HELMINTH PARASITISM IN ISOLATED POPULATIONS OF A NEOTROPICAL FOREST RODENT

By Annette L. Ireland

Parasitism is an extremely common life style that has evolved independently many times, and parasites are diverse with respect to that life style. Parasitic nematodes are commonly found in rodents and can serve as excellent model systems for understanding parasite-host interactions. *Proechimys semispinosus* (the Central American spiny rat) is a widely-distributed and common rodent in Neotropical forests. Several species of intestinal nematodes have been isolated from this rat, including *Heligmostrongylus* sp. I analyzed data collected from isolated populations of *P. semispinosus*. The data set included counts of eggs of *Heligmostrongylus* sp. that were shed in the feces of their rat hosts. The data were collected over a 13-month period (January 1997 through January 1998) from rat populations on seven small islands in Gatun Lake, central Panama. Rats were censused monthly by live trapping, and monthly fruit availability was assessed by counting the numbers of trees and lianas that were producing ripe fruits. Rat populations on five islands were provisioned with supplemental food during the period of least food availability (November and December 1997 and January 1998) to test the effects of host nutritional status on reproductive activity of *Heligmostrongylus* sp. Rat fecal samples were collected from each captured individual, and nematode eggs were counted from each sample. I estimated monthly rat densities, fruit densities, and per capita fruit availability for each island. I also calculated three indices (egg density, prevalence, and egg density of egg-shedding individuals) of *Heligmostrongylus* sp. reproductive activity. Egg density and density of egg-shedding individuals were $\log_{10}$+1-transformed, and prevalence was arcsine square root-transformed. I computed cross-correlation functions of each pair-wise island combination to search for synchrony in nematode reproductive activity among insular populations of rats. I computed Spearman rank correlation coefficients of island-wide means of the three *Heligmostrongylus* sp. indices and rat density, fruit density, and per capita fruit availability. I used repeated measures analysis of variance (ANOVA) to search for differences in mean parasite indices with respect to treatment period, treatment group, population nested within treatment group, month, and the month x treatment group interaction. I then searched for differences in the mean number of eggs shed by rats according to age and sex by constructing a full ANOVA model that included age, sex, and the interaction. I compared the proportions of male and female rats that shed nematode eggs at some time in their capture histories. I used linear regression analysis to search for a relationship between the number of eggs shed and rat body weight. Reproductive activity of *Heligmostrongylus* sp. varied widely over time, but there was little evidence of synchrony among islands. There were no associations of the parasite indices with rat density, fruit density, or per capita fruit availability. Food provisioning had no effect on reproductive activity, but such activity varied among islands. There

were no differences in *Heligmostrongylus* sp. reproductive activity between age classes of rats, but female rats shed more eggs than did males. By contrast, the proportions of male and female rats shedding eggs did not differ, and there was no relationship between the number of eggs shed by a rat and it body weight. Results suggest that reproductive activity of *Heligmostrongylus* sp.is infrequent and aseasonal but spatially variable. Host nutritional status has little effect on nematode reproductive activity, but dietary or physiological consequences of female rat reproduction may increase nematode activity. I suggest that *Heligmostrongylus* sp. has little impact on host fitness or population-level processes.

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by

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Chapter I

Introduction

Parasitism is one of seven evolutionarily-important interspecific interactions. I follow Price (1980) in defining a parasite along strict lexicographical lines as "an organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host". Using this definition, parasitism is an extremely common life style that has evolved independently in a diverse array of lineages. The unique relationships that parasites have developed with their hosts can range from relatively simple to extremely complex. A parasite obtains almost all of its nutritional and physiological needs from its host. Effects on the host of this way of feeding may range from minor to severe and can even cause mortality if pathogenicity is sufficiently high. Parasites can be endoparasites, whereby they live inside the host, and can include bacteria, protists, nematodes, and cestodes. They can also be ectoparasites, whereby they live on the external surfaces of the host, and can include leeches, ticks, mites, and fleas. Tenure of association of a parasite with its host can be ephemeral, as in the case of mosquitoes, or more permanent, as in the case of parasites that spend their entire lives living in or on their host.

Parasites may infect only one host through direct transmission or multiple intermediate hosts through indirect transmission. Thus, parasites may be very specialized in the type of hosts that they inhabit, or they may be more generalized and associate with

a broad range of hosts. There are advantages to both host specialization and generalization. Generalist parasites have the advantage in that they do not need to wait for a certain type of host, but there is also the risk of associating with an inappropriate host. Specialized parasites have the advantage in that their host will most likely provide a hospitable environment for them to complete their lifecycle and be able to reproduce. Specialists also do not need to evolve in different directions simultaneously in response to diverse host antiparasite adaptations.

The ultimate goal of a parasite, as with any living organism, is to successfully reproduce. In general, a parasite is under selection pressures to not kill its hosts because, because most parasites have little to no ability to survive outside of their host for extended periods and have poor mobility, killing the host would result in the death of the parasite. Some ectoparasites have the ability to remove themselves from the host if it is no longer a viable source of nutrition or if the parasite has fulfilled its nutritional requirements. Parasites can range in size from microscopic to macroscopic and therefore can infect unicellular or multicellular organisms (Agosta, Janz, and Brooks 2010).

Parasitism is an exploitative relationship (Bush et al. 2001), whereby the parasite harms the host and may even eventually kill it in the process of concluding its lifecycle. Female mosquitoes (Culicidae) feed for a short period of time on their numerous hosts, including humans, but their actions rarely result in host exsanguination and death. However, mosquitoes frequently serve as vectors of other parasites, thereby providing a vehicle for other potentially more damaging parasites to be transmitted to a common host. By contrast, the sea lamprey (*Petromyzon marinus)* is a parasitoid, which invariably kills

its host by creating large wounds on the skin of the fish on which it is feeding (Vélez-Espino et al. 2008).

Parasites cause considerable morbidity and mortality in humans. In 1999, over 1.4 billion humans, close to 25% of the world's population, were estimated to be infected with *Ascaris lumbricoides,* a parasitic nematode (Bush et al. 2001; Carneiro et al. 2002); 342 species of parasitic helminths alone have been found in humans (Bush et al. 2001). Other devastating human diseases caused by parasites include, but are not limited to, 300 million cases of malaria, 100 million cases of filariasis (tissue-dwelling nematodes), and greater than 500 million cases of amoebiasis (a gastrointestinal infection that can lead to death) (Bush et al. 2001). Parasitism in humans can cause great economic loss and extreme physical and psychological impact and can result in death when humans inadvertently intrude into the transmission cycle of parasites.

Rodents (order Rodentia) comprise approximately 1,500 of the 4,000 living species of mammals and are naturally distributed worldwide except in Antarctica and on remote oceanic islands. The largest family of rodents is Muridae, which accounts for over 700 species, including rats, mice, and voles. Rodents harbor a large number of parasites, many of which infect humans, including *Crytosporidium*, *Pasturella*, *Listeria*, *Yersinia*, and many nematodes (Fagir and El-Rayah 2009; Rafique et al. 2009). These parasites cause diseases such as cryptosporidiosis (an intestinal disease), pastuerellosis (tissue disease, sepsis, and pneumonia), and plague (lymphatic, pulmonary, and septicemic forms). Over 20 parasitic infections in rodents can be transmitted directly to humans and cause disease states through zoonotic transmission (Singla et al. 2008).

Rodents are the ultimate hosts for many parasites but can also be used as an indirect, or intermediate, host (Singla et al. 2008).

Intestinal parasites in rats are particularly common. *Cryptosporidium* sp., *Eimeria* sp., *Entamoeba* sp., *Giardia* sp., *Hexamastix* sp., *Monocercomonoides* sp., *Retortamonas* sp., *Spironucleus* sp., *Trichomonas* sp., and others are often found in murids. Coomansingh et al. (2009) conducted a study on the Norway rat (*Rattus norvegicus)* and found six different types of endoparasitic helminthic infections. Some infections were of zoonotic importance, and some caused physical damage to the infected rats.

Tropical rodents, in particular, have high rates of infection by many parasitic nematodes. For instance, Digiani et al. (2003) described a new genus of *Nippostrongylinae* from the intestines of the water rat (*Scapteromys aquaticus*) in Argentina. This newly-described parasite coexisted with three other known intestinal parasites. Because rodents harbor many parasites that can affect human health, there is a great need to understand those parasites, their interactions with rodent hosts, and their transmission cycles. Such understanding can have important implications not only for developing a comprehensive theory of parasite-host coevolution but also for improving human public health.

Chapter II

Helminth Parasitism in Isolated Populations of a Neotropical Forest Rodent

Introduction

Parasites are extremely diverse with respect to taxonomic affinities, morphology, host spectrum, and life cycles. By definition, the host is negatively affected by the parasite and also reacts defensively to parasite invasion (Price 1980; Slansky 2007; Careau et al. 2010). Parasites usually use the host as an "insular habitat", while simultaneously using it as their main food source (Price 1980; Poulin 1995; Nunn et al. 2003). Parasites may reach enormous population sizes within the host and are also able to modify host physiological and behavioral activities (Price 1980; Loreau and Tilman 2005). Using the host for energy and metabolism negatively impacts the host's overall fitness through influences on growth, fecundity, and survival (Lemaître et al. 2009). Although parasites compose a large proportion of the organisms on earth, in general, they are not uniformly distributed; a relatively small number of hosts may harbor the majority of parasites, while many potential hosts carry far fewer parasites (Anderson and May 1978).

