PARASITE COMMUNITIES OF TROPICAL FOREST RODENTS: INFLUENCES OF MICROHABITAT STRUCTURE AND SPECIALIZATION

By Ashley M. Winker

Parasitism is the most common life style and has important implications for the ecology and evolution of hosts. Most organisms host multiple species of parasites, and parasite communities are frequently influenced by the degree of host specialization. Parasite communities are also influenced by their habitat – both the host itself and the habitat that the host occupies. Tropical forest rodents are ideal for examining hypotheses relating parasite community composition to host habitat and host specialization. *Proechimys semispinosus* and *Hoplomys gymnurus* are morphologically-similar echimyid rodents; however, *P. semispinosus* is more generalized, occupying a wider range of habitats. I predicted that *P. semispinosus* hosts a broader range of parasite species that are less host-specific than does *H. gymnurus* and that parasite communities of *P. semispinosus* are related to microhabitat structure, host density, and season.

During two dry and wet seasons, individuals of the two rodent species were trapped along streams in central Panama to compare their parasites, and *P. semispinosus* was sampled on six plots of varying microhabitat structure in contiguous lowland forest to compare parasite loads to microhabitat structure. Such structure was quantified by measuring thirteen microhabitat variables, and dimensions were reduced to a smaller subset using factor analysis to define overall structure. Ectoparasites were collected from each individual, and blood smears were obtained to screen for filarial worms and trypanosomes.

In support of my prediction, the habitat generalist (*P. semispinosus*) hosted more individual fleas, mites, and microfilaria; contrary to my prediction, the habitat specialist (*H. gymnurus*) hosted more individual lice, ticks, and species of ticks. Also contrary to my prediction, none of the tick species found on *P. semispinosus* were host-specific. The sole flea species I collected was *Polygenis klagesi*, which may be host-specific largely to *P. semispinosus*, only rarely infesting other mammals. Fleas were associated with forest openness with respect to trees and were more abundant during the rainy season. Lice were more abundant during the dry season, and ticks were more abundant on male hosts. Male-biased parasitism is common in mammals and presumably results from greater mobility and lower immune response than females. This descriptive study is the first to investigate the relationships between parasite communities and microhabitat, host density, and season in a lowland Neotropical forest. It lays the foundation for an experimental approach to study the interactions of these hosts and their parasites.

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By

Ashley M. Winker

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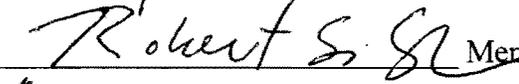
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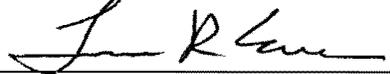COMMITTEE APPROVAL

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_____ Member

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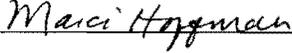
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Introduction

Parasitism is the most common lifestyle, having evolved multiple times in all major biotic taxa (Price 1980). Because the parasite benefits from and the host is harmed by the relationship, coevolutionary arms races have raged since the first organism adopted a parasitic lifestyle. The parasite benefits from the relationship and is under selection pressures to maintain the relationship. Therefore, selection pressures are placed on parasites to maintain and enhance the relationship, increase the odds of transmission, and become silent in the host. By contrast, the host is harmed and is under selection pressures to adopt defensive measures against their parasites in an attempt to dissociate from the relationship. Parasites therefore apply unique ecological and evolutionary pressures on their hosts and vice versa.

Parasites can alter host behavior, physiology, and ecology and are frequently pathogenic, particularly when hosts unwittingly intrude into the life cycle of a parasite (Price 1980). This pathogenicity is of particular importance to humans and the organisms on which humans depend. Consequently, the understanding of parasites and their ecology is crucial to combating disease-causing parasites. Unfortunately, our knowledge of parasites is, in many cases, limited. This deficiency of knowledge is particularly problematic in biotically-rich ecosystems such as tropical forests. Not surprisingly, it is in such ecosystems that humans have unwittingly intruded most frequently into host-parasite relationships that cause the greatest human morbidity and mortality, including malaria, leishmaniasis, and Chagas disease.

The goal of this thesis is to examine parasite-host relationships in a tropical forest in central Panama. I focus on two species of echimyid rodents (Neotropical spiny rats), *Proechimys semispinosus* (the Central American spiny rat) and *Hoplomys gymnurus* (the armored rat), both of which are known to serve as hosts to a wide variety of parasites, including ectoparasitic arthropods and endoparasitic blood parasites (Mendez 1993). Both species of rodents also have coincident geographical distributions. Various species of echimyids serve as reservoirs for such anthropogenically-important parasites as *Leishmania* sp., the etiologic agents of various forms of leishmaniasis, and *Trypanasoma cruzi*, the etiologic agent of Chagas disease (Mendez 1993).

The first chapter focuses on the parasites of *P. semispinosus*. This rat is a habitat generalist and can maintain persistent populations in lowland forests that range from dry to pluvial and from very young and newly-regenerating to old-growth (Adler 2000, Lambert and Adler 2000). In that chapter, I examine the influences of season, rat abundance, rat gender, and microhabitat associations of the rats on parasite burdens. I predict that parasitic burdens increase with increasing spiny rat density, vary according to host gender and season, and that such burdens are influenced by microhabitat use by *P. semispinosus*.

The second chapter compares the parasitic burdens of *P. semispinosus* with those of *H. gymnurus*. In contrast to *P. semispinosus*, *H. gymnurus* is a habitat specialist and is confined to cooler and wetter situations, although both species may occur syntopically in appropriate microhabitats (Tomblin and Adler 1998). Thus, *P. semispinosus* typically is distributed throughout a single tract of forest, while *H. gymnurus* is often restricted to

only a subset of the same tract. I predict that the more generalized *P. semispinosus* has greater parasitic burdens that are characterized by more generalized and less host-specific parasites.

Chapter I

Parasite Communities of Tropical Forest Rodents: Influences of Microhabitat Structure, Host Density, Host Gender, and Season

Abstract

The habitat of a parasite includes both the body of its host and the habitat that the host occupies. Parasite community structure therefore depends on a relationship between host body and host habitat. Tropical forest rodents are ideal for examining hypotheses of parasites and habitat structure because they are often abundant and occupy a wide range of habitats. *Proechimys semispinosus* is a common forest rodent in central Panama and is distributed widely throughout lowland forests but is more commonly associated with young and disturbed forest. I predicted that parasite loads would vary with microhabitat structure, host density, and season. During two dry and wet seasons, *P. semispinosus* was trapped in varying microhabitats within contiguous lowland forest, and its parasite communities were catalogued. Microhabitat structure was quantified by measuring 13 microhabitat variables and dimensions were reduced to a smaller subset using factor analysis to define overall structure. The sole species of flea found, *Polygenis klagesi*, may be host-specific to *P. semispinosus*. Fleas were associated with forest openness with respect to trees and were more abundant during the rainy season. Lice were more abundant during the dry season, and ticks were more abundant on male hosts. Male-biased parasitism is common in mammals and presumably results from greater mobility and lower immune response than females. This descriptive study is the first to

investigate the relationships between parasite communities and microhabitat, host density, and season in a lowland Neotropical forest.

Introduction

The host of a parasite can be considered a biological island, providing the parasite with the resources it needs – food, shelter, and opportunities for reproduction (Mize et al. 2011). Parasite distributions are influenced by host sex, age, and density; however, a parasite's habitat is not only its host but also the environment that the host occupies (Krasnov et al. 1997, Krasnov et al. 2006). A complex host-habitat relationship is therefore important in parasite community structure (Krasnov et al. 1997), and many studies have examined this relationship (e.g., Krasnov et al. 1997, Krasnov et al. 2006, Mize et al. 2011).

