Ectoparasite presence, density, and unit load in relation to tent-roosting behavior of neotropical bats

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ABSTRACT

Behavioral defenses have evolved in response to the negative effects caused by ectoparasitism. Within neotropical bats, roosting behaviors have been studied as a possible reaction to the presence of parasitic bat flies and mites. Tent-making, the process of actively constructing protective roosts in foliage, was studied in order to assess its specific impact on ectoparasitism. Bats that exclusively utilized tents were predicted to suffer a lower level of ectoparasitism as their roosting behavior can disrupt ectoparasite lifecycles. I captured different bat species, categorized as either tent-roosting or non-tent-roosting, at several sites in Costa Rica, including Monteverde, San Luis and Peñas Blancas. All ectoparasites were collected with forceps and ultimately used to calculate presence, density, and unit load. After analysis, the bat species grouped as tent-makers, *Artibeus toltecus* and *Platyrrhinus helleri*, contained significantly lower levels of ectoparasite presence, density, and load in comparison with the species of bats that do not exclusively use tent roosts. These results, though suggestive, are derived from a relatively small sample of tent-making bats and can be strengthened by further replication on a larger scale.

RESUMEN

Defensas en el comportamiento han evolucionado en respuesta a efectos negativos causados por ectoparasitismo. Entre los murciélagos neotropicales, comportamiento de refugios han sido estudiados como una reacción posible a la presencia de moscas parasíticas y ácaros. Estudié el comportamiento de construcción de tiendas, proceso donde los murciélagos activamente elaboran refugios protegidos en el follaje, para determinar su impacto específico en ectoparásitos. Predije que los murciélagos que utilizan tiendas exclusivamente, tuvieran un nivel mas bajo de ectoparasitismo ya que su comportamiento de refugio puede rompar con los ciclos de vida de los ectoparásitos. Capturé diferentes especies de murciélagos en Costa Rica, incluyendo Monteverde, San Luis y Peñas Blancas. Los clasifiqué como especies que se refugian en tiendas y los que no. Todos los ectoparásitos fueron colectados con un forceps y luego usados para calcular la presencia, densidad y la unidad de carga. Las especies de murciélagos agrupados como aquellos hacen tiendas, *Artibeus toltecus* and *Platyrrhinus helleri*, contuvieron niveles de ectoparásitos significativamente mas bajos de presencia, densidad y carga, comparados con las especies de murciélagos que no se refugian en tiendas. Estes resultos, aunque sugerente, son derivados por una muestra de murciélagos que se refugian que es relativamente pequena y serían reforzado por replicación en una escala más grande.

INTRODUCTION

Many species of neotropical bats coexist with ectoparasites, ranging from host-specific streblid bat flies to mites (1, 2). The presence of these ectoparasites can lead to a reduction in the health or reproductive success of bats carrying a high parasitic load (3, 4). Streblids, in particular, have been identified as potentially significant in spreading and maintaining disease-causing organisms among bats, and host defenses have evolved over time in response to these potential decreases in fitness (2, 5). Many potential hosts employ behavioral strategies by moving from geographical areas of high to low ectoparasitism, reducing associated costs through habitat selection (6). This also takes place on an evolutionary scale, where species adapt to habitats and behaviors that provide the fitness enhancements linked to lower ectoparasite abundances (2). Elk grooming patterns in Canada, for example, have been observed to reflect an internal clock that is selected for to optimize the benefits of tick removal when the threat of infestation is at its highest (7).

Several studies have suggested that roosting behaviors in neotropical bats can significantly impact levels of ectoparasitism (2, 8, 9, 10). One specific roosting behavior of bats, tent-making, involves manipulation of the environment by cutting leaves in key places to form protective refugia known as "tents" (1, 11). While some species can passively roost in foliage, the active process of altering leaves is a unique characteristic of tent-makers/tent-roosters (1). All 19 known species of tent-roosting bats are found in the tropics, 15 of which are located in the New World and all belong to the leaf-nosed family Phyllostomidae (12).

Bat flies belonging to the families Streblidae and Nycteribiidae and mites belonging to the order Acarina are common ectoparasites of bats in the neotropics (2, 9, 13, 14, 15). Bats take refuge in various habitats (such as caves, tree hollows, foliage, and human constructions) during the day, where the female imago bat fly leaves its host to deposit a single larva, already at the third-instar, on the roosting substrate (9, 13, 14). The larva pupates immediately after being deposited and the newly emerged adult begins to search for a host bat (2, 9). Deposition of pupae directly on a host is unusual as they can be easily removed by bat grooming at that stage (14, 16). While mites require continuous contact with their hosts, the non-parasitic developmental stages of the bat flies are reliant on roosting habitat (14). Based on this, it is thought that bat flies are better suited to bats that roost in more stable locations for longer periods of time, such as caves or various other cavities (8, 10).

Bats that roost in foliage more frequently change their roosting sites, potentially acting as a defense by limiting the ectoparasites that are able to establish (1). Leaf roosts also support fewer bats in close proximity and several studies have tested that larger colonies of bats support higher densities and species richness of parasites (2, 8, 9, 10). One tent-making bat, *Artibeus watsoni*, supports colony sizes of around only 2-14 individuals, while *Carolia brevicauda*, in comparison, can live in caves and cavities with colonies reaching up to 1,000 conspecifics (17).