Parasites affect not only host fitness but may also affect population-level processes and can sometimes regulate host populations (Dobson and Hudson 1992; Hudson, Newborn and Dobson 1992; Witting 2000; Hanski et al. 2001; Turchin and

Hanski 2001; Eccard and Ylonen 2002; and Gilg et al. 2006). Hudson et al. (1998) showed that by removing the helminth *Trichostrongylus tenuis* from their hosts, the red grouse (*Lagopus lagopus scoticus)*, there was a decrease in the periodic crashes in the abundances of the red grouse. Hudson et al. (1992) showed that there was a correlation between infection with these parasites and the loss of eggs and chicks within the red grouse population. Fewer offspring, as a result of parasitic infection, may have a great impact on the host's population size (Lively 2006). This same impact on offspring also was shown in a study by Albon et al. (2002), where helminthic parasitism regulated populations of reindeer (*Rangifer tarandus*) by reducing calving rate but not by affecting the host's survival. This regulation of a host's population most likely occurs only early in a host's life (Møller 2005). Some ectoparasites also affect host survival (Lemaître et al. 2009). Studies conducted on parasitic species richness and parasitic diversity have also shown a connection to the host's population density (Nunn et al. 2003).

Geography may also influence parasitic infection and diversity. While Rohde and Heap (1998) showed that there were no latitudinal differences in relation to the diversity and abundance of endoparasites within teleost fish, they did find that parasites were "distributed with a low degree of aggregation", and hosts that were parasitized had reduced reproductive output. Other host factors, such as sex (Poulin 1996; Zuk and McKean 1996; Morand et al. 2004), body mass, age, and population density (Arneberg 2002; Nunn et al. 2003; Krasnov et al. 2004; Ezenwa et al. 2006; Hawlena et al. 2006; and Lindenfors et al. 2007) also may influence the number of parasites that a host harbors. For instance, Ezenwa et al. (2006) compared parasitic species richness to host traits. As

host body size increased, parasitic species richness also increased, but as the lifespan of the host increased, the diversity of parasites decreased. Lindenfors et al. (2007) found that although parasitic species richness was correlated with body mass, host population density, host range, and latitudinal differences in wild carnivores, there were differences in whether parasitic species richness could be predicted by host specialization and transmission mode. Only generalist parasites showed relationships of parasite species richness to density, geographical distribution, and latitude. Specialist and vector-borne parasites had no correlations with any of the host characteristics. Ectoparasites typically do not have any correlation between species richness and host's age, size, or other individual-level variables (Krasnov et al. 2004; Hawlena et al. 2006). Some of the correlation of endoparasites with body size and parasitic species richness may be explained by the need for increased food intake to sustain increased body size (Nunn et al. 2003).

Heligmostrongylus spp. (Trichostrongylidae) are poorly characterized nematodes. However, their life cycles may be similar to those of other trichostrongylids, some of which are well known and cause a disease state in humans and ruminants. Adult trichostrongylids enter the gastrointestinal tract of the host, and females produce eggs that are passed out in the feces of the host (Poole 1956; Audebert et al. 2003). The time that elapses between the egg and the infective stage varies in response to temperature and humidity; higher temperatures and humidity accelerate the process. Infection occurs when the host inadvertently ingests the infective stage while feeding. Poulin (2004) described helminthic parasite populations as being fragmented spatially, where each

parasite has an ideal habitat in its host but is separated by a hostile environment from other suitable habitats, thus making infection of a new host dependent upon host characteristics and chance. Some species of *Heligmostrongylus* have been recovered from Neotropical rodents, including *Proechimys semispinosus* (the Central American spiny rat).

Proechimys semispinosus is widely distributed in Neotropical lowland forests, ranging from southern Honduras to northwestern South America (Eisengberg 1989; Oaks et al. 2008). This species is one of the most abundant rodents in lowland forests throughout its geographical range (Eisenberg 1989). Its diet consists mostly of fruits, seeds, and fungi (Adler 1995; Mangan and Adler 2002; Oaks et al. 2008). These rodents are important in the dispersal of seeds of many species of plants and spores of mycorrhizal fungi and are an important food resource for many predators (Hoch and Adler 1997; Adler and Kestell 1998; Mangan and Adler 2002; Oaks et al 2008). This rodent's abundance renders it an ideal model organism for the study of helminthic parasitism.

In this thesis, I focus on *Heligmostrongylus* sp. infecting the Central American spiny rat (*Proechimys semispinosus*) in seven populations isolated on small islands in the Panama Canal. With previous studies showing effects of a host's age, sex, and population characteristics, I focus on those relationships. I also examine the effects of food availability and host nutritional status on infection by analyzing data from control and food-supplemented populations.

Materials and methods

Study Area

This study was conducted over a 13-month period from January 1997 through January 1998 in central Panama on seven small islands in Gatun Lake, central Panama. The islands were formed during construction of the Panama Canal, when low-lying areas were inundated after the Chagres River was dammed (Leigh & Wright 1990; Dietrich et al. 1996; Mangan et al. 2004). Many hilltops remained emergent and were isolated as islands. The sizes of those islands vary from less than one hectare to 1,500 hectares, and most islands are covered with tropical moist forest of varying ages. *Proechimys semispinosus* is widely distributed on the islands and is the only rodent to maintain persistent populations on all but the largest islands. This species also maintains greater abundances than other rodents, constituting up to 84% of captured mammals in surrounding mainlands forest (Adler 1995; Lambert & Adler 2000).

The seven islands (designated islands 8, 12, 51, 52, 53, 54, and 55, Mangan and Adler 2002) ranged in size from 1.8 to 3.5 ha. The sizes of the islands permitted each insular rat population to be thoroughly censused on a regular basis and to provide sufficiently-robust samples. All islands were located within a 40-km^2 area and therefore experienced similar climatic conditions (Adler 1994).

The climate of the study area is highly seasonal, with mean annual rainfall of 2600 mm and a four-month dry season that begins near the end of December (Dietrich et al. 1996; Adler 1998; Asquith and Mejia-Chang 2005). Approximately 90% of annual precipitation falls during the rainy season (Windsor 1990; Adler 1998; Shapiro and

Pickering 2000). Fruit production by most tree species is related to rainfall, with greatest fruit production occurring from the end of the dry season until late in the rainy season (Foster 1982; Adler 1998). Thus, fruit production is least from November through February, and famine conditions for frugivorous mammals are evident during that time (Adler 2008).

Sampling procedures

Abundances of spiny rats vary widely across islands (Adler and Seamon 1991; Adler 1994, 1996, 1998). To provide estimates of rat density on each of the seven study islands, rats were live-trapped monthly throughout the study. A matrix of sampling stations was established across the entirety of each island, with 20 m between adjacent stations. A single Tomahawk live trap (38.4 x 12.0 x 12.0 cm) baited with cut, ripe banana was set for four consecutive nights and checked each subsequent morning. Individuals that were captured for the first time were marked for permanent identification by toe clipping. Upon initial capture during a month, each rodent was sexed and weighed, and its reproductive status (abdominal or scrotal for males and lactating or obviously pregnant for females) was determined. Based upon pelage, each individual was assigned to one of three age classes: juvenile, sub-adult, or adult (Adler 1994). All captured individuals were released after data collection at the station at which they were captured.

Five fecal pellets (if present) from each rat were collected from the forest floor beneath the trap upon first capture each month and placed into vials with 70% ethanol

(Mangan and Adler 2002). To avoid sampling bias, multiple samples from a given individual were not collected upon subsequent capture within a month. A single adult female rat that was shedding *Heligmostrongylus* sp. eggs was sacrificed, and its digestive tract was removed and preserved in 70% ethanol. Adult *Heligmostrongylus* sp. were extracted from the tract, mounted on slides, and examined microscopically for identification by Humberto Carvajal (Universidad del Valle, Cali, Colombia).

Fruit availability

Fruit availability was estimated on each island by conducting monthly censuses of ripe fruits that were known or suspected to be eaten by spiny rats (Adler 1995, 1998). For this purpose, each island was thoroughly searched by walking between the transects that constituted the sampling grid. All individual trees and lianas that were producing ripe fruits were recorded. To facilitate these surveys, all trees $\geq$10 cm in diameter at breast height (dbh, 1.3 m above ground level) had been previously marked, measured, and identified to species (Adler 2000). For animals with small home ranges, this method yields less bias than fruit traps and transect surveys (Chapman et al. 1994).

Experimental food provisioning

Of the seven study populations, two (islands 8 and 52) were designated as controls, whereby monthly censuses of rats and fruit availability were conducted, and fecal pellets were collected. The remaining five populations (islands 12, 51, 52, 53, 54, and 55) were designated as experimental populations and provisioned with supplemental food during the three months of least fruit availability (November and December 1997

and January 1998). For this purpose, 5 kg of cracked corn were placed monthly into semipermeable exclosures that were placed uniformly across each island at a density of 10 per ha (Mangan and Adler 2002). Exclosures were constructed of galvanized wire mesh (40x33x33 cm), with a mesh size of 1 cm. Each exclosure contained two opposing portals (6.5x7.6 cm) that allowed spiny rats access to the corn but excluded larger frugivores and granivores, if present on an island. Thus, rats on each provisioned island had access to 50 kg per ha of supplemental food, and the density of exclosures ensured that there was at least one exclosure within the home range of each rat. While corn is not a natural dietary constituent of spiny rats, the scarcity of natural fruits made it logistically infeasible to collect sufficient quantities of such fruit for provisioning. However, the rats consumed most of the corn each month, indicating that corn was an effective dietary substitute for naturally-occurring fruit (Mangan and Adler 2002).