When studying a parasite's habitat, study sites are classified as specific habitat types based on variables such as soil type, vegetation structure, and humidity. For example, Krasnov et al. (1997) studied parasites found in six habitat types in the Negev Desert. Flea species composition and abundance did indeed differ spatially across those habitats and temporally across seasons. Another factor determining how habitat affects parasite communities is the quantifiable aspects of microhabitat structure (i.e. number of trees and lianas) at various sampling locations. Microhabitat structure influences populations and communities of tropical rodents (Lambert and Adler 2000, Lambert et al. 2006, Tomblin and Adler 1998) and therefore may influence parasite communities.

The ectoparasites examined in this study have different levels of host interaction (Mize et al. 2011). Ticks have the least host interaction, attaching for feeding before detaching and returning to the environment. Fleas and mites have moderate levels of host interaction, attaching for repeated feedings, then returning to the host burrow or nest to reproduce and develop. Lice are permanent on the host, reproducing and feeding while only being transferred to other hosts via direct contact. These different life histories result in each ectoparasite being exposed to different environmental characteristics.

Central American spiny rats (*Proechimys semispinosus*) serve as hosts for a wide variety of parasites (e.g., ectoparasitic arthropods and endoparasitic blood parasites, Mendez 1993) and maintain populations in lowland forests ranging from dry to pluvial and from young and newly-regenerating to old-growth (Adler 2000, Lambert and Adler 2000). This study focuses on the relationships between the ectoparasites and blood parasites of *P. semispinosus* and microhabitat structure and the influences of seasonality, host abundance, and host gender on the parasites. I predict that parasite loads on *P. semispinosus* will vary with microhabitat structure, season, host density, and host gender.

Methods

Study area. The study was conducted in Soberania National Park along Pipeline Road near Gamboa, Panama (Figure 1-2). I sampled *P. semispinosus* on six 1.8-ha plots adjacent to Pipeline Road. Plots were established at three sites along a 2-km stretch of Pipeline Road, starting approximately 10 m from the road, with one plot on each side of the road. These study sites were located within second-growth tropical moist forest that

has been regenerating for approximately 70 years. The close proximity of the study sites allowed for similar climatic conditions. The climate of this study area is highly seasonal with respect to rainfall; the eight-month rainy season generally occurs from late April or early May through December and is followed by a four-month dry season. Mean annual precipitation is approximately 2188 mm with less than 10% falling during the dry season (Windsor 1990).

Sampling procedures. I live-trapped *P. semispinosus* at each of the six plots during two wet seasons and two dry seasons from January 2011 to July 2012. Each plot consisted of three rows spaced 50 m apart, with each row having ten sampling stations spaced 20 m apart. Each sampling station had one Tomahawk live-trap (40.6 by 12.7 by 12.7 cm) baited with cut ripe plantain. Once during each season, traps were set for 10 consecutive nights and checked every morning. During January 2012, traps were heavily disturbed by coatis and set for a maximum of six consecutive nights (Table 1-1).

All captured *P. semispinosus* were ear-tagged with a unique identification number, weighed, and placed into sex and age classes. Age was determined by stage of pelage development (juvenile, sub-adult, or adult, Adler 1994). An ear snip was taken and a blood smear made from the cut site to screen for blood parasites. I combed each spiny rat twice with a fine-toothed metal comb to obtain relative counts of lice and mites, and I used a forceps to remove all ticks and fleas. All ectoparasites were preserved in 70% ethanol. Rat individuals were released at their respective sampling station immediately after data collection, and recaptured individuals in the same sampling season were released without further data collection.

Microhabitat measurements. During June 2011, I measured 13 variables at each sampling station to quantify microhabitat structure (Table 1-2). These variables have been used previously to determine microhabitat associations of *P. semispinosus* (Lambert and Adler 2000). I estimated variables 2 through 7 within a 15-m^2 circle centered on the sampling station. Variables 9 through 12 were based on the point-quarter method, whereby I used the first tree ≥10 cm in diameter at breast height (dbh) encountered in each of the four cardinal compass directions.

Parasite identification. I fixed blood smears in 100% methanol for 30 seconds and stained them in a 10% Giemsa stain for 30 minutes. I scanned the entire blood smear under a 10x objective lens to search for microfilariae. Under the 40x objective lens, I searched 10 random fields for the presence of trypanosomes. Fleas and ticks were identified to genus or species with a dissection scope using the following dichotomous keys: Brinton and Beck 1963, Fairchild et al. 1966, Jones and Clifford 1972, Jones et al. 1972, Martins et al. 2010, and Tipton and Mendez 1966. Lice and mites were not identified.

Data analysis. I performed a factor analysis to quantify forest microhabitat structure with a reduced number of variables (Seamon and Adler 1996). The factor analysis followed the factoring protocols of Cureton and D'Agostino (1983). To determine communalities, I executed an initial principal-axes factoring and then used the communalities as the diagonals in the correlation matrix. A final factoring was performed with a promax rotation of the axes. I determined the salient number of axes, or composite variables, to be retained for further analysis by examining a scree plot. The

retained factors represented gradients in microhabitat structure (Seamon and Adler 1996) defined by the original (raw) variables most correlated with each factor. To show the distribution of the total sampled microhabitat, I plotted all sampling stations in multivariate space as defined by the first three axes derived from the factor analysis.

I then used multiple logistic regression analysis to determine microhabitat gradients with which *P. semispinosus* was associated. If an individual was captured multiple times, only the first capture was included to avoid problems of statistical dependence. I used the presence or absence of spiny rats at each trap station as the dichotomous dependent variable and the factors retained from the analysis as the independent variables. To avoid problems associated with stepwise analysis, I used a full logistic regression model that included all salient (retained) factors. The factors were therefore explanatory variables that could predict the presence or absence of a spiny rat at a sampling station. I also analyzed the relationship between the raw microhabitat variables and the presence-absence data by calculating separately the significance level of each such variable entering into a simple logistic regression model.

To determine microhabitats with which parasites of *P. semispinosus* were associated, I used multiple logistic regression analysis with the salient composite microhabitat variables. For this purpose, I calculated the median number of parasites per rat in each ectoparasite category (fleas, ticks, mites, and lice). Those burdens below the median were classified as low and those above as high burdens. Burden (low or high) thereby represented the dichotomous dependent variable. I also analyzed the relationship between the parasites and the raw microhabitat variables by calculating separately the

significance level of each such variable entering into a simple logistic regression model.
For the two categories of blood parasites (trypanosomes and microfilariae), I used simple
presence-absence as the dependent variable and otherwise performed the same analysis as
with ectoparasites.

I used simple chi-square analysis and Fischer's exact P tests (in cases where at
least one cell size was less than five) to determine differences in the distributions of
parasites with respect to rat gender or season (dry or rainy). ANCOVA was used to test
for differences in mean burdens between seasons while controlling for rat abundance.

Results

I recorded 87 captures of 70 individual *P. semispinosus* during 6120 trapnights
(Table 1-1). Overall capture success, including recaptures, was 1.42%. Only three
individuals were captured in two consecutive seasons. One of those individuals moved
from plot 4 to plot 2. *Proechimys semispinosus* was most abundant on plot 3 (24
individuals) and least abundant on plot 2 (3 individuals) during the study (Table 1-3).
January 2011 yielded the most samples (30), and June 2012 had the fewest (4).