While relationships between roosting sites and ectoparasites of bats have been studied, less is known about the specific impact of the active roosting behaviors unique to tent-making species (1, 2, 17, 18, 19, 20). Earlier studies have shown that foliage-roosters suffer less ectoparasites than their cave and cavity dwelling counterparts, so one would expect tent-makers to similarly show lower levels of parasitism (2, 8, 9, 10). However, Kunz (2005) suggested that tents might not play a significant role in controlling ectoparasites. Kunz noted that some species of tent-roosters may occupy the same tent continuously for several weeks, leaving their roosts more susceptible to ectoparasites compared to general foliage-roosters that more frequently change locations (21). This suggests that the energy devoted to constructing tents is providing different benefits that would outweigh potentially lower defenses against parasitism. This may be explained as tents are thought to attract female bats for mating purposes, provide better protection from predators and the elements, and more efficiently retain metabolic heat (21, 22)

How, then, does the incidence of ectoparasitism specifically associated with neotropical tent-roosting bats compare to non-tent-roosting species? In order to investigate this question, I sampled ectoparasites on individuals from the species *Artibeus toltecus* and *Platyrrhinus helleri*, two known tent-makers found in the lowlands and mid-elevations of Costa Rica (1, 20). Due to the evidence that foliage roosts in general support fewer ectoparasites, I predicted that *A. toltecus* and *P.*

helleri, grouped together as tent-makers, would have lower levels of ectoparasitism, across several different metrics, compared non-tent-roosting species found in the same regions.

MATERIALS AND METHODS

I set mist-nets for bats between the dates of 4 November 2007 and 29 November 2007. My netting locations included the garden near the Monteverde Biological Station (1500 m), La Finca Bella in San Luis (1100 m), the University of Georgia Station in San Luis (1100 m), and Eladio's Refuge in Peñas Blancas (800 m). Between one and four mist-nets were used at each site, ranging from six to twelve meters in length. In general, the nets were set around dusk and kept open for several hours into the night, ultimately totaling 1659.75 mist-netting hours over the duration of the study. Mist-netting hours reflect the total length of net (in meters) multiplied by the time kept open (3, 17, 18, 19, 23).

At each site, I checked the mist-nets at roughly 30-minute intervals over the period of 3-4 hours in order to assure that the bats did not damage themselves or the nets after being tangled for too long. Once a bat was captured in the net, I untangled the individual using gloves. After being liberated from the net, the bats were placed in a clean cloth bag for further processing. Each individual was weighed and forearm length was measured (in millimeters) with a hand caliper or ruler. I determined gender visually and categorized each specimen as either a juvenile or adult. I assessed age categories by examining the joints of the fourth and fifth fingers. Adult bats show a distinct line between the bones, while juveniles do not, as their cartilage has not yet solidified (18). I identified all bats to the species level using a dichotomous key (15). Finally, I cut off a small patch of fur from the shoulder of each bat before release in order to recognize any future recaptures.

In addition to mist-netting at night, I searched for tents during the day in Peñas Blancas. This was accomplished by walking along a trail and visually scanning for altered leaves that match the characteristics of tents. I examined any observed tents to determine if they were occupied, ultimately catching two bats of the species *Artibeus toltecus* with a butterfly net. One additional bat of the species *Glossophaga commissarisi* was found freshly deceased during the early morning at the Hummingbird Gallery in Monteverde. This bat and those found in tents were immediately processed in the same manner as all of the other specimens in the study to insure consistency.

Bat Species	**Sample Size (n)**
Total Bats Caught	**76**
Total Species Caught	**16**
Recaptures	**2**
Non-Tent-Roosting Bats Caught	**64**
Carollia brevicauda	18
Myotis nigricans	1
Sturnira ludovici	10
Anoura geoffroyi	8
Artibeus lituratus	7
Artibeus jamaicensis	4
Glossophaga commissarisi	1
Carollia perspicillata	5
Myotis albescens	1
Pteronotus parnelli	1
Platyrrhinus vittatus	4
Hylonycteris underwoodi	1
Desmodus rotundus	1
Sturnira mordax	2
Tent-Roosting Bats Caught	**10**
Artibeus toltecus	9
Platyrrhinus helleri	1

Table 1: Total species composition and sample size of bats captured in Monteverde, San Luis, and Peñas Blancas, separated into two groups based on roosting behavior.

I extracted ectoparasites from each bat with a pair of fine tweezers. While processing, I visually examined all of the bats, approximately for the same length of time across samples, for any obvious parasites crawling on or through fur. More cryptic ectoparasites were revealed by carefully blowing on the bat to part patches of hair and expose skin. I placed all ectoparasites from each individual bat into a vial with ethyl alcohol. I later counted and keyed all ectoparasites; those from the family Streblidae were identified to the genus level, while mites were keyed to order (24). Using a stereoscope at 40x magnification, I measured the area of all ectoparasites with an eyepiece grid, later converting to millimeters (18).