Screening for *Heligmostrongylus* sp. infection

Fecal pellets were examined for *Heligmostrongylus* sp. eggs by randomly selecting three pellets from each sample and dividing those pellets into thirds and then combining the three subsamples together. These composite samples were then air-dried and weighed to the nearest 0.001 g. They were then placed in a gridded petri dish, rehydrated with distilled water, and distributed uniformly throughout the petri dish and examined under a dissecting microscope at 40x magnification. All *Heligmostrongylus* sp. eggs were counted and recorded.

Data analysis

I began the analysis by estimating monthly densities of spiny rats and fruiting trees and lianas on each island. Spiny rat densities were estimated using a modified minimum number known alive per hectare estimator (Adler 1994). Known individuals included all those that were 1) captured during a given month, 2) captured previously and subsequently but not during that month, and 3) estimated to have been born prior to that month but not captured until a later month. Month of birth was estimated based on growth curves, and all individuals captured on a given island were assumed to have been born on that island because over-water dispersal was rare (Adler 1994). Density of fruiting trees and lianas was estimated as the total number of individual trees and lianas producing ripe fruits per hectare. I then calculated three estimates of *Heligmostrongylus* sp. infection: density, prevalence, and density of egg-shedding individuals . Helminth density was estimated as the total number of eggs per captured individual (for which a fecal sample was collected), prevalence was estimated as the proportion of individuals that were shedding eggs, and density of egg-shedding individuals was estimated as the number of eggs per individual that was shedding eggs. Per capita fruit availability was calculated monthly for each island as fruit density/rat density.

For all subsequent analysis, *Heligmostrongylus* sp. egg density and density of egg-shedding individuals were $\log_{10}+1$ transformed, and prevalence was arcsine square root transformed to achieve normal distributions. All analysis was conducted using SAS version 9.2 (SAS 2008). To measure synchrony in *Heligmostrongylus* sp. reproductive activity among islands, I calculated cross-correlation functions between each possible

pairwise island combination separately for *Heligmostrongylus* sp. egg density, prevalence, and density of egg-shedding individuals. I then calculated the island-wide means of those three variables and used Spearman rank correlation analysis to identify associations between each of those variables and rat density, fruit density, and per capita fruit availability.

I used repeated measures analysis of variance (ANOVA) to compare means of the three *Heligmostrongylus* sp. variables among island populations, between treatment periods (before and during food provisioning), and between treatment groups (control and food-provisioned). For this purpose, I constructed a model that included treatment period, island population nested within treatment group, month, and the month x treatment group interaction separately for *Heligmostrongylus* sp. egg density, prevalence, and density of egg-shedding individuals.

I then searched for patterns in *Heligmostrongylus* sp. reproduction according to age, sex, and weight within an individual rat. I compared the mean number of eggs ($\log_{10}$+1 transformed) shed by an individual by sex and age by constructing a full ANOVA model (sex, age, and the interaction). I included only those individuals that shed eggs, and of the individuals that shed eggs more than one time, I included only the capture in which it shed the most eggs. Thus, each individual in this analysis was included only once to avoid problems of dependence. I then included those individuals in a linear regression analysis of number of eggs shed ($\log_{10}$+1 transformed) on body weight during that month of capture.

Finally, I compared the proportion of males and females that shed *Heligmostrongylus* sp. eggs at some time in their capture histories. Because an individual rat would be more likely to be recorded as shedding eggs the more frequently it was captured, I first conducted a Spearman rank correlation test between the number of months in which an individual rat was captured and the number of times it was recorded as shedding eggs. I initially included all individuals that shed eggs at least once and were captured ≥1 time and then sequentially eliminated individuals that were captured more than one time until there was no statistical association between those two variables. I then retained those individuals that were captured at least that minimum number of times for further analysis. Using those retained individuals, I conducted a chi-square analysis to test for a difference in the proportions of males and females that shed eggs at some point in their capture history.

Results

Included in this study were 1163 fecal samples collected over the thirteen-month study period (Table 2-1). Of those samples, 644 were from female rats, and 519 were from males; samples from 56 female and 39 males contained *Heligmostrongylus* sp. eggs. Mean *Heligmostrongylus* sp. egg density, prevalence, and density of egg-shedding individuals varied widely (Table 2-2). Rats on island 52 had the lowest mean *Heligmostrongylus* sp. egg density (3.72 eggs per gram), while those on island 8 had the highest such density (132.78 eggs per gram). Mean prevalence (proportion) ranged from 0.02 on island 52 to 0.09 on island 8. Mean density of egg-shedding individuals ranged

from 18.62 eggs per gram of fecal sample from egg-shedding rats on island 52 to 1064.67 eggs per gram from egg-shedding rats on island 8. Mean rat density was lowest on island 52 and highest on island 8. By contrast, island 52 had the highest mean fruit density, while island 55 had the lowest such density. On a per capita basis, islands 8, 12, and 53 had the least fruit availability, while island 52 had the greatest fruit availability.

Heligmostrongylus sp., rat, and fruit estimates varied widely among islands and over time (Table 2-3, Figures 2-2, 2-3, 2-4, and 2-5). *Heligmostrongylus* sp. egg density gram was greatest on island 8 during March 1997 (441.00 eggs per gram) but was generally low on each island throughout the study (Table 2-4). *Heligmostrongylus* sp. egg prevalence was highest in January 1997 on island 53 (0.38) and in October 1997 on island 55 (0.38) (Table 2-5). Density of eggs by egg-shedding individuals was greatest in November 1997 on island 8 (Table 2-6) and was >1000 during seven months. By contrast, rats on island 52 shed eggs in only October 1997.

There was little evidence of synchronous *Heligmostrongylus* sp. reproductive activity across islands (Tables 2-7, 2-8, and 2-9). Only four of 21 cross-correlation functions were positive for *Heligmostrongylus* sp. density and prevalence, while only one was positive for density of egg-shedding individuals. Positive correlations bore no relationship to geographical proximity; *Heligmostrongylus* sp. reproductive activity on even the most distantly-separated islands was sometimes positively correlated, while such activity on the most proximally-located islands was frequently not correlated.

Repeated measures ANOVA showed differences in mean *Heligmostrongylus* sp. egg density and density of egg-shedding individuals among island populations nested

within experimental group, while prevalence was marginally significant (Tables 2-10, 2-11, and 2-12). No differences were found over time or between treatment periods or treatment groups. Thus, increasing the nutritional status of spiny rats by food provisioning had no influence on *Heligmostrongylus* sp. reproductive activity, and no consistent differences over time were evident. Similarly, no interactions were found between month and experimental group.

Helminth reproductive activity (as measured by mean *Heligmostrongylus* sp. egg density, prevalence, and density of egg-shedding individuals) was not associated with spiny rat density, fruit density, or per capita fruit availability (Table 2-13).

The number of months in which a rat was captured and the number of times it shed eggs was correlated until a rat was captured $\geq$5 times (S=0.20532, P=0.0713). Thus, individuals that were captured at least five times (N=78) were retained in the analysis to compare sex and age classes. There was no difference between age classes in the mean number of eggs shed (young mean=696.08, N=12; adult mean=991.32; F=0.77, P=0.3826), but female rats shed more eggs than males (female mean=1333.04, N=51; male mean=408.81, N=36; F=7.05, P=0.0095). There was no interaction between age and sex (F=0.18, P=0.6701). The proportions of male (0.075) and female (0.087) rats that shed eggs did not differ (χ^2=0.8365, P=0.3604). Thus, although the proportions of females and males shedding eggs did not differ, of those rats that did shed eggs, females shed more eggs. There was no relationship between the number of eggs shed by an individual rat and its body weight (F=1.72, P=0.1936).

Figure 2-1
Map of the study area in central Panama (modified from Boyett et al.2000).

