomids, are not known to parasitize tree-roosting bats.

Incidence and prevalence can be estimated without regard to the taxonomic identity of the parasites. These numbers can be directly compared among host species. Of the 3 species of bats

for which adequate sample sizes exist, *A. jamaicensis* had the highest overall incidence (87.2%) and a much higher overall prevalence (6.32 ectoparasites per bat). *M. redmani* was 2nd, with an incidence of 56.5% and a prevalence of 1.61 ectoparasites per individual, followed by *S. rufum*, of which 34.7% were infested, with a prevalence of 1.48 ectoparasites per bat. Sample size limitations allowed us to examine only the composition of the ectoparasite community of 1 host, *A. jamaicensis*; however, we did detect differences in species abundance distributions attributable to age–sex host groups. The proportional representation of ectoparasite species (species abundance distributions) can be used as a measure of community composition (Pielou 1974). These findings indicate a great deal of complexity in bat–ectoparasite population and community relationships on Puerto Rico that vary at intraspecific, interspecific, and community levels, where coevolution occurs not just between parasite–host populations, but within entire parasite–host communities.

Although low, both incidence and prevalence levels of particular ectoparasite species on these bat hosts are similar to levels observed for other bat species (Marshall 1982). Host behavior and ecology must have a substantial impact on regulating the ectoparasite communities, but without more detailed information on host attributes, it is not possible to identify ecological factors affecting the complexity we observe in ectoparasite ecology.

Even though extensive taxonomic and morphological works on ectoparasites for many species of bats exist, the exact nature of most host–parasite relationships remains unexplored. Nonetheless, bats often have large geographic ranges, occupy a diversity of habitats, employ a number of foraging strategies, and exhibit a variety of roosting behaviors. They have the potential to serve as models for comparative study in the interaction of ectoparasites and their hosts at both the population and community level. The vast majority of ectoparasite work is still qualitative, based on surveys stressing host–parasite occurrences and interactions. More field research needs to develop a wider range of experiments and techniques that can obtain detailed quantitative information on parasite community ecology that examine multiple use of host populations by different species of parasites.

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