To compare ectoparasite presence between tent-makers and non-tent-makers, I counted the number of bats of each group with parasites present and per-

Ectoparasite	**Number of Parasites**	**Host Bat Species**
Family: Streblidae	**80**	
Genus: *Paratrichobius*	1	*Sturnira ludovici*
	3	*Artibeus lituratus*
	1	*Carollia brevicauda*
	3	*Platyrrhinus vittatus*
	1	*Artibeus toltecus*
Genus: *Trichobius*	12	*Carollia brevicauda*
	10	*Pteronotus parnelli*
	1	*Desmodus rotundus*
	2	*Platyrrhinus vittatus*
	1	*Sturnira ludovici*
Genus: *Anastrebla*	3	*Anoura geoffroyi*
	1	*Glossophaga commissarisi*
	3	*Hylonycteris underwoodi*
	2	*Desmodus rotundus*
Genus: *Paradyschiria*	20	*Anoura geoffroyi*
Genus: *Masoptera*	1	*Anoura geoffroyi*
Genus: *Strebla*	1	*Anoura geoffroyi*
Genus: *Megistopoda*	7	*Sturnira ludovici*
	1	*Artibeus lituratus*
	1	*Artibeus jamaicensis*
	2	*Carollia brevicauda*
	2	*Sturnira mordax*
Genus: *Joblingia*	1	*Myotis albescens*
Order: Acarina	**31**	
Mites	1	*Anoura geoffroyi*
	2	*Artibeus lituratus*
	14	*Platyrrhinus vittatus*
	3	*Artibeus jamaicensis*
	1	*Artibeus toltecus*
	7	*Carollia perspicillata*
	3	*Sturnira mordax*

Table 2: Ectoparasite identification and association with host bat species. A total 80 streblids were found, spanning eight genera. In addition, 31 mites were collected of the order Acarina.

formed a Chi-Squared test to assess statistical differences between groups. Next, I compared mean ectoparasite density between tent-making and non-tent-making bats. Density was calculated by counting the number of parasites found on each bat (categorized as either a tent or non-tent-rooster) and dividing by forearm length (in millimeters) in order to standardize size (2). I used forearm measurements instead of weight, as it is overall a more stable indicator of bat size (25). This index was analyzed with a non-parametric Mann-Whitney U test. In order to further examine density levels within roosting groups, I used a Kruskal-Wallis test to analyze density differences with non-tent-makers and a Mann-Whitney U test with tent-makers.

Finally, I compared ectoparasite load between tent-making and non-tent-making bats, with a standard index that factors the number of parasites found and their respective size (calculated by body area). In order to standardize the effects of different parasites across hosts, I calculated a "unit parasite" by averaging the total area of all ectoparasites sampled (18). The total area of all parasites found on each bat was then, in turn, divided by the unit parasite. As with the density index, this parasite load value was divided by the forearm length of each bat (in millimeters) to standardize body size. I then compared the mean parasite load values between tent-making and non-tent-making groups using a Mann-Whitney U test. Once again, I tested within groups, using a Kruskal-Wallis test to assess differences in parasite load with non-tent-roosting bats and a Mann-Whitney U test with tent-roosters.

I excluded all bat recaptures from data analysis. The rest of the bats were all included in the comparison of ectoparasite presence between roosting groups. However, some of the bats were never fully processed and lacking certain measurements (such as forearm length or number of ectoparasites present). These samples were excluded from the ectoparasite density and load calculations, which required the missing information (10 tent-roosters and 58 non-tent-roosters for density analysis and 10 tent-makers and 57 non-tent-makers for load).

RESULTS

A total of 76 individual bats were captured, and of these, there were 16 different species, which were categorized as either tent-roosters or non-tent-roosters. After excluding two recaptures, the tent-making group was comprised of 10 bats and the non-tent-makers totaled 64 individuals (Table 1). Of the 111 ectoparasites found, I identified a total of 80 individuals to eight genera within the family Streblidae