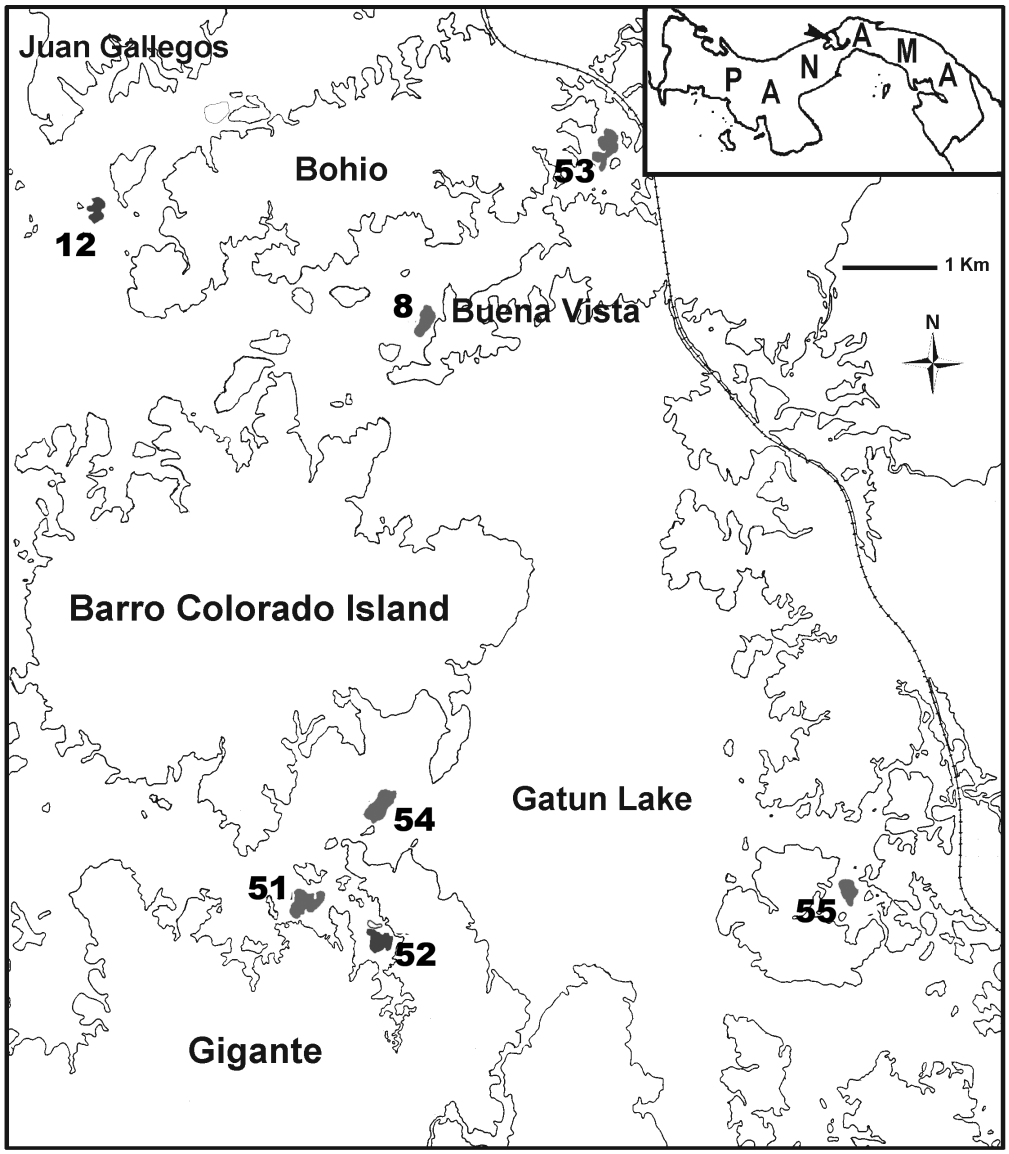
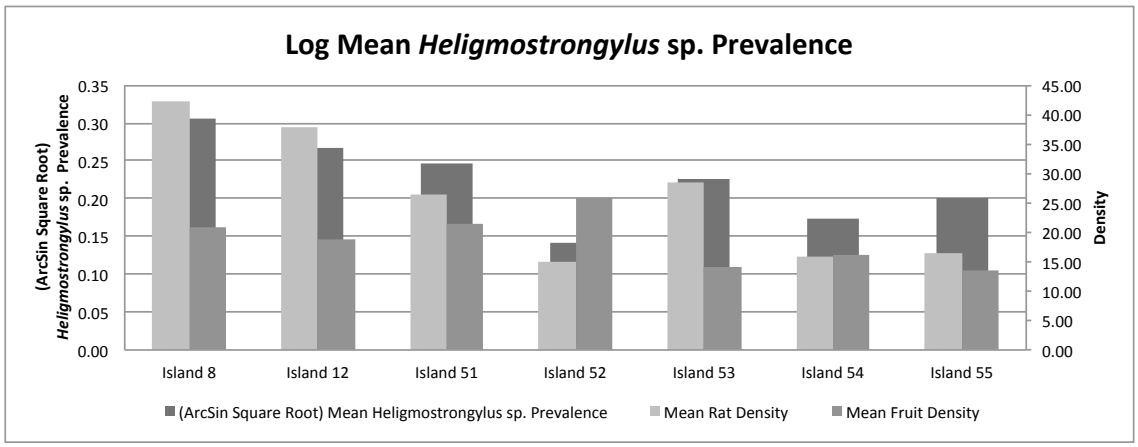
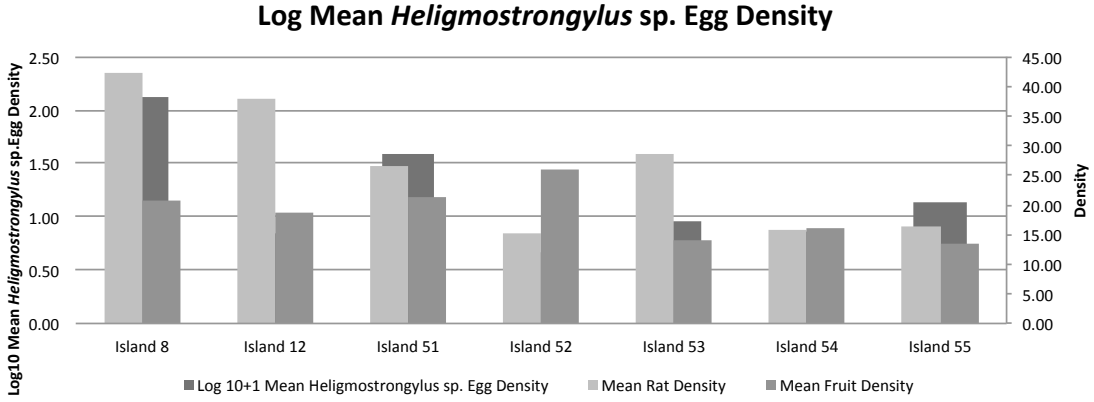


Figure 2-2

Log mean *Heligmostrongylus* sp. prevalence, *Heligmostrongylus* sp. egg density, and *Heligmostrongylus* sp. density of egg-shedding individuals for all islands.





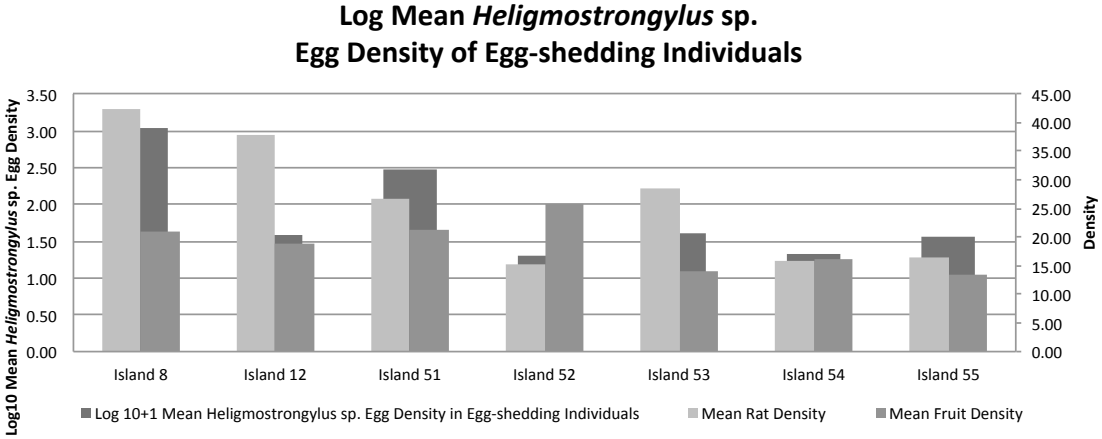


Figure 2-3

Log *Heligmostrongylus* sp. density of egg-shedding individuals for each island over the study period.