All fleas were *Polygenis klagesi*; 50.0% of *P. semispinosus* were infested with
fleas, and the mean intensity of infestation was 4.3 fleas/rat. Of the 58 spiny rats sampled
for ticks, 43.1% were infested. I identified larval ticks to genus, nymphal ticks to genus
or species, and adult ticks to species (Table 1-4). I found one soft tick (Argasidae), a
larval *Ornithodoros puertoricensis,* while the remaining ticks were hard ticks (Ixodidae).
No host was infested with more than two species of ticks (unless they harbored multiple

species of the same genus in larval form) or two life stages at one time. Only one adult tick was found, a male *Amblyomma oblongoguttatum*. I grouped other parasites as mites, lice, microfilariae (likely *Molinema* sp. or *Litomosoides* sp., Odile Bain, personal communication), and trypanosomes (*Trypanosoma cruzi* or *Trypanosoma rangeli*) because I was unable to identify them to species. Mites infested 96.6% of *P. semispinosus*, lice 63.8%, microfilaria 15.8%, and trypanosomes 17.5%.

I retained six salient factors from the microhabitat factor analysis that I interpreted, based on factor loadings, as forest openness with respect to trees (i.e. negatively correlated with tree density), few large logs (i.e. negatively correlated with large logs), lianas, forest age, small logs, and medium logs (Table 1-5). Figure 1-2 plots each trap station in microhabitat space as defined by the first three factors; trapping stations were not evenly distributed throughout microhabitat space. *Proechimys semispinosus* was associated with the sixth factor (medium logs, $X^2 = 4.66$, p = 0.0308), and the raw variable medium logs ($X^2 = 5.68$, p = 0.0171). Fleas were associated with the first factor (forest openness, $X^2 = 6.84$, p = 0.0089) and microfilariae were associated with the raw variable tree distance (i.e. less likely to be found by trees, $X^2 = 4.01$, p = 0.0451). Ticks were found more frequently on male spiny rats ($X^2 = 8.28$, p = 0.0040), fleas were more common in the rainy season (Fisher's exact P = 4.111E-04), and lice were more common in the dry season ($X^2 = 4.67$, p = 0.0307). These two seasonal differences were not influenced by rat abundance (Table 1-6).

Discussion

Proechimys semispinosus has been the focus of numerous studies in the Panama Canal Area (Adler 1994, Endries and Adler 2005, Fleming 1971, Gliwicz 1984), including habitat associations (Lambert and Adler 2000, Tomblin and Adler 1998). Tomblin and Adler (1998) found that *P. semispinosus* used all available microhabitats, suggesting its generalized habits. By contrast, Lambert and Adler (2000) found that *P. semispinosus* was associated with younger forest (smaller trees and lianas and lower forest canopies) and tree-fall gaps within older forest. In this study, *P. semispinosus* was sampled in younger forest and was associated with medium-sized logs.

Flea species previously found on *P. semispinosus* include *Adoratopsylla intermedia copha*, *Polygenis dunni*, *P. klagesi*, *P. roberti beebei*, *Rhopalopsyllus australis tupinus*, *R. cacicus saevus*, and *R. lugubris lugubris* (Tipton and Mendez 1966). In Tipton and Mendez's review (1966), 99 percent of fleas collected from *P. semispinosus* were *P. klagesi*. In the present study, the only flea species found on the spiny rat was *P. klagesi*. It is apparently rare for a different flea species to be found on *P. semispinosus* in the study area. *Polygenis klagesi* is most commonly found on *P. semispinosus* (91% of *P. klagesi* collected by Tipton and Mendez 1966) and is second most common on the spiny rat's close relative, *Hoplomys gymnurus* (3.2% of *P. klagesi*). Other hosts include *Tylomys watsoni, Nasua narica, Zygodontomys brevicauda,* and *Didelphis marsupialis*, accounting for less than 1.7% total collected *P. klagesi* each.

In this study, fleas found on *P. semispinosus* were more abundant during the rainy season and were associated with forest openness (i.e., negatively associated with tree

density). Fleas are acquired in the host burrow (Krasnov et al. 1997); therefore, the burrows the flea-infested rats are using may be located in areas with lower tree density. Endries and Adler (2005) found that spiny rat burrows have little herbaceous cover. They also found that spiny rats occupy more burrows and share burrows more often during the rainy season. This finding supports my results because burrow co-habitation may promote flea transmission to spiny rats during the rainy season. Further support is derived from temperate forests, where increased burrow sharing increased host switching of fleas (Krasnov et al. 2006). In the Negev Desert, Krasnov et al. (1997) found different species of fleas on rodents during different seasons; many other flea studies found high seasonal abundances of different flea species (Krasnov et al. 1997, Lang 1996, Osacar et al. 2001).

Proechimys semispinosus hosts the following tick species: *Amblyomma* sp., *A. ovale*, *A. dissimile, A. pacae, Ixodes* sp., *I. luciae, I. venezuelensis, Ornithodoros puertoricensis* and *Haemaphysalis juxtakochi* (Fairchild et al. 1966 and Mendez 1993). In the present study, *A. cajennense, A. naponense*, *A. oblongoguttatum*, and *I. boliviensis*, were found for the first time on *P. semispinosus*. *Amblyomma cajennense* is an important vector of *Rickettsia rickettsi*, the causative agent of Rocky Mountain spotted fever in humans and paralysis in livestock (Kolonin 2009). Spiny rats may be an important reservoir host for *R. rickettsi* if *A. cajennense* infestations are sufficiently abundant because spiny rats are common in young forests, where this tick is also common. *Amblyomma naponense* is commonly found on *Pecari tajacu*, *A. oblongoguttatum* is

commonly found on livestock and various wild mammals, and immature *I. boliviensis* are generally found on carnivores and opossums (Kolonin 2009).

In this study, ticks were more closely associated with male rats. The larger home ranges of male spiny rats (Endries and Adler 2005) allows males to encounter a greater number of questing ticks and may be the reason that males host more ticks than females. Greater male mobility is a common hypothesis for male-biased parasitism; another hypothesis suggests that a male's lower immunocompetence, due to the immunosuppressive effect of androgens, allows a parasite to better establish itself on a male host (Khokhlova et al. 2011, Krasnov et al. 2012). These two causes of male-biased parasitism are not mutually exclusive but probably occur together (Grear et al. 2009). Male-biased parasitism has been documented for fleas, ticks, mites, lice, and filarial worms in birds and mammals (Krasnov et al. 2012).

Previous studies have found nine species of mites, 21 species of sucking lice, and 10 species of chewing lice on *P. semispinosus* (Mendez 1993). In this study, sucking and chewing lice were grouped together and, as a whole, were more common in the dry season than the rainy season. Mize et al. (2011) found lice on *Peromyscus leucopus* to be associated with dry vegetation. Conversely, Calvete et al. (2003) found lice on *Alectoris rufa* to be associated with higher humidity. Identifying the lice and mites on the spiny rat could reveal different species-specific associations.

Host abundance frequently promotes ectoparasite abundance. However, I found no influence of rat abundance on any of the groups of ectoparasites. Rat abundance was much lower relative to previously-recorded abundances in central Panama (Adler 1998).

Thus, rat abundance in this study may have been far below a critical threshold whereby ectoparasite transmission would have been facilitated.