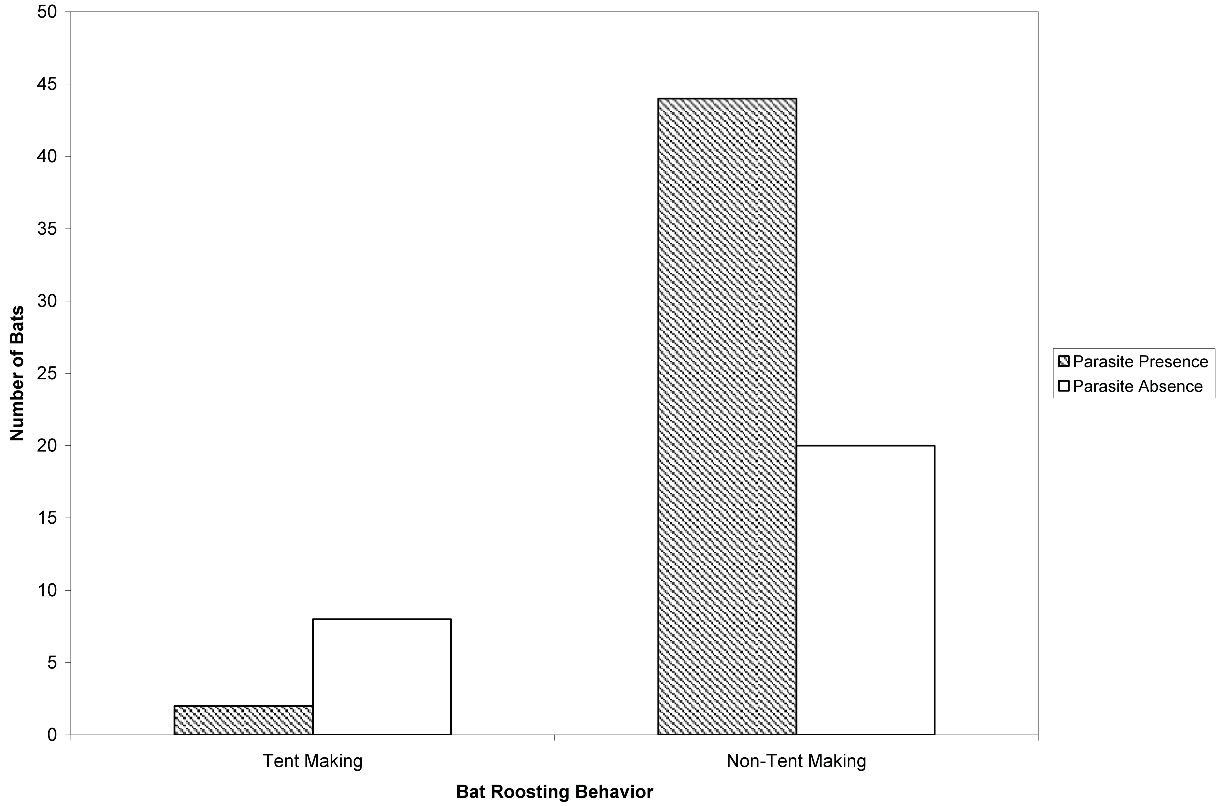

Figure 1: A comparison of ectoparasite presence between tent-making and non-tent-making bats ($\chi^2 = 8.738$, df = 1, $p < 0.005$). The cross-hatched bars note parasite presence and the white bars note parasite absence.

(Table 2). I keyed the additional 31 ectoparasites to the order Acarina. Of the eight Streblidae genera, only one genus, *Paratrichobius*, was found on tent-roosting bats. In addition, only one mite was found on a single tent-making bat. I found mites and all of the eight Streblidae genera on non-tent-roosting bats.

Tent-roosters showed a lower presence of ectoparasites than non-tent-makers ($\chi^2 = 8.74$, df = 1, $p < 0.005$). Of the 10 tent-making bats, two individuals had ectoparasites, while 44 of the 64 non-tent-roosters had ectoparasites (Figure 1). In addition, tent-making bats showed a significantly lower mean level of ectoparasite density as compared to non-tent-makers (Mann-Whitney U test: $U_{58,10} = 2.78$, $p = 0.005$). Using an ectoparasite density index, tent-roosting bats had a mean density of 0.005, while non-tent-roosters showed a mean density of 0.04 (Figure 2). A lower index value indicates a lower ectoparasite density.

Ectoparasite density was also calculated within the two roosting groups (Figure 3). There is a less significant difference found in density levels within non-tent-roosters than in comparison to the tent-roosting group (Kruskal-Wallis test: $\chi^2 = 26.27$, df = 13, $p = 0.02$). Similarly, there is no significant difference in ectoparasite density found within the tent-makers (Mann-Whitney U test: $U_{9,1} = 0.248$, $p = 0.804$). These calculations were performed in order to determine the weight of the density difference found between groups; the level of ectoparasitism is more significantly related to roosting behavior as opposed to simple species differences.

Using an index of mean ectoparasite load, tent-roosting bats also showed significantly lower levels of ectoparasitism in comparison with non-tent-roosters (Mann-Whitney U test: $U_{57,10} = 2.958$, $p = 0.0031$). After calculating a unit parasite of 0.9213, non-tent-making bats had a mean ectoparasite load of 0.041, while tent-makers had a mean load of 0.003 (Figure 4).

The mean unit ectoparasite load was similarly compared within the roosting groups (Figure 5). Non-tent-roosting bats had less of a significant difference within their group as opposed to in comparison to tent-makers. (Kruskal-Wallis test: $\chi^2 = 21.91$, df = 13, $p = 0.06$). There was also no significant difference in mean ectoparasite load within tent-roosting bats (Mann-Whitney U test: $U_{9,1} = 0.25$, $p = 0.8$).