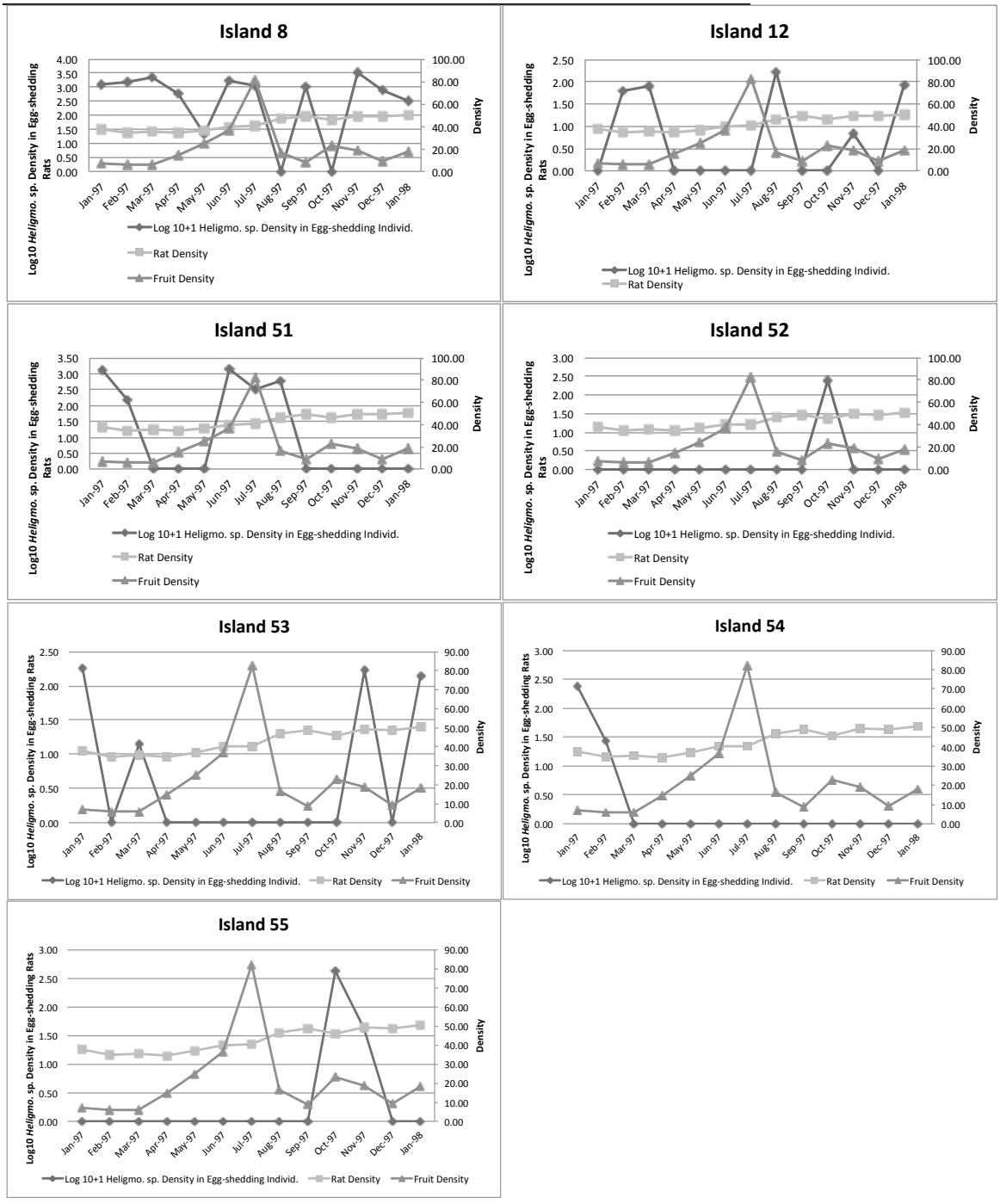


Figure 2-4

Log *Heligmostrongylus* sp. egg density for each island over the study period.

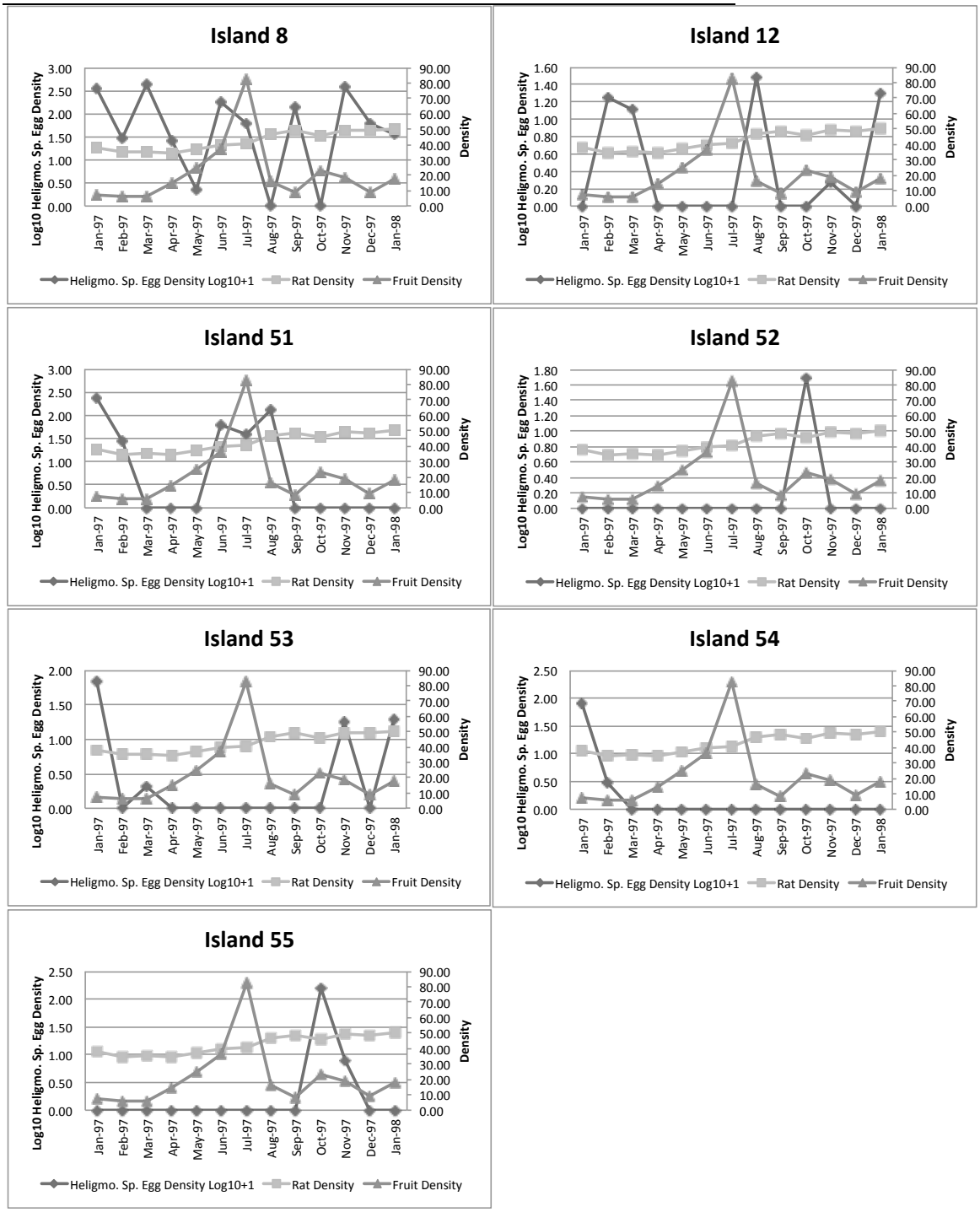


Figure 2-5

ArcSin square root *Heligmostrongylus* sp. prevalence for each island over the study period.

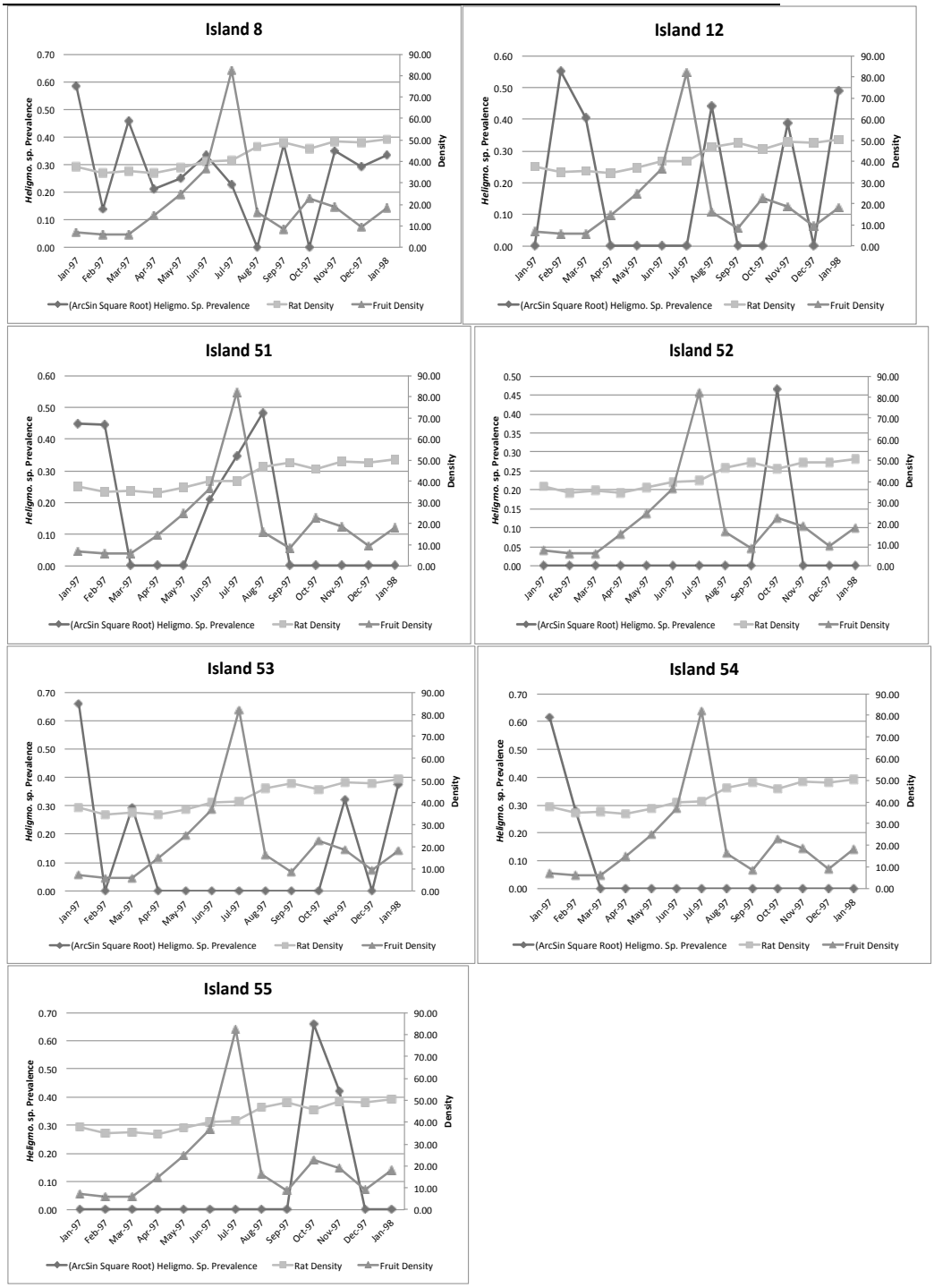


Table 2-1

Total numbers of samples collected by sex and infection status.