Two species of filarial worms have been found in *P. semispinosus*, *Litomosoides hoplomyis* and *Dipetalonema raposoensis* (Mendez 1993). The microfilaria found in this study are most likely in the genera *Litomosoides* or *Molinema* (Odile Bain, personal communication)*. Proechimys semispinosus* and *H. gymnurus* are the only two echimyid rodents known to host *Litomosoides* spp. (Guerrero et al. 2011). *Litomosoides* is more commonly found in murid rodents, but it is also found in other rodents, marsupials, and bats. By contrast, echimyids, including other species of *Proechimys*, frequently host filariae from the genus *Molinema,* which is found only in echimyids and erethizontids (Guerrero and Bain 2001). Perhaps this association is related to the vector ecology, as *Molinema* are vectored by mosquitoes (Loiseau et al. 1996) and *Litomosoides* by mites (Guerrero et al. 2011)

Two species of *Trypanosoma* (*cruzi* and *rangeli*) have been found in *P. semispinosus* (Mendez 1993). Rodents are an important reservoir host for *T. cruzi*, the causative agent of Chagas disease in humans. In Brazil, species of spiny rats living in close proximity to livestock play a secondary role in the transmission cycle of *T. cruzi* (Rademaker et al. 2009). *Trypanosoma rangeli* is not pathogenic to mammals; however, it is important because of its antigenic cross-reactivity and overlapping distribution with *T. cruzi* (Pinto et al. 2006). Further research to determine which *Trypanosoma* spp. are present in the spiny rats in the present study is necessary.

My prediction that parasites were influenced by microhabitat and varied according to season, rat density, and host gender was supported to varying degrees; not every parasite was associated with aspects of the microhabitat that we measured or did not vary in abundance according to host density or season. Ticks were associated with male hosts, fleas with the rainy season and forest openness with respect to trees, lice with the dry season, and filariae with tree distance. However, because I combined ticks, mites, and lice into categories, doing so may have masked the biology of the constituent species. Nonetheless, while the associations with seasons and host gender are common findings (Krasnov et al. 2012, Krasnov et al. 1997, Osacar et al. 2001), this is the first study to describe the relationship between Neotropical ectoparasites and microhabitat structure. Identification of the lice and mites in this study as well as further studies on parasite-microhabitat associations would help elucidate parasite ecology.

Table 1-1. Sampling dates, effort, and numbers of individuals and captures of *Proechimys semispinosus*. * indicates trapping suspended due to coati disturbance: plot 1 closed on day 2; plot 2 closed on day 1, reopened on day 3, and closed again on day 4; plot 3 closed on day 5; plot 4 closed on day 4; plot 5 closed on day 5; plot 6 closed on day 6.

Season	Dates	Trapnights	Individuals	Captures
Dry	31 Dec – 9 Jan 2011	1800	30	33
	31 Dec – 6 Jan 2012*	720	18	24
Wet	10 Jun – 20 Jun 2011	1800	18	25
	3 Jun – 13 Jun 2012	1800	4	5
Total		6120	70	87

Table 1-2. Descriptions of the thirteen microhabitat variables measured.

Name	Description
1. Gap	Presence or absence of a tree-fall gap at the station (0 = no gap, 1 = tree-fall gap, 2 = road-side gap)
2. Rock cover	Amount of rock cover, ranging from 0 to 4 (0 = no cover, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%)
3. Woody cover	Amount of live woody ground cover (values same as rock cover)
4. Herbaceous cover	Amount of live herbaceous ground cover (values same as rock cover)
5. Small logs	Number of logs 5-10 cm in diameter
6. Medium logs	Number of logs 11-20 cm in diameter
7. Large logs	Number of logs >20 cm in diameter
8. Log distance	Distance to nearest log >20 cm in diameter
9. Tree distance	Mean distance to the nearest tree in each of the four cardinal compass directions
10. Tree size	Mean diameter of the nearest tree in each of the four cardinal compass directions
11. Number of lianas	Mean number of lianas supported by the four trees described above
12. Liana size	Mean diameter of the largest liana on each of the four trees described above
13. Tree density	Number of trees ($\geq$10 cm dbh) within a 100-m^2 circle centered on the sample station

Table 1-3. Captures of *Proechimys semispinosus* on each plot during each trapping season. * denotes when a single individual travelled between plot 1 and 4 or 3 and 6; individual is counted once on each plot for abundance estimates (parasite samples were not recollected).

Plot	January 2011 (dry)	June 2011 (wet)	January 2012 (dry)	June 2012 (wet)	Total
1	4*	5*	1	1	11
2	2	0	1	0	3
3	9*	6	7	2	24
4	8*	4*	1	1	14
5	4	3	3	0	10
6	5*	1	5	0	11
Total	32	19	18	4	73

Table 1-4. Ticks sampled on *Proechimys semispinosus*. L is larval, N is nymphal, and M is adult male.

Tick	Quantity	# hosts
Amblyomma sp. (L)	1	1
	14	1
Haemaphysalis sp. (L)	1	6
	2	1
	39	1
Ornithodoros puertoricensis (L)	1	1
Amblyomma ovale (N)	1	3
	2	1
Amblyomma naponense (N)	1	1
Haemaphysalis sp. (N)	1	1
Ixodes boliviensis (N)	1	1

Mixed infections

Tick	Quantity	# hosts
Amblyomma sp. (L) & *Amblyomma ovale* (N)	1 & 1	1
	1 & 3	1
Haemaphysalis sp. (L) & *Amblyomma oblongoguttatum* (M)	1 & 1	1
Haemaphysalis sp. (L) & *Amblyomma cajennense* (N)	1 & 1	1
Haemaphysalis sp. (L) & *Amblyomma ovale* (N)	1 & 1	1
	1 & 2	1
	4 & 2	1
none		33

Table 1-5. Factor loadings of the six salient factors retained for analysis. Bold faced font

indicates raw variables used in interpreting the factors. For a description of raw

variables, see Table 1-2.

	Factor 1 - forest openness	Factor 2 - few large logs	Factor 3 - lianas	Factor 4 - forest age	Factor 5 - small logs	Factor 6 - medium logs
Gap	0.18454	-0.20578	0.22408	**0.4254**	-0.0141	0.08802
Rock cover	-0.01565	0.01811	0.03261	0.32023	0.04196	-0.06135
Woody cover	0.1086	-0.26878	0.17512	0.35198	0.22448	-0.19905
Herbaceous cover	0.16967	0.13338	0.03815	0.15288	-0.10978	0.17056
Small logs	-0.05575	-0.08341	-0.02095	-0.04859	**0.7829**	0.20219
Medium logs	0.119	-0.2217	-0.01406	-0.04777	0.26174	**0.72448**
Large logs	0.12974	**-0.71031**	-0.04652	0.18681	0.04546	0.1914
Log distance	-0.11677	**0.74541**	-0.00125	-0.00005	-0.12672	-0.05854
Tree distance	**0.7827**	-0.2044	0.1485	0.02858	-0.0103	-0.00277
Tree size	0.23056	-0.0378	0.25851	**-0.56208**	0.26934	-0.13039
Number of lianas	0.17343	-0.01812	**0.64106**	**0.41873**	-0.09142	-0.14104
Liana size	0.16596	0.02961	**0.81856**	-0.08201	0.08322	-0.05076
Tree density	**-0.77615**	0.0847	-0.2088	0.04069	-0.005	-0.15343

Table 1-6. Results from ANCOVA testing for differences between seasons while controlling for rat abundance.