DISCUSSION

Tent-roosting bats showed significantly lower levels of ectoparasitism across all calculations in this

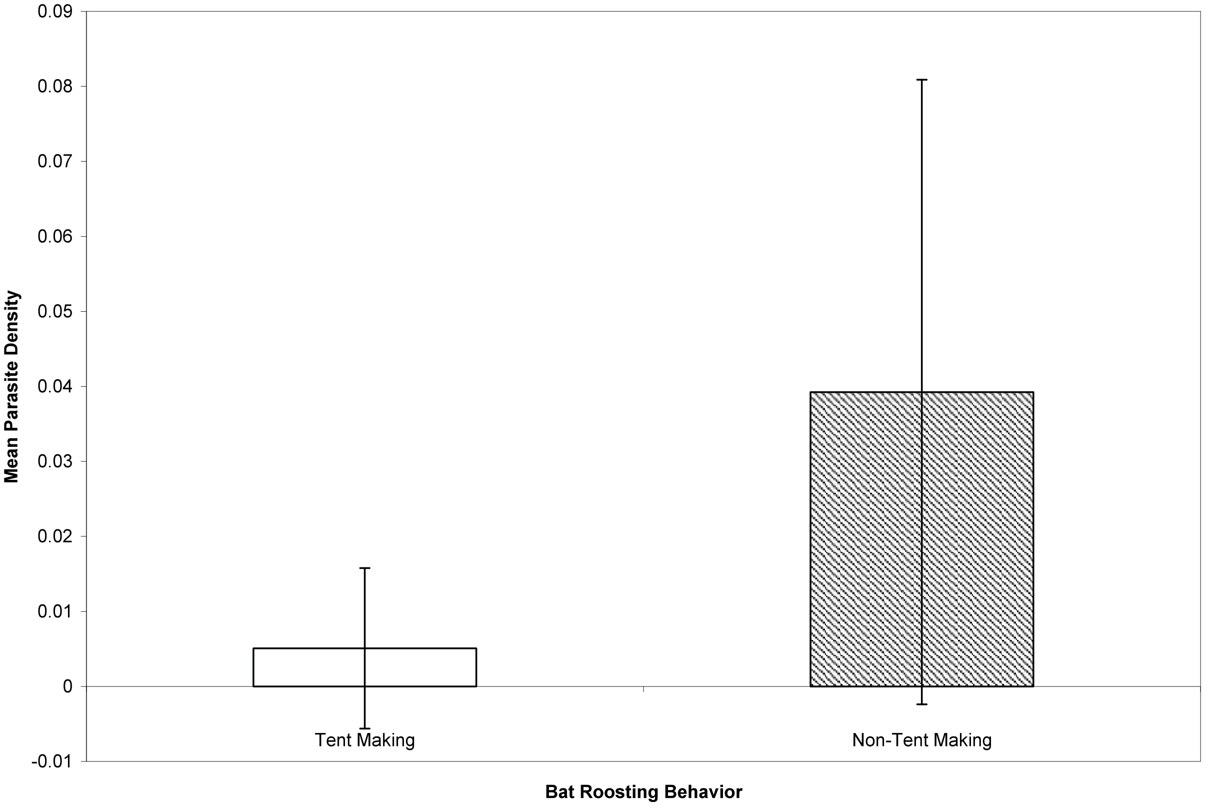

Figure 2: Ectoparasite mean density levels and their standard deviations between tent-making (n=10) and non-tent-making bats (n=58). A lower index value represents a lower ectoparasite density (Mann-Whitney U test: $U_{58,10} = 2.78$, $p = 0.005$).