	Total captures		
	Non-infected	Infected	Total
Male	480	39	519
Female	588	56	644
Total	1068	95	1163

Table 2-2

Island characteristics of mean *Heligmostrongylus* sp. egg density, mean *Heligmostrongylus* sp. prevalence, mean *Heligmostrongylus* sp. density of egg-shedding individuals, mean rat density, mean fruit density, and mean fruit/rat density (per capita).

Island	Mean *Heligmostrongylus* sp. egg density	Mean *Heligmostrongylus* sp. prevalence	Mean *Heligmostrongylus* sp density of egg-shedding individuals	Mean Rat Density	Mean Fruit Density	Mean Fruit/Rat Density
8	132.78	0.09	1064.67	42.31	20.87	0.49
12	6.08	0.07	37.16	37.90	18.73	0.49
51	38.16	0.06	289.49	26.55	21.33	0.80
52	3.72	0.02	18.62	15.11	25.88	1.71
53	8.11	0.05	38.87	28.49	14.06	0.49
54	6.32	0.03	20.50	15.72	16.12	1.03
55	12.63	0.04	35.44	16.41	13.46	0.82

Table 2-3

Total numbers of samples from *Proechimys semispinosus* collected on each island per month.

Month	Island 8	Island 12	Island 51	Island 52	Island 53	Island 54	Island 55
Jan 97	33	6	32	10	8	12	5
Feb 97	52	11	27	6	15	13	9
Mar 97	46	13	24	6	12	9	9
Apr 97	23	8	27	4	9	14	5
May 97	49	8	21	5	14	1	6
Jun 97	47	8	23	0	6	1	2
Jul 97	39	11	35	1	11	3	4
Aug 97	25	11	14	3	1	1	4
Sep 97	45	5	7	5	4	4	0
Oct 97	34	2	5	5	2	4	8
Nov 97	34	7	8	8	10	11	6
Dec 97	48	2	0	0	4	3	1
Jan 98	37	9	9	4	15	8	7

Table 2-4

Heligmostrongylus sp. egg density on each island per month. Density was calculated by dividing the total number of eggs found by the total number of all rats captured.

Month	Island 8	Island 12	Island 51	Island 52	Island 53	Island 54	Island 55
Jan 97	363.67	0.00	244.38	0.00	68.75	80.17	0.00
Feb 97	28.73	17.00	27.48	0.00	0.00	2.00	0.00
Mar 97	441.00	12.08	0.00	0.00	1.08	0.00	0.00
Apr 97	24.52	0.00	0.00	0.00	0.00	0.00	0.00
May 97	1.33	0.00	0.00	0.00	0.00	0.00	0.00
Jun 97	182.13	0.00	60.39	0.00	0.00	0.00	0.00
Jul 97	61.08	0.00	38.66	0.00	0.00	0.00	0.00
Aug 97	0.00	29.91	125.21	0.00	0.00	0.00	0.00
Sep 97	139.89	0.00	0.00	0.00	0.00	0.00	0.00
Oct 97	0.00	0.00	0.00	48.40	0.00	0.00	157.38
Nov 97	387.50	0.86	0.00	0.00	16.70	0.00	6.83
Dec 97	62.04	0.00	0.00	0.00	0.00	0.00	0.00
Jan 98	34.22	19.22	0.00	0.00	18.93	0.00	0.00

Table 2-5

Heligmostrongylus sp. prevalence per island per month.

Month	Island 8	Island 12	Island 51	Island 52	Island 53	Island 54	Island 55
Jan 97	0.30	0.00	0.19	0.00	0.38	0.33	0.00
Feb 97	0.02	0.27	0.19	0.00	0.00	0.08	0.00
Mar 97	0.20	0.15	0.00	0.00	0.08	0.00	0.00
Apr 97	0.04	0.00	0.00	0.00	0.00	0.00	0.00
May 97	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Jun 97	0.11	0.00	0.04	0.00	0.00	0.00	0.00
Jul 97	0.05	0.00	0.11	0.00	0.00	0.00	0.00
Aug 97	0.00	0.18	0.21	0.00	0.00	0.00	0.00
Sep 97	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Oct 97	0.00	0.00	0.00	0.20	0.00	0.00	0.38
Nov 97	0.12	0.14	0.00	0.00	0.10	0.00	0.17
Dec 97	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Jan 98	0.11	0.22	0.00	0.00	0.13	0.00	0.00

Table 2-6

Heligmostrongylus sp. egg density of egg-shedding individuals per island per month. Mean *Heligmostrongylus* sp. density of egg-shedding individuals is calculated by dividing the number of *Heligmostrongylus* sp. eggs by the number of infected individuals.

Month	Island 8	Island 12	Island 51	Island 52	Island 53	Island 54	Island 55
Jan 97	1200.10	0.00	1303.33	0.00	183.33	240.50	0.00
Feb 97	1494.00	62.33	148.40	0.00	0.00	26.00	0.00
Mar 97	2254.00	78.50	0.00	0.00	13.00	0.00	0.00
Apr 97	564.00	0.00	0.00	0.00	0.00	0.00	0.00
May 97	21.67	0.00	0.00	0.00	0.00	0.00	0.00
Jun 97	1712.00	0.00	1389.00	0.00	0.00	0.00	0.00
Jul 97	1191.00	0.00	338.25	0.00	0.00	0.00	0.00
Aug 97	0.00	164.50	584.33	0.00	0.00	0.00	0.00
Sep 97	1049.17	0.00	0.00	0.00	0.00	0.00	0.00
Oct 97	0.00	0.00	0.00	242.00	0.00	0.00	419.67
Nov 97	3293.75	6.00	0.00	0.00	167.00	0.00	41.00
Dec 97	744.50	0.00	0.00	0.00	0.00	0.00	0.00
Jan 98	316.50	86.50	0.00	0.00	142.00	0.00	0.00

Table 2-7

Cross correlation functions of *Heligmostrongylus* sp. egg density (critical function = 0.61489). Boxes show significant values.

Density						
	12	51	52	53	54	55
8	-0.13306	0.22465	-0.09079	0.49122	0.44915	-0.07191
12	-----	0.12947	-0.14798	-0.13929	-0.19567	-0.15613
51		-----	-0.16124	0.73891	0.84906	0.16846
52			-----	0.12607	-0.08893	0.99906
53				-----	0.93990	-0.09212
54					-----	-0.08782

Table 2-8

Cross correlation function of *Heligmostrongylus* sp. prevalence (critical function = 0.61489). Boxes show significant values.

	Prevalence					
	12	51	52	53	54	55
8	0.02560	0.18137	-0.27345	0.83943	0.73372	-0.24261
12	-----	0.33027	-0.21949	0.08613	-0.01729	-0.12543
51		-----	0.06122	0.09340	0.40618	-0.01514
52			-----	-0.14819	-0.10688	0.90807
53				-----	0.87774	-0.04524
54					-----	-0.11563

Table 2-9

Cross correlation functions for mean *Heligmostrongylus* sp. egg density within infected individuals (critical function = 0.61489). Boxes show significant values.

Intensity						
	12	51	52	53	54	55
8	-0.17572	0.09596	-0.32981	0.36557	0.05651	-0.26324
12	-----	-0.03130	-0.17682	-0.02579	-0.15750	-0.19135
51		-----	-0.17348	0.21392	0.60034	-0.19108
52			-----	-0.16224	-0.09264	0.99522
53				-----	0.58725	-0.11037
54					-----	-0.10203

Table 2-10

Repeated measures ANOVA of *Heligmostrongylus* sp. egg density

Source	DF	F Value	PR > F
Treatment period	1	0	0.9865
Treatment group(Population)	6	6.54	<0.0001
Month	11	1.28	0.2592
Treatment groupXMonth	12	0.7	0.7497

Table 2-11

Repeated measures ANOVA of *Heligmostrongylus* sp. prevalence.

Source	DF	F Value	PR > F
Treatment period	1	0.1	0.7582
Treatment group(Population)	6	2.16	0.0597
Month	11	1.59	0.1249
Treatment groupXMonth	12	0.56	0.866

Table 2-12

Repeated measures ANOVA of *Heligmostrongylus* sp. egg density of egg-shedding individuals

Source	DF	F Value	PR > F
Treatment period	1	0.05	0.8232
Treatment group(Population)	6	7.67	<0.0001
Month	11	1.06	0.4073
Treatment groupXMonth	12	0.62	0.8166

Table 2-13

Spearman correlation analysis using transformed data for mean *Heligmostrongylus* sp. egg density, *Heligmostrongylus* sp. prevalence, and *Heligmostrongylus* sp. egg density of egg-shedding individuals compared to mean rat density, mean fruit density, and mean per capita density. Upper numbers are correlation coefficients (S), and lower numbers are P values.