Parasite	Main effects	F value	p value
Fleas	Season	26.16	<.0001
Fleas	Rat abundance	0.00	0.9560
Lice	Season	10.26	0.0023
Lice	Rat abundance	1.35	0.2498
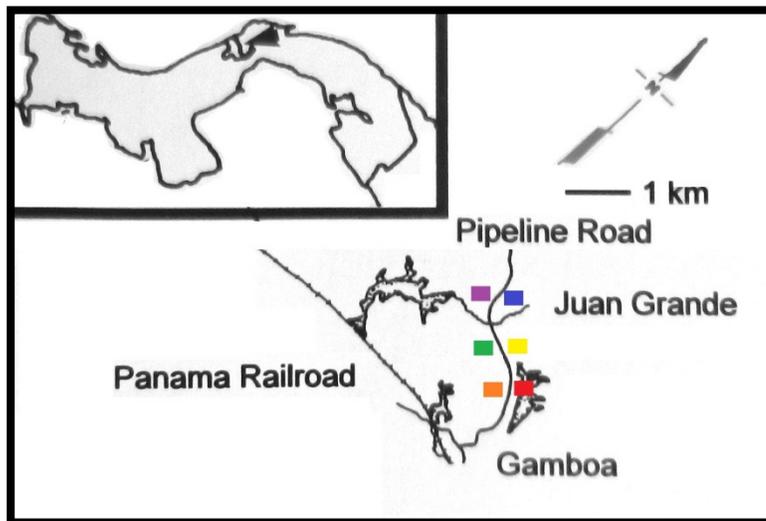
Figure 1-1. Plot locations along Pipeline Road. Plot 1 is shown in red, 2 in orange, 3 in yellow, 4 in green, 5 in blue, and 6 in purple. Inset shows the location of Soberania National Park and Pipeline Road in Panama (indicated by the arrow).

Figure 1-2. Sampling stations plotted in total microhabitat space as defined by the first three composite variables (factors). The x-axis is factor 1 which is defined by tree density; the y-axis is factor 2, defined by the number of large logs; the z-axis is factor 3, defined by the number of lianas. Plot 1 is shown in red, 2 in orange, 3 in yellow, 4 in green, 5 in blue, and 6 in purple.
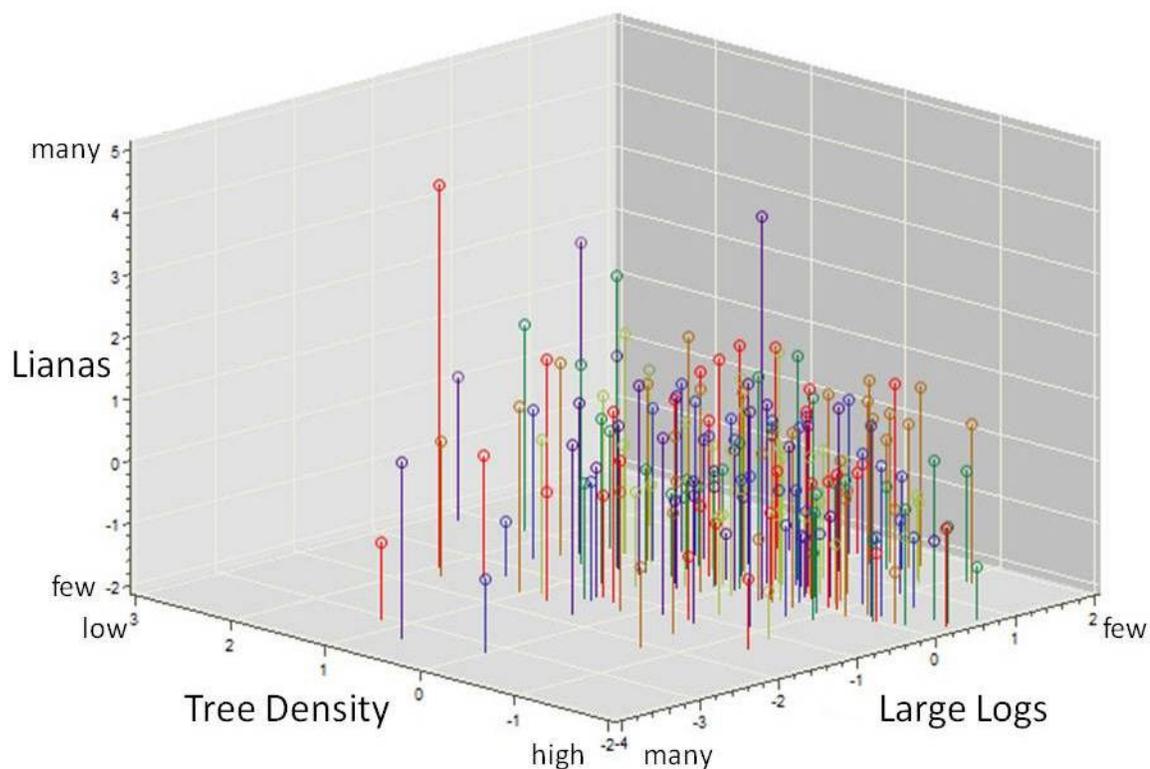
Chapter II

Parasite Communities of Tropical Forest Rodents: Influences of Host Specialization

Abstract

Most organisms host multiple species of parasites, and parasite communities are frequently influenced by the degree of host specialization. Tropical forest rodents are ideal for examining hypotheses related to host habitat specialization and parasite community composition because they are often abundant, diverse, and differ widely with respect to habitat specialization. *Proechimys semispinosus* and *Hoplomys gymnurus* are sympatric and morphologically similar; however, *P. semispinosus* is more generalized, occupying a wider range of forested habitats. I predicted that *P. semispinosus* hosts a broader range of parasite species that are less host-specific than does *H. gymnurus*. During two dry and wet seasons, rodents were trapped in central Panama to compare their parasites. In support of my prediction, the habitat generalist (*P. semispinosus*) hosted more fleas, mites, and microfilariae; contrary to my prediction, the habitat specialist (*H. gymnurus*) hosted more lice and ticks. Also contrary to my prediction, none of the tick species found on the habitat specialist were host-specific. The sole flea species I collected was *Polygenis klagesi*, which may be largely specific to *P. semispinosus*. This descriptive study lays the foundation for an experimental approach to study the interactions of these hosts and their parasites.

Introduction

Parasitism is the most common lifestyle and is a driving force of evolution, having evolved countless times in all major biotic taxa (Price 1980). A parasitic relationship causes a coevolutionary arms race, whereby the parasite is under selection pressures to maintain the relationship, and the host is under selection pressures to dissociate from it. These selection pressures change the genetic constitution of both organisms involved and alter behavior, physiology, and consequently fitness.

A host's phylogeny, physiology, age, sex, feeding ecology, and habitat preferences are important in the establishment of a parasitic relationship (Krasnov et al. 2005). Phylogenetically-related hosts with similar niches may harbor the same or similar parasites (Munoz et al. 2006). Parasites differ in their degree of host specificity; they may be either generalists or specialists (Holmes and Price 1980). A specialist parasite is typically closely coevolved with its host, which frequently leads to phylogenetically-related hosts having the same specialist parasite species. Generalist parasites are less specific and can use multiple and even phylogenetically-unrelated hosts to complete their lifecycle.