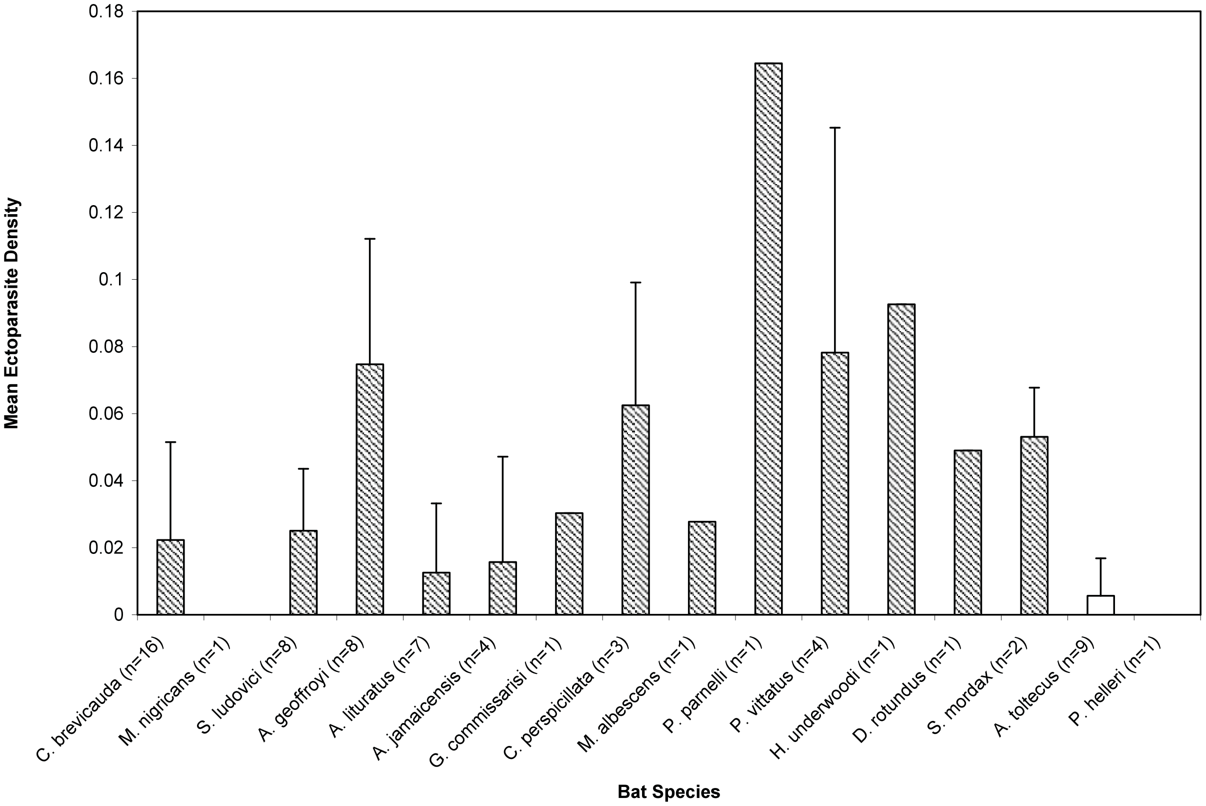

Figure 3: Ectoparasite mean density levels and their standard deviations between all 16 species of bats. The cross-hatched bars represent non-tent-making bats, while the white bars represent tent-making species. This allows for a comparison within roosting behavior groups. (Within Non-Tent-Roosters: Kruskal-Wallis test: $\mathcal{X}^2 = 26.27$, df = 13, $p = 0.02$. Within Tent-Roosters: Mann-Whitney U test: $U_{9,1} = 0.248$, $p = 0.804$).

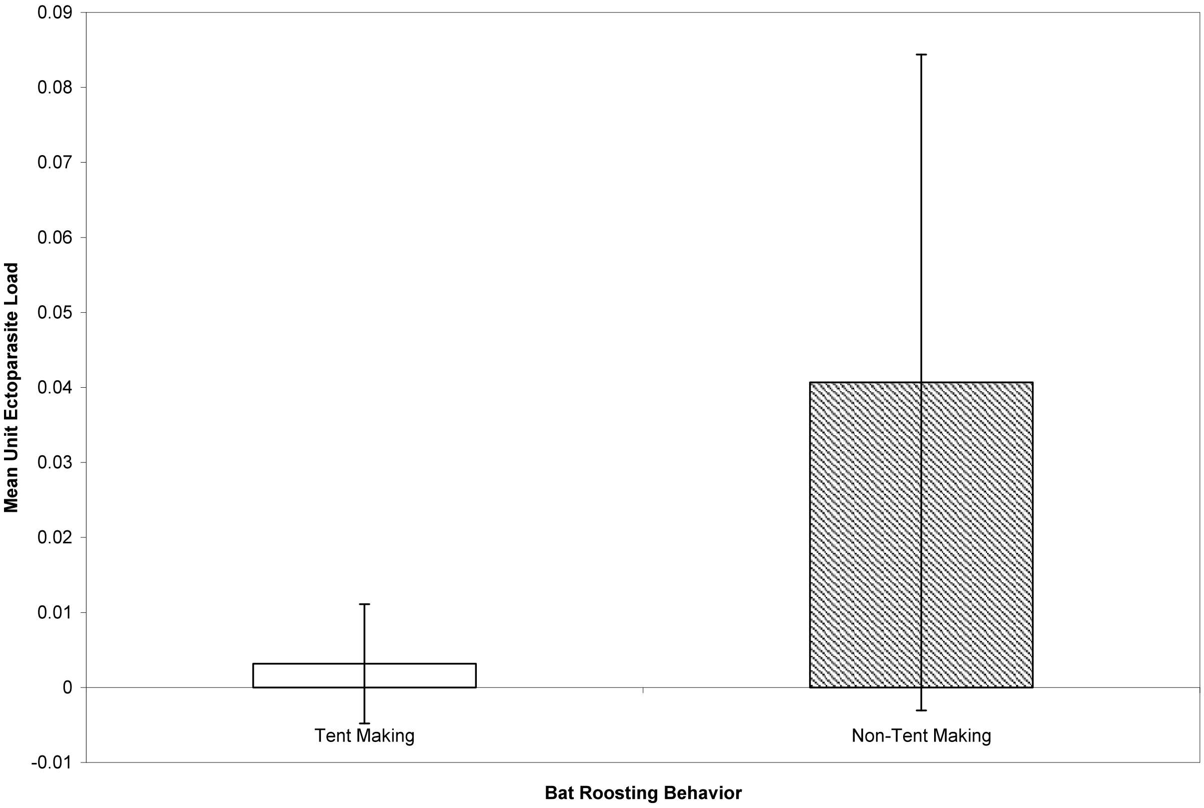

Figure 4: Mean unit ectoparasite load and their standard deviations between tent-making (n=10) and non-tent-making groups (n=57). A lower index value represents a lower parasite load (Mann-Whitney U test: $U_{57,10} = 2.958$, $p = 0.0031$).