	Transformed *Heligmostrongylus* sp. Egg Density	Transformed *Heligmostrongylus* sp. Prevalence	Transformed *Heligmostrongylus* sp. Egg Density of Egg-shedding Individuals
Mean Rat Density	0.03571 0.9394	0.00000 1.0000	0.03571 0.9394
Mean Fruit Density	0.53571 0.2152	0.67857 0.0938	0.53571 0.2152
Mean Per Capita Density (Fruit/Rat)	0.01802 0.9694	0.05406 0.9084	0.01802 0.9694

Discussion

The insular study system provided an ideal opportunity to examine parasitism in discrete, essentially-closed populations of hosts. Thus, the nearly complete lack of immigration ensured that infections were acquired on a given island rather than having been imported from elsewhere. The relatively small sizes of the islands ensured that a representative proportion of each host population was regularly sampled, providing longitudinal histories of individual hosts. The islands also provided an ideal experimental system to examine the influence of host nutritional status on parasite activity. It is important to note, however, that my measures of parasitism by *Heligmostrongylus* sp. were based on parasite reproductive activity rather than directly on infection. Thus, I do not know how many rats hosted *Heligmostrongylus* sp. that were not actively reproducing. To determine actual infection status would have required either sacrificing nearly all individual rats within each population or using possible molecular techniques to screen for infection by adults. Neither method was feasible. However, based on the low rates at which individual rats shed eggs, I suggest that infection rates were commensurately low. Furthermore, most rats that shed eggs did so only once or twice in consecutive months, suggesting that infection was ephemeral or that fecundity of *Heligmostrongylus* sp. in reinfected rats was reduced.

Distinct seasonality with respect to precipitation in tropical forests imposes pronounced seasonal fluctuations in the reproductive activities of most organisms within such forests (Leigh 1999). I found no evidence of seasonal reproduction by *Heligmostrongylus* sp. (i.e., eggs were shed throughout the year), despite distinctly-

seasonal activity in both their hosts and that of their hosts' food resources. I also found little evidence of synchronous reproductive activity among islands. Thus, *Heligmostrongylus* sp. females produced eggs during any month in both the rainy and dry seasons, indicating that nematode reproductive activity is not triggered by an external environmental cue.

Although there were no temporal patterns evident in the reproductive activity of *Heligmostrongylus* sp. , such activity varied spatially (i.e., among host populations). Although Rohde and Heap (1998), and Lindenfors et al. (2007) found that latitudinal differences may influence parasite diversity of hosts, latitudinal differences in our study were minimal (approximately 4 minutes) and unlikely to influence parasite burdens within the rats. Reproductive activity was highest on island 8 and virtually absent on island 52. Not surprisingly, host population densities were highest on island 8, suggesting that a minimum critical host density must be sustained for regular and direct transmission of *Heligmostrongylus* sp. to new hosts and subsequent reproduction. If such transmission does not occur regularly, then most rats will remain uninfected throughout their life spans. These findings agree with previous studies (Arneberg 2002; Nunn et al. 2003) that show an increase in rat density being accompanied by an increase in parasite density. Anderson and May (1978), Arneberg (2002), and Nunn et al.(2003) also found a positive relationship between infection and host density.

In general, *Heligmostrongylus* sp. prevalence was very low, frequently being zero within each population and reaching a monthly maximum of 0.38. Low infection rates accord with those of previous studies (Poulin 2004; Bordes et al. 2009), which showed

that only a small proportion of hosts harbored *Heligmostrongylus* sp. eggs, and of those that did, an even smaller proportion had high parasite burdens. Overall prevalence in my study was near the lower range of values reported by Rafique et al. (2009).

Hosts that are in poor physiological condition and under conditions of food stress frequently have higher parasite burdens. This situation occurs in the rats in my study system with respect to ectoparasites such as mites (Adler 2008). Surprisingly, however, I found no relationship between the quantity of food available to rats on a per capita basis and *Heligmostrongylus* sp. egg reproductive activity. This lack of a statistical relationship was verified experimentally when rats were provisioned with supplemental food during the period of least resource availability and therefore greatest food stress.

The previous discussion focused largely on population-level patterns. With respect to individuals, female rats shed more eggs than did males, but there were no age differences. This female bias agrees with results from other studies (Zuk and McKeon 1996; Moura et al. 2003; Behnke et al. 2004; Morales-Monter et al. 2004; Morand et al. 2004; Rossin et al. 2010). By contrast, some studies have found male host bias (Poulin 1996; Zuk 1996; Zuk and McKean 1996; Schalk and Forbes 1997). Dietary or physiological (hormonal) differences, unrelated to food availability but rather stemming from the increased burden of reproduction by female rats, may have contributed to greater nematode reproductive activity. Although females shed, on average, more eggs than did males, the proportions of males and females that hosted reproductively-active nematodes did not differ.

Because of low *Heligmostrongylus* sp. prevalence within each host population and infrequent, aseasonal, and ephemeral nematode reproductive activity, I suggest that it is unlikely that *Heligmostrongylus* sp. substantially lowers host fitness. Consequently, I further suggest that this nematode has minimal population-level impact and does not limit or regulate rat populations.

Conclusions

In concluding, two caveats with respect to the current study should be mentioned. First, I did not assess additional parasitic loads that the rodents certainly carried. Spiny rats harbor many other types of parasites, including other nematodes, and competition with such parasites may have affected the reproductive activity of *Heligmostrongylus sp.* Second, many rats may have been infected with adult *Heligmostrongylus* sp. nematodes that were not reproductively active throughout the entire sampling period. The frequency of reproduction by this nematode and the duration of infection of an individual rat are simply not known. Therefore, additional studies are sorely needed to develop a more complete understanding of this parasite-host system.

References

Adler, G. H. 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. *Journal of Animal Ecology.* 63: 903-911.

Adler, G. H. 1995. Fruit and seed exploitation by Central American spiny rats, *Proechimys semispinosus*. *Studies on Neotropical Fauna and Environment.* 30: 237–244.

Adler, G. H. 1996. The island syndrome in isolated populations of a tropical forest rodent. *Oecologia*. 108: 694–700.

Adler, G. H. 1998. Impacts of resource abundance on populations of a tropical forest rodent. *Ecology*. 79: no. 1: 242.

Adler, G. H. 2000. Tropical tree diversity, forest structure and the demography of a frugivorous rodent, the spiny rat (*Proechimys semispinosus)*. *Journal of Zoology.* 250: 57-74.

Adler, G. H. 2008. Resource limitation of insular animals: causes and consequences. Pages 322-333 in W. Carson and S. Schnitzer, Tropical Forest Ecology. Blackwell.

Adler, G. H. and D. W. Kestell. 1998. Fates of neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica.* 30: 677-681.

Adler, G. H., and J.O. Seamon. 1991. Distribution and abundance of a tropical rodent, the spiny rat, on islands in Panama. *Journal of Tropical Ecology.* 7: 349–360.

Agosta S. J., N. Janz, D.R. Brooks. 2010. How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. *Zoologia.* 27: 151–62.

Albon, S. D., A. Stien, R. J. Irvine, R. Langvatn, E. Ropstad, and O. Halvorsen. 2002. The role of parasites in the dynamics of a reindeer population. *The Royal Society.* 269: 1625-1632.

Anderson, R. M., and R. M. May. 1978. Regulation and stability of host-parasite population interactions. *Journal of Animal Ecology.* 47: 219-247.

Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography.* 25: no. 1: 88-94.

Asquith, Nigel M., and Mejía-Chang Mønica. 2005. Mammals, edge effects, and the loss of tropical forest diversity. *Ecology.* 86: no. 2: 379-390.

Audebert F., Vuong, P.N., Durette-Desset, M.C. 2003. Intestinal migrations of Trichostrongylus retortaeformis (Trichostrongylina, Trichostrongylidae) in the rabbit. *Veterinary Parasitology.* 112: No. 1–2, 28: 131-146.

Bordes, Frédéric, Serge Morand, Douglas A. Kelt, Dirk H. Van Vuren. 2009. Home range and parasitic diversity in mammals. *The American Naturalist.* 173: 4. 467-474.

Behnke J. M., P. D. Harris, A. Bajer, C. J. Barnard, N. Sherif, L. Cliffe, J. Hurst, M. Lamb, A. Rhodes, M. James, S. Clifford, F. S. Gilbert, S. Zalat. 2004. Variation in the helminth community structure in spiny mice (*Acomys dimidiatus*) from four montane wadis in the St. Katherine region of the Sinai Peninsula in Egypt. *Parasitology*. 129:379–398.

Bush, A. O., J. C. Fernandez, G. W. Esch, and J. R. Seed. 2001. *Parasitism: The diversity and ecology of animal parasites.* Cambridge University Press, Cambridge, U.K., 566 p.

Careau, Vincent, Donald W. Thomas, and Murray M. Humphries. 2010. Energetic cost of bot fly parasitism in free-ranging eastern chipmunks. *Oecologia.*162: no. 2: 303-312.

Carneiro FF, E. Cifuentes, MM. Tellez-Rojo, I. Romieu. 2002. The risk of Ascaris lumbricoides infection in children as an environmental health indicator to guide preventive activities in Caparao and Alto Caparao, Brazil. *Bull World Health Organization* 80: 40–46.

Chapman C.A.R., R. Wrangham, L. J. Chapman. 1994. Indices of habitatwide fruit abundance in tropical forests. *Biotropica* 26: 160–171.

Coomansingh, C., R. D. Pinckney, M. I. Bhaiyat, A. Chikweto, S. Bitner, A. Baffa, R. Sharma. 2009. Prevalence on endoparasites in wild rats in Grenada. *West Indian Veterniary Journal*. 9(1): 17-21.