Rodents are common hosts for parasites because of their wide geographical distribution and ubiquity throughout various environments. They are important reservoirs of many zoonotic diseases (e.g. leishmaniasis and trypanosomiasis) because they are frequently in close contact with humans and domestic animals. Parasites of two abundant sympatric rodents (*Apodemus flavicollis* and *A. sylvaticus*) have been studied in Germany; the rodents have very similar parasites and show that phylogenetically-related

species and those with similar life styles harbor similar parasites (Klimpel et al. 2007). However, similar studies of parasites of closely-related habitat specialists and generalists have not been studied in tropical forests, despite the importance of many of those rodents in transmitting zoonotic diseases.

Echimyid rodents occur in tropical regions of Central and South America and are terrestrial, arboreal, and fossorial (Eisenberg 1989, Eisenberg and Redford 1999, Redford and Eisenberg 1992). *Proechimys semispinosus* (the Central American spiny rat) and *Hoplomys gymnurus* (the armored rat) serve as hosts for a wide variety of parasites (e.g., ectoparasitic arthropods and endoparasitic blood parasites, Mendez 1993). *Proechimys semispinosus* is an abundant habitat generalist, maintaining persistent populations in lowland forests ranging from dry to pluvial and from young and newly-regenerating to old-growth (Adler 2000, Lambert and Adler 2000). *Hoplomys gymnurus* is morphologically similar, closely related to, and occurs syntopically with *P. semispinosus* but is restricted to wetter and cooler habitats (Tomblin and Adler 1998).

Proechimys semispinosus has been the focus of numerous studies in the Panama Canal Area (Adler 1994, Endries and Adler 2005, Fleming 1971, Gliwicz 1984, Lambert and Adler 2000) and has previously been compared to *H. gymnurus* with respect to distribution, habitat use, and morphology (Adler et al. 1998, Tomblin and Adler 1998). Previous studies have described ectoparasites from the two rats from various locations in Central and South America (Fairchild et al 1966, Mendez 1993, Tipton and Mendez 1966). However, this study is the first to describe the ectoparasites of these two tropical forest rats from syntopic locations.

This study focuses on the ectoparasites and blood parasites of these two closely-related echimyid rodents, one a habitat generalist and the other a habitat specialist, in a tropical forest in Panama. These habitat-use differences may be important because - previous studies in the Negev desert and central Europe found that parasite communities vary with habitat (Krasnov et al. 1997, Krasnov et al. 2006). I predict that the habitat generalist, being exposed to more microhabitats, has greater parasitic burdens that are characterized by more generalized and less host-specific parasites than the habitat specialist.

Methods

    Study area. The study was conducted along Pipeline Road in Soberania National Park near Gamboa, Panama (Figure 2-1). I sampled *P. semispinosus* and *H. gymnurus* along three streams (Rio Limbo, Rio La Seda, and Juan Grande) that flowed approximately perpendicular to the road and one stream (Rio Stu, a tributary of Juan Grande) that flowed parallel to the road, where both rodents were known to occur (Tomblin and Adler 1998). These study sites were located mostly within second-growth tropical moist forest that has been regenerating for approximately 70 years. The termini of the sampling transects along Rios Limbo and La Seda were located mostly in old-growth forest. The study sites experienced similar climatic conditions because they were in close proximity (within a 4 km span) to each other (Tomlin and Adler 1998). The climate of the study area is highly seasonal with respect to rainfall, with an eight-month rainy season from late April through December followed by a four-month dry season.

Mean annual precipitation is approximately 2200 mm, with less than 10% falling during the dry season (Windsor 1990).

Sampling procedures. I live-trapped *P. semispinosus* and *H. gymnurus* along the streams during two wet seasons and two dry seasons from January 2011 to July 2012 (Table 2-1). Rio Stu was trapped during all sampling seasons, although there were no captures during June 2012 due to low rat population densities. I could not trap Rios Limbo or La Seda during the dry seasons due to poor road conditions. Juan Grande was only sampled during June 2011. I established transects of sampling stations 20 m apart along the banks of each stream. The number of sampling stations varied by stream: Rio Stu had 17, Rio Limbo had 45, La Seda had 50 during June 2011 and 85 during June 2012, and Juan Grande had 30. Each sampling station had one Tomahawk live-trap (40.6 by 12.7 by 12.7 cm) baited with fresh-cut ripe plantain. I set traps for four to ten consecutive nights and checked them every morning, with the exception of Rio Limbo, having one night in June 2012.

All captured *P. semispinosus* and *H. gymnurus* were ear-tagged with a metal band stamped with an unique identification number, weighed, and placed into sex and age classes. I determined age by stage of pelage development (juvenile, sub-adult, or adult, Adler 1994). An ear snip was taken and blood smear made from the cut site to screen for blood parasites. I used forceps to remove all ticks and fleas from each rat and combed them twice with a fine-toothed metal comb to obtain relative counts of lice and mites. I preserved all ectoparasites in 70% ethanol. Rats were released at their respective

sampling station immediately after data collection, and recaptured individuals in the same sampling season were released without further data collection.

Parasite identification. Blood smears were fixed in 100% methanol for 30 seconds and stained in a 10% Giemsa stain for 30 minutes. At a magnification of 100x, I scanned the entire blood smear to search for microfilariae, and I searched 10 random fields for the presence of trypanosomes at 400x. I identified fleas to species, larval ticks to genus, and nymphal ticks to species with a dissecting scope using the following dichotomous keys: Brinton and Beck 1963, Fairchild et al. 1966, Jones and Clifford 1972, Jones et al. 1972, Martins et al. 2010, and Tipton and Mendez 1966. Lice and mites were not identified.

Data analysis. To determine the differences in the distribution of parasites with respect to rat species, I used simple chi-square analysis and Fischer's exact P tests (in cases where at least one cell size was less than five). Although these tests are sensitive to violations of independence, very few rats were captured in more than one sampling season.

Results

In 2500 trap nights accumulated along the regular stream transects, I captured 16 individual *P. semispinosus* 17 times and 24 individual *H. gymnurus* 29 times (Table 2-2). One *P. semispinosus* was caught in two seasons, January and June 2011. To increase sample sizes, an additional *H. gymnurus* and six additional *P. semispinosus* were captured downstream on Rio Stu at another study location. All fleas were *Polygenis*

klagesi. Only 20.8% of *H. gymnurus* were infested with fleas, with no individuals having more than two fleas. The 57.1% of *P. semispinosus* hosting fleas had between two and 16 fleas, with a mean intensity of infestation of 6.6 fleas.

Only one *P. semispinosus* individual hosted a tick (a nymphal *Amblyomma cajennense*), which was not found on *H. gymnurus* (Table 2-3). I found three genera of larval ticks (*Haemaphysalis*, *Ixodes*, and *Amblyomma*) and one species of nymphal tick (*A. ovale*) on *H. gymnurus*. Of the nine tick-infested *H. gymnurus*, only one was infested with more than one life stage or species (one larval *Amblyomma* sp. and two *A. ovale*). I grouped other parasites as mites, lice, microfilariae (likely *Molinema* sp. or *Litomosoides* sp., Odile Bain, personal communication), and trypanosomes (*Trypanosoma cruzi* or *Trypanosoma rangeli*).