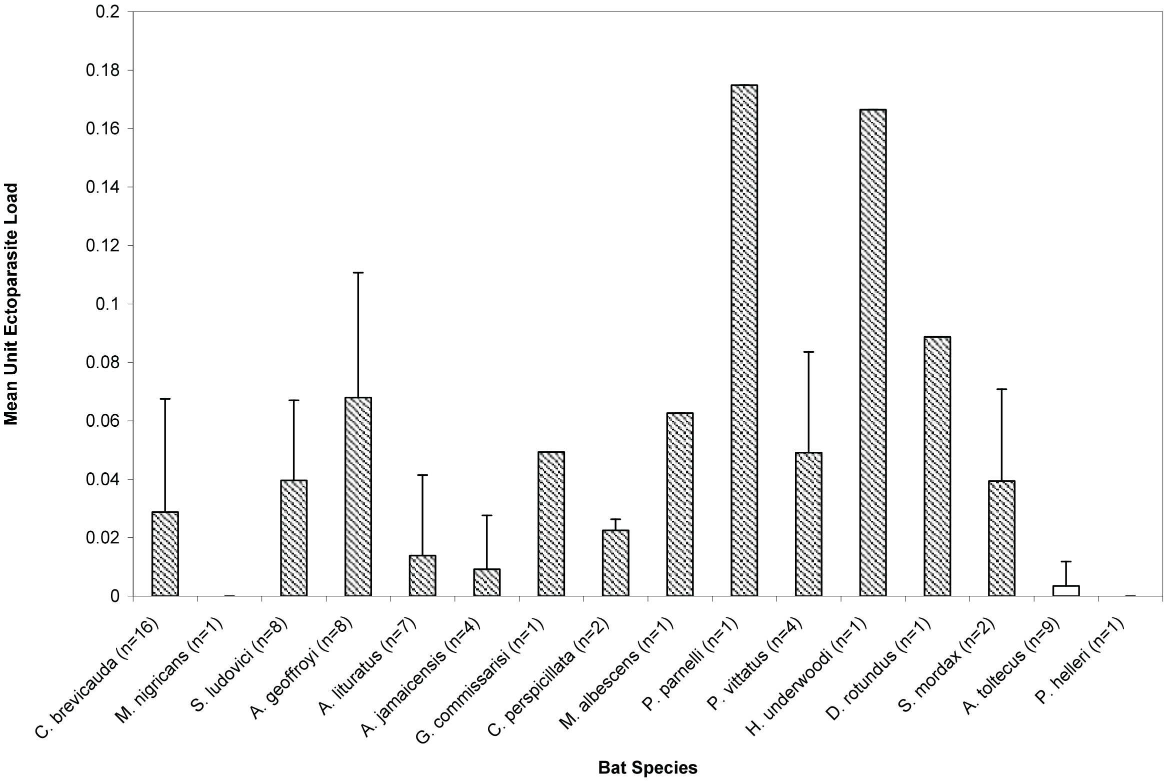

Figure 5: Mean unit ectoparasite load and the standard deviations between all 16 species of bats. The cross-hatched bars represent non-tent-making bats, while the white bars represent tent-making species. This allows for a comparison within roosting behavior groups. (Within Non-Tent-Roosters: Kruskal-Wallis test: $\mathcal{X}^2 = 21.91$, df $= 13$, $p = 0.06$. Within Tent-Roosters: Mann-Whitney U test: $U_{9,1} = 0.25$, $p = 0.8$).

study in comparison to non-tent-roosters. The analysis of presence/absence, density, and unit load was used by Quan (2004) as a metric of evaluating degrees of ectoparasitism and similarly is applied in this study with focus specifically on the tent-making behavior.

First, there were proportionally more non-tent-making bats with ectoparasites compared to tent-makers. Going beyond this, analyzing ectoparasite density provides an additional perspective by also considering the number of parasites found on each bat (18). For example, certain individuals captured over the duration of this study were infested with many parasites, and this index weights these bats more heavily than others that might only have one parasite (2). Tent-making bats had a lower density than non-tent-roosters. I continued to analyze ectoparasites within the two roosting groups and there was no difference between the densities of the two tent-making species. There was a significant difference of ectoparasite density within the 14 species of non-tent-roosting bats, however, but it was less pronounced than in comparison to the tent-roosting group. These results suggest that the differences found between the roosting groups may be due in part to tent-making behavior, instead of just general interspecies differences that do not account for roosting strategy.

The ectoparasite load index provides an even deeper level in which tent-making and non-tent-making bats can be compared. This particular index evaluates the total area of all parasites found on a bat (18). This is important because, in theory, the number of ectoparasites on a host is negatively correlated with parasite size (18). Hosts can only support a certain carrying capacity, and larger ectoparasites have a greater overall negative effect (26). Hypothetically, a particular bat may be able to survive supporting 50 small mites, but only 10 large streblid flies. The bat with 50 mites would then be over inflated in the ectoparasite density index when compared to an individual carrying the 10 large flies, even though the cumulative detrimental effect should be roughly the same. Using this ectoparasite load index, tent-roosting bats once again showed significantly lower levels on average compared to non-tent-roosting species. As with the density index, differences within roosting groups were less significant than between tent and non-tent-making bats. This shows that the roosting behavior has an impact on mean ectoparasite load instead of simply interspecies differences.