Dietrich, W. E. , D. M. Windsor, and T. Dunn. 1996. *Geology, climate, and hydrology of Barro Colorado Island. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, pp 21-46. Smithsonian Institution Press, Washington DC.

Digiani, Marîa Celîna, Carola A. Sutton, Marie-Claude Durette-Desset. 2003. A new genus of Nippostrongylinae (Nematoda: Heligmonellidae) from the water rat *Scapteromys Aquaticus* (Sigmodontinae) in Argentina. *Journal of Parasitology.* 89(1): 124-132.

Dobson, A. P., and P.J. Hudson. 1992. Regulation and stability of a free-living host-parasite system - *trichostrongylus tenuis* in red grouse. 2. Population-models. *Journal of Animal Ecology.* 61: 487-498.

Eccard, Jana A., and Hannu Ylönen. 2002. Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. *Oikos.* 99: no. 3: 580-590.

Eisenberg, J. F. 1989. *Mammals of the Neotropics: the northern Neotropics*. University of Chicago Press, Chicago, Illinois.

Ezenwa, Vanessa O., Samantha A. Price, Sonia Altizer, Nicholas D. Vitone, and Katherine C. Cook. 2006. Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. *Oikos.*115: no. 3: 526-536.

Fagir, Dina M., and El-Amin El-Rayah. 2009. Parasites of the Nile rat in rural and urban regions of Sudan. *Integrative Zoology.* 4: no. 2: 179-187.

Foster, R. B.1982 The seasonal rhythm of fruitfall on Barro Colorado island. Pages 151-172 *in* E.G. Leigh, Jr., A.s. Rand, and D.M. Windsor, editors. *The ecology of tropical forest: seasonal rhythms and long-term changes.* Smithsonian Institution Press, Washington D.C., USA.

Gilg, Olivier, Benoît Sittler, Brigitte Sabard, Arnaud Hurstel, Raphaël Sané, Pierre Delattre, and Ilkka Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos*. 113: no. 2: 193-216.

Hanski, Ilkka, Heikki Henttonen, Erkki Korpimaki, Lauri Oksanen, and Peter Turchin. 2001. Small-rodent dynamics and predation. *Ecology.* 82: no. 6: 1505.

Hawlena, Hadas, Zvika Abramsky, and Boris R. Krasnov. 2006. Ectoparasites and age-dependent survival in a desert rodent. *Oecologia.* 148: no. 1: 30-39.

Hoch, G. A. and G. H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum)* seeds by spiny rats *(Proechimys semispinosus*). *Journal of Tropical Ecology.* 13: 51-58.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. *Science.* 282: 2256-2258.

Hudson, Peter, David Newborn, and Andrew P. Dobson. 1992. Regulation and stability of a free-living host-parasite system: *trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reduction experiments. *Journal of Animal Ecology.* 61: 477-486.

Krasnov, Boris R., Georgy I. Shenbrot, Irina S. Khokhlova, and A. Allan Degen. 2004. Flea species richness and parameters of host body, host geography and host' milieu'. *Journal Of Animal Ecology* 73: no. 6: 1121-1128.

Lambert, Thomas D., and Gregory H. Adler. 2000. Microhabitat Use by a Tropical Forest Rodent, *Proechimys Semispinosus*, in Central Panama. *Journal Of Mammalogy* 81: no. 1: 70.

Leigh, E. G., Jr. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, Oxford, UK.

Leigh, E. G., Jr. and S. J. Wright. 1990. *Barro Colorado Island and Tropical Biology. Four Neotropical Forests*. 28-47. Yale University Press, New Haven CT.

Lemaître, Jérôme, Daniel Fortin, Pierre-Olivier Montiglio, and Marcel Darveau. 2009. Bot fly parasitism of the red-backed vole: host survival, infection risk, and population growth. *Oecologia.* 159: no. 2: 283-294.

Lindenfors, Patrik, Charles L. Nunn, Kate E. Jones, Andrew A. Cunningham, Wes Sechrest, and John L. Gittleman. 2007. Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Global Ecology & Biogeography* 16: no. 4: 496-509.

Lively, Curtis M. 2006. The ecology of virulence. *Ecology Letters* 9: no. 10: 1089-1095.

Loreau M, Roy J, Tilman D. 2005. "Linking ecosystem and parasite ecology." In: Thomas F, Guégan J, Renaud F, editors. *Parasitism and Ecosystems.* New York: Oxford University Press. pp. 13–21.

Mangan, S. A., and Adler, G. H. 2002. Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a neotropical forest. *Oecologia.* 131:587–597.

Mangan, Scott A., Ahn-Heum Eom, Gregory H. Adler, Joseph B. Yavitt, and Edward A. Herre. 2004. Diversity of arbuscular mycorrhizal fungi across a fragmented forest in Panama: insular spore communities differ from mainland communities. *Oecologia* .141: 687-700.

Møller, Anders Pape. 2005. "Parasitism and the regulation of host populations." In: Thomas F, Guégan J, Renaud F, editors. *Parasitism and Ecosystems.* New York: Oxford University Press. pp. 43-53.

Morand, S., J. Gouy De Bellocq, M. Stanko, D. Mikilisova. 2004. Is sex-biased ectoparatism related to sexual size dimorphism in small mammals of Central Europe? *Parasitology.* 129: 505-510.

Morales-Montor J., A. Chavarri, M. A. De Leon, L. I. Del Castillo, E. G. Escobedo, E. N. Sanchez, J. A. Vargas, M. Hernandez-Flores, T. Romo-Gonzalez, T. Larralde. 2004. Host gender in parasitic infections of mammals: an evaluation of the females host supremacy paradigm. *Journal of Parasitology.* 90:531–546.

Moura, M.O. M. Bordignon, G. Gracioli. (2003) Host characteristics do not affect community structure of ectoparasites on the fishing bat. *Noctilio leporinus* (Mammalia: Chiroptera). *Mem Inst Oswaldo Cruz* 98: 811-815.

Nunn, Charles L., Sonia Altizer, Kate E. Jones, and Wes Sechrest. 2003. Comparative Tests of Parasite Species Richness in Primates. *American Naturalist* 162: no. 5: 597-614.

Oaks Jamie R., Jason M. Daul, and Gregory H. Adler. 2008. Lifespan of a tropical forest rodent, *Proechimys semispinosus*. *Journal of Mammology.* 89(4): 904-908.

Poole, John. 1956. Reaction to temperature by infective larvae of *Nematodirus Filicollis* trichostrongylidae (Nematoda). *Can J Comp Med Vet Sci.* 20(5): 169–172.

Poulin, R. 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* 65: 283-302.

Poulin, R. 1996. Sexual inequalities in helminth infections: a cost of being male? *Am Nat* 147: 289-295.

Poulin, Robert. 2004. Parasites and the neutral theory of biodiversity. *Ecography* 27: no. 1: 119-123.

Price, P. W. 1980. Evolutionary biology of parasites. Princeton University Press, Princeton, NJ.

Rafique, A., S. A. Rana, H. A. Khan, and A. Sohail. 2009. Prevalence of some helminths in rodents captured from different city structures including poultry farms and human population of Faisalabad, Pakistan. *Pakistan Veterinary Journal*. 29: no. 3: 141-144.

Rohde, Klaus and Maureen Heap. 1998. Latitudinal differences in species and community richness and in community structure of metazoan endo- and ectoparasties of marine teleost fish. *International Journal for Parasitology.* 28: 461-474.

Rossin, M. A., A. I. Malizia, J.T. Timi and R. Poulin. 2010. Parasitism underground: determinants of helminth infections in two species of subterranean rodents (Octodontidae). *Parasitology.* 137: 1569–1575.

SAS Institute Inc. 2008. SAS® 9.2. Cary, NC.

Schalk G, M. R. Forbes. 1997. Male biases in parasitism of mammals: effects of study type, host age, and parasite taxon. *Oikos*. 78:67–74.

Shapiro, B. A., and J. Pickering. 2000. Rainfall and parasitic wasp (Hymenoptera: Ichneumonoidea) activity in successional forest stages at Barro Colorado Nature Monument, Panama, and La Selva Biological Station, Costa Rica. *Agricultural & Forest Entomology.* 2: no. 1: 39-47.

Singla, Lachhman D., Neena Singla, Vir R. Parshad, Prayag D. Juyal, and Naresh K. Sood. 2008. Rodents as reservoirs of parasites in India. *Integrative Zoology.* 3: no. 1: 21-26.

Slansky, Frank. 2007. Insect/Mammal Associations: Effects of Cuterebrid Bot Fly Parasites on Their Hosts. *Annual Review Of Entomology* 52: no. 1: 17-36.

Turchin, Peter, and Ilkka Hanski. 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology.* Letters 4, no. 3: 267-276.

Véléz-Espino, Luis Antonio, Robert L. McLaughlin, and Thomas C. Pratt. 2008. Management inferences from a demographic analysis of sea lamprey (Petromyzon marinus) in the Laurentian Great Lakes. *Canadian Journal Of Fisheries & Aquatic Sciences* 65: no. 2: 227-244.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences.* 29: 145.

Witting, Lars. 2000. Population cycles caused by selection by density dependent competitive interactions. *Bulletin of Mathematical Biology* 62: 1109-1136.

Zuk M. 1996. Disease, endocrine–immune interactions, and sexual selection. *Ecology* 77:1037–1042.

Zuk M, McKean K. A. 1996. Sex differences in parasite infections: patterns and processes. *Int J Parasitol.* 26:1009–1024.