I found no difference in trypanosome infection between the two species of rodents (Fisher's exact P = 0.4286, Table 2-4). *Proechimys semispinosus* hosted more fleas (X^2 = 6.28, p = 0.0122), mites (Fisher's exact P = 0.0069), and microfilariae (Fisher's exact P = 0.0012) than *H. gymnurus*, while the latter species hosted more lice (Fisher's exact P = 0.0120) and ticks (Fisher's exact P = 0.0086).

Discussion

Proechimys semispinosus hosts the following flea species: *Adoratopsylla intermedia copha*, *Polygenis dunni*, *P. klagesi*, *P. roberti beebei*, *Rhopalopsyllus australis tupinus*, *R. cacicus saevus*, and *R. lugubris lugubris* (Tipton and Mendez 1966). In Tipton and Mendez's review (1966), 99 percent of fleas collected from *P.*

semispinosus were *P. klagesi*, and 91 percent of collected *P. klagesi* were from this host. Also, all fleas they collected from *H. gymnurus* were *P. klagesi*, and 3.2 percent of individuals (the second highest percentage) collected were from this host. *Polygenis klagesi* has also been found in low numbers (less than 1.7 percent of the total number of individuals collected) on *Tylomys watsoni, Nasua narica, Zygodontomys brevicauda,* and *Didelphis marsupialis* (Tipton and Mendez 1966). In the present study, the only flea species found on the two rodents was *P. klagesi*, which more frequently infested *P. semispinosus*; of the 85 fleas collected, 92.9% were from *P. semispinosus*.

Taking into account Tipton and Mendez's review (1966), I suggest that *P. semispinosus* is the most common host for *P. klagesi*, which does not commonly infest other small mammals. This would support my finding *P. semispinosus* with more fleas than *H. gymnurus*. Fleas reproduce in the host's nest, and pre-imaginal development is usually off-host (Krasnov et al. 2004). *Proechimys semispinosus* does not excavate their own burrows and frequently uses different burrows (Endries and Adler 2005), which can facilitate the transfer of this flea to other small mammals. Because *P. semispinosus* and *H. gymnurus* occur synoptically, are morphologically similar, and may intermittently use the same burrows, it is likely *H. gymnurus* will be an accidental host of *P. klagesi*.

Tick species previously found on *P. semispinosus* include *Amblyomma* sp., *A. ovale*, *A. dissimile, A. pacae, Ixodes* sp., *I. luciae, I. venezuelensis, Ornithodoros puertoricensis* and *Haemaphysalis juxtakochi* (Fairchild et al. 1966, Mendez 1993). *Hoplomys gymnurus* hosts *Amblyomma* sp. that could not be further identified (Fairchild et al. 1966). Both rat species have been previously documented to host larval and

nymphal forms, and only nymphs were identified to species (Fairchild et al. 1966). In the present study, nymphal *A. cajennense* was found for the first time on *P. semispinosus* and was the only tick found on the 21 hosts sampled. Larval *Haemaphysalis* sp., larval *Ixodes* sp., and nymphal *A. ovale* were found on *H. gymnurus* for the first time in this study.

Amblyomma cajennense is medically important as a vector of *Rickettsia rickettsi*, the causative agent of Rocky Mountain spotted fever and paralysis in livestock (Kolonin 2009). This tick parasitizes humans and a wide range of domestic and wild mammals from Texas to Argentina. Because *P. semispinosus* is a widespread generalist, it may be an important reservoir host for *R. rickettsi* if *A. cajennense* infestations are sufficiently great. *Amblyomma ovale* ranges from Mexico to Argentina and may be an important vector for *Rickettsia* spp. (Murgas et al. 2013). It may also be a vector of *Hepatozoon canis*, a hemoparasite of dogs (Forlano et al. 2005). Canids are thought to be the main host of *A. ovale*, and rodents and marsupials are important hosts for immature stages (Murgas et al. 2013).

Previous studies have found 21 species of sucking lice and 10 species of chewing lice on *P. semispinosus* (Mendez 1993). Only one species of sucking louse and six species of chewing lice have been reported from *H. gymnurus*. In this study, lice were more common on *H. gymnurus* than on *P. semispinosus*. This may be due to physiological differences; *H. gymnurus* retains heat better than *P. semispinosus* (unpublished data) and in the cool stream microclimate, the lice may be sensitive to those differences.

Proechimys semispinosus has been infested by nine species of mites: *Androlaelaps fahrenholzi*, *Gigantolaelaps gilmorei*, *Laelaps dearmasi*, *L. nuttali*, and *L. pilifer*, *Ornithonyssus bacoti*, *Hirstionyssus parvisona*, *Acanthonyssus dentipes*, and *A. Proechimys* (Mendez 1993). *Hoplomys gymnurus* has been found hosting the mites *A. fahrenholzi*, *Tur anomalus* and *T. uniscutatus*. *Androlaelaps fahrenholzi* is a generalist mite and is found on many mammal hosts and occasionally birds (Bittencourt and Rocha 2003). *Ornithonyssus bacoti* is a mite of both wild and domestic rats (Green and Baker 1996). *Tur* spp., by contrast, are closely associated with echimyid rodents (Bitterncourt and Rocka 2003). In this study, mites were more common on *P. semispinosus* but were not identified to species. Like lice, mites may be sensitive to the host's body temperature and prefer the cooler body of *P. semispinosus*.

Previously, *P. semispinosus* has been found to host the filarial worms *Litomosoides hoplomyis* and *Dipetalonema raposoensis* (Mendez 1993). *Hoplomys gymnurus* has been infected with the filaria *L. hoplomyis* and has not been found infected with trypanosomes (Mendez 1993). Only two echimyid rodents have been found to host *Litomosoides* spp., *P. semispinosus* and *H. gymnurus* (Guerrero et al. 2011). *Litomosoides* is more commonly found in murids, but is also found in other rodents, marsupials, and bats. By contrast, echimyids, including many *Proechimys* spp., are frequently found hosting filariae from the genus *Molinema* (Guerrero and Bain 2001). *Molinema* is found only in echimyids and erethizontids. Molecular research methods or examining adult morphology is necessary to determine which microfilariae are present in the rodents in this study, which are more common in *P. semispinosus*.

Proechimys semispinosus has been found to be infected with *Trypanosoma cruzi* and *T. rangeli* (Mendez 1993). In this study, blood smears revealed the presence of both filarial worms and trypanosomes in *P. semispinosus*, but neither were found in blood smears from *H. gymnurus*, consistent with previous studies. Rodents play an important role as reservoir hosts for *T. cruzi*, the causative agent of Chagas disease in humans. For instance, other species of spiny rats in Brazil living in close proximity with livestock play a secondary role in the transmission cycle of *T. cruzi* (Rademaker et al. 2009). *Trypanosoma rangeli* is not believed to be pathogenic to mammals but is important because of its antigenic cross-reactivity and overlapping distribution with *T. cruzi* (Pinto et al. 2006). Further research to determine which *Trypanosoma* spp. are present in the rodents in the present study is necessary.

My prediction was supported with some parasites and refuted with others. The habitat generalist (*P. semispinosus*) had greater burdens of fleas, mites, and microfilariae than the habitat specialist (*H. gymnurus*) and was the sole host of *Trypanosoma* spp. Contrary to the prediction, however, the habitat specialist (*H. gymnurus*) hosted more lice, tick species, and tick individuals than the habitat generalist (*P. semispinosus*). The tick species found on *H. gymnurus* are not host-specific, also contrary to my prediction. The prediction may have been supported if *P. semispinosus* had been sampled in areas where *H. gymnurus* was not found. Different areas of the forest will have different characteristics and will likely support other parasite faunas. Indeed, in a related study in the same contiguous area of forest where *H. gymnurus* was absent, I found six additional species of ticks on *P. semispinosus*. However, my goal in this study was to compare

parasite faunas of the two host species occurring syntopically within the same microhabitats rather than to describe complete parasite faunas across the entire spectrum of available microhabitats.