The data from this study support the hypothesis that tent-makers, as represented by *A. toltecus* and *P. helleri*, would have a lower incidence of ectoparasitism compared to other non-tent-roosting species. In turn, this upholds those findings that suggested foliage-roosters incurred fewer ectoparasites than cavity and cave dwellers. Both Patterson *et al.* (2007, 2008) and ter Hofstede and Fenton (2005) tested for the impact of roosting behavior on ectoparasitism and found that cavity-roosting species had generally higher densities of both bat flies and mites. Given that tent-makers are a subset of general foliage-roosters, the results from this study agrees with these past findings.

This, however, does not support the hypothesis offered by Kunz (2005), suggesting that tents, rather than aiding in defenses against parasitism, mainly provide benefits associated with mating patterns and protection against predators and harsh environmental conditions. Kunz does state that this may not be the case for all tent-makers, as some tent-roosting species change roosts more frequently than others. With only two species of tent-making bats, this study would benefit from additional research further examining the interspecies differences in ectoparasitism of tent-roosters. *A. toltecus*, for example, has been known to roost in plants belonging to the family Araceae, cutting the leaves basally and near the midrib to cause the structure to fold downwards, while *P. helleri* has been observed constructing conical tents in plants within the subfamily Compositae (1, 20). These differences in roosting behaviors within the tent-makers may result in different ectoparasite relationships.

While frequently switching roosts may help bats defend against ectoparasites, the type of roosting structure may prove to be an even more significant factor (27). A recent study by Dittmar *et al.* (2009) showed that a bat fly species in the genus *Trichobius* in fact deposits its pupae as far away as 20 meters from the bat hosts' roost. This indicates that the streblid parasites may seek out hosts as bats pass by to leave their caves for night foraging. While it might seem critical for the parasites to remain in close proximity to their hosts, Dittmar only found 5 pupae in the bat roosting area of the cave. They suggested that the hot and humid roost itself might actually be an unsuitable environment for the flies to complete their lifecycles. If the streblids cannot develop in the close proximity of a warm roost, this may explain a facet of how tents defend against ectoparasites. While some tent-making bat species do frequently revisit the same roost, all tents provide an environment that better traps heat compared to unmodified foliage (21). Do to the open nature of leaf roosts, bat flies would not be able to pupate away from the roost itself and then easily seek a host passing by as compared to cave exits that funnel large numbers of bats though a single area. Therefore, tents, like all foliage roosts, may help to protect against ectoparasitism simply by being in more open spaces.

The data from this study also suggested that there was less diversity of ectoparasites found on tent-roosters. Only one of the eight identified streblid genera, *Paratrichobius*, was found on tent-making bats. In contrast, all eight Streblidae genera were present on non-tent-making species. These results support past research by Bordes *et al*. (2008) and Patterson *et al*. (2007), who found that bats roosting in more permanent, enclosed structures harbored a higher species richness of ectoparasitic flies. While this may indicate that fewer species of ectoparasites can successfully live with tent-making bats, it is difficult to draw definite conclusions from my data, as my sample size is limited with only one bat fly collected across all tent-roosters. In addition, continued research examining levels of ectoparasitism between flies and mites would be beneficial as their lifecycles may be differently impacted by roosting behaviors in bats.

Further analysis of the ectoparasite metrics, especially for testing within roosting groups, would also greatly benefit from a larger data set. Similarly, collecting more individuals and species of tent-roosting bats would be advantageous. Only *A. toltecus* and *P. helleri* comprise the tent-making group in this study as they are known to exclusively modify leaves as roosting sites in the areas of my sampling (1). Other bats such as *A. jamaicensis* are known to use tents, but they also frequent other types of roosting habitats (12, 28). It would not be possible to know if any particular *A. jamaicensis* caught in a mist-net was using tents or other roosts at the time. I therefore grouped those that did not exclusively make tents into the non-tent-roosting category. Additional research further examining roosting behaviors of bat species would also help to more accurately group bats into tent-makers and non-tent-makers. Another constraint of using the roosting groups is that other factors can influence ectoparasitism, such as colony size, body size, and sex (20, 29). More analysis that can further isolate the impact of the active tent-making behavior on ectoparasite levels would be valuable. Due to the limitations of time and the small sample size in this study, the results, though suggestive, can be strengthened by further research and replication on a larger scale.

CONCLUSION

Ultimately, understanding the relationship between tent-making bats and their ectoparasites can help to provide insight on the lives and health of bats, giving evidence to explain daily behaviors and evolutionary forces. This study suggests that tent-making as a roosting behavior potentially provides defenses against ectoparasitism. With the ability to quickly spread pathogens from one host to another, some blood-fed ectoparasites can have a significant impact on bat populations as disease vectors, and consequently warrant attention in epidemiological investigations (4). The increasing interface between people and wildlife also presents a concern for emerging zoonoses (30). With bats themselves as potential vectors, it is important to better understand how disease can spread amongst bat populations. From a conservation perspective, tent-roosting bats, as habitat specialists, are particularly threatened by the increasing deforestation that is encroaching upon environments across the tropics (31). Tent-makers depend upon the availability of specific plants for roosting habitat, and knowing more about the details of their roosting behavior may help to better preserve bat populations and their ecological roles into the future.

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