Acknowledgements

Table 2-1. Streams sampled from January 2011 to June 2012.

	Rio Stu	Rio Limbo	Rio La Seda	Juan Grande
January 2011	X			
June 2011	X	X	X	X
January 2012	X			
June 2012	X		X	

Table 2-2. Sampling dates, effort, and numbers of individuals and captures of

Proechimys semispinosus and *Hoplomys gymnurus*.

Stream	Date	Trap-nights	*P. semispinosus* individuals	*P. semispinosus* captures	*H. gymnurus* individuals	*H. gymnurus* captures
Rio Stu	Jan 2011	68	3	3	0	0
Rio Stu	Jun 2011	170	2	2	2	2
Rio Limbo	Jun 2011	450	0	0	5	6
Rio La Seda	Jun 2011	465	6	7	8	10
Juan Grande	Jun 2011	180	1	1	1	1
Rio Stu	Jan 2012	102	2	2	4	6
Rio Stu	Jun 2012	170	0	0	0	0
Rio Limbo	Jun 2012	45	0	0	1	1
Rio La Seda	Jun 2012	850	2	2	3	3
TOTAL		2500	16	17	24	29

Table 2-3. Ticks sampled on *Proechimys semispinosus* and *Hoplomys gymnurus*. L is larval and N is nymphal.

Host	# hosts	Tick
P. semispinosus	1	1 *Ablyomma cajennense* (N)
	20	None
H. gymnurus	1	1 *Haemaphysalis* sp. (L)
	1	3 *Haemaphysalis* sp. (L)
	1	1 *Ixodes* sp. (L)
	1	1 *Amblyomma* sp. (L)
	1	1 *Amblyomma* sp. (L) & 2 *Amblyomma ovale* (N)
	1	1 *Amblyomma ovale* (N)
	2	2 *Amblyomma ovale* (N)
	1	3 *Amblyomma ovale* (N)
	15	None

Table 2-4. Two-by-two contingency tables with the presence (+) or absence (-) of a

parasite and the host rodent (Ps= *Proechimys semispinosus*, Hg= *Hoplomys gymnurus*).

Fisher's exact P test or chi square value is also included. * denotes significance.

	Fleas	
	Ps	Hg
+	12	5
-	9	19

$X^2 = 6.28$

df = 1

p = 0.0122*

	Lice	
	Ps	Hg
+	11	20
-	10	3

p = 0.0120*

	Microfilariae	
	Ps	Hg
+	7	0
-	11	24

p = 0.0012*

	Mites	
	Ps	Hg
+	20	14
-	1	9

p = 0.0069*

	Ticks	
	Ps	Hg
+	1	9
-	20	15

p = 0.0086*

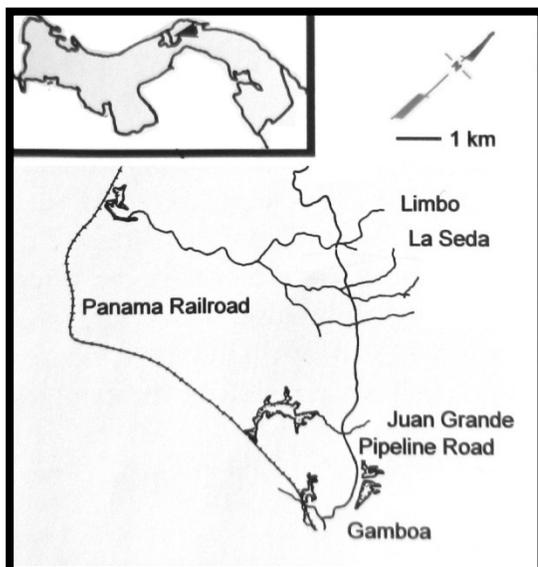|	Trypanosomes	
	Ps	Hg
+	1	0
-	17	24

p = 0.4286

Figure 2-1. Stream locations along Pipeline Road. Inset shows the location of Soberania

National Park and Pipeline Road in Panama (indicated by the arrow).

Conclusion

Proechimys semispinosus and *Hoplomys gymnurus* have been the focus of numerous studies in tropical forests (Adler et al 1998, Tomblin and Adler 1998, Adler 2000). This thesis is the first study that analyzes their parasite communities within an evolutionary context with respect to host specialization. It is also the first to describe how parasite communities are influenced by microhabitat structure within a Neotropical forest. Together, these two studies describe four species of ticks not previously recorded from *P. semispinosus* (*Amblyomma cajennense, A. naponense, A. oblongoguttatum, and Ixodes boliviensis*) and three species not previously found on *H. gymnurus* (*Haemaphysalis* sp., *Ixodes* sp., and *A. ovale*).

Ectoparasites are commonly associated with male hosts; this phenomenon has been documented with fleas, ticks, mites, and lice (Krasnov et al. 2012). My work presented in the first chapter corroborates this phenomenon because I found ticks to be more common on male hosts. Male-biased parasitism is likely the result of higher male mobility and a lower immunocompetence than females (Grear et al. 2009). Indeed, male spiny rats have larger home ranges than do females (Endries and Adler 2005).

The sole flea found in these studies, *Polygenis klagesi*, was more abundant during the rainy season. Fleas are commonly more abundant during a particular season because of their sensitivity to humidity and temperature (Osacar et al. 2001). Fleas are associated with the host burrow; *P. klagesi* may also be more abundant in the rainy season because spiny rats occupy more burrows and share burrows more frequently in the rainy season

(Endries and Adler 2005). Sharing burrows thereby allows for increased host switching of fleas (Krasnov et al. 2006). I also found fleas to be associated with forest openness with respect to trees; therefore, the host burrows might be in areas of lower tree density.

In my second chapter, *P. semispinosus* hosts more fleas than *H. gymnurus*. Based on past studies (Tipton and Mendez 1966), *P. klagesi* occurs on *P. semispinosus* 91% of the time and *H. gymnurus* 3.2% of the time. I believe *P. klagesi* is largely specific to *P. semispinosus*, but host switching may sometimes occur with *H. gymnurus* because the two species of rats are morphologically similar and may intermittently use the same burrows. *Proechimys semispinosus* does not excavate its own burrows and frequently uses different burrows (Endries and Adler 2005), which may facilitate the transfer of this flea to other accidental hosts.

In my studies, I did not identify lice and mites. Identifying them in the future could reveal different species-specific patterns with respect to microhabitat, season, host abundance, or host species. I also did not identify the microfilariae or trypanosomes. Molecular work is needed to identify the *Trypanosoma* spp, present. These data would add to knowledge about reservoir hosts for Chagas disease (caused by *T. cruzi*) or trypanosomes with similar surface antigens to *T. cruzi* (*T. rangeli*). Currently, molecular work is in progress to identify the filarial worms present in these rodent populations, which are likely *Molinema* spp. or *Litomosoides* spp.; these two genera have very different evolutionary histories. It would also be beneficial to identify the vector of the filaria and trypanosomes from this study. More studies of *P. semispinosus* and *H. gymnurus* parasites are needed to further elucidate their community structure